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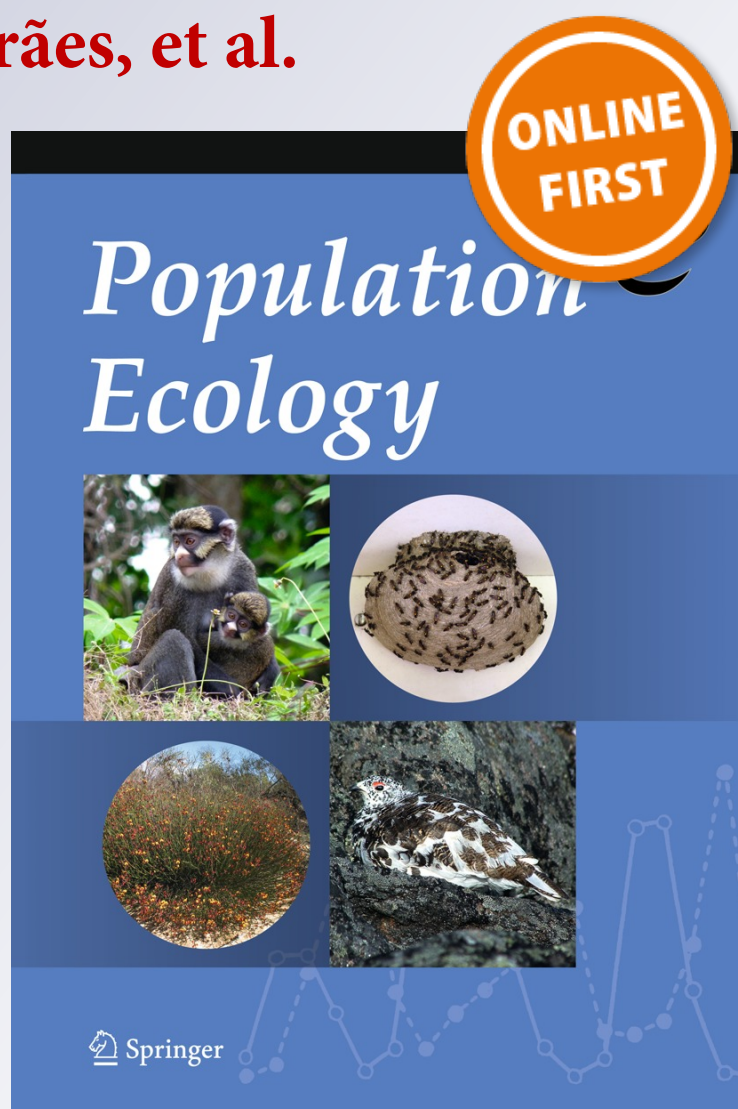
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Population Ecology

ISSN 1438-3896

Popul Ecol

DOI 10.1007/s10144-012-0352-3



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Impacts of enemy-mediated effects and the additivity of interactions in an insect trophic system

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Received: 6 December 2011 / Accepted: 28 October 2012
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Abstract In this study, we used data from both experiments and mathematical simulations to analyze the consequences of the interacting effects of intraguild predation (IGP), cannibalism and parasitism occurring in isolation and simultaneously in trophic interactions involving two blowfly species under shared parasitism. We conducted experiments to determine the short-term response of two blowfly species to these interactions with respect to their persistence. A mathematical model was employed to extend the results obtained from these experiments to the long-term consequences of these interactions for the persistence of the blowfly species. Our experimental results revealed that IGP attenuated the strength of the effects of cannibalism and parasitism between blowfly host species, increasing the probability of persistence of both populations. The simulations obtained from the mathematical model indicated that IGP is a key interaction for the long-term dynamics of this

system. The presence of different species interacting in a tri-trophic system relaxed the severity of the effects of a particular interaction between two species, changing species abundances and promoting persistence through time. This pattern was related to indirect interactions with a third species, the parasitoid species included in this study.

Keywords Calliphoridae · Cannibalism · Host-parasitoid interaction · Intraguild predation · Population dynamics · Shared enemy

Introduction

Ecological assemblages reflect the direct and indirect interactions that occur in communities of species. The consequences of these interactions within the structure of

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the community have great importance for the stabilization and persistence of trophic systems (McCann et al. 1998; Van Veen et al. 2006). Among insects, there are particular types of species interactions such as parasitism, intraguild predation and cannibalism, which can lead the community to exhibit complex dynamics (Holt 1977; Van Veen et al. 2006).

Predation and parasitism are interactions that exhibit direct impacts on prey or hosts; however, they can also have indirect effects on the trophic structure of the community by intensifying or relaxing other interactions in the trophic web (Wootton 1994; Chaneaton and Bonsall 2000). Predator-predator interactions may also be present in food webs, further complicating the species relationships in a community. In this case, it is common for generalist predators to engage in competition with one another for resources via cannibalism and intraguild predation (Polis 1981; Polis et al. 1989).

Intraguild predation (IGP) is a common type of interaction observed when competing species exhibit different competitive abilities, often resulting in one species becoming the predator of its competitor (Holt 1977). IGP may also allow an intraguild predator (IG-predator) to survive under conditions of resource scarcity, leading to a decrease in intraspecific competition (Polis et al. 1989).

Community dynamics may be significantly influenced by IGP in different ways because IGP allows species to persist or coexist (Kondoh 2008). Moreover, IGP involves the killing and consumption of individuals of species that use similar and limiting resources (Polis et al. 1989). This interaction is common between predators, frequently minimizing top-down impacts on shared prey (Snyder and Ives 2001), altering food web dynamics (McCann et al. 1998), influencing ecosystem functions (Ostrom et al. 1997), and strongly reducing or eliminating local populations of IG-prey (Polis et al. 1989; Rosa et al. 2006). IGP may also affect other interactions depending on the simultaneity among them or their chronological order (Polis and Holt 1992). However, the consequences of IGP occurring simultaneously with other ecological processes such as parasitism and cannibalism for species persistence and community structure are not known.

Cannibalism is common in insects and can be an important regulation mechanism for population sizes. Its incidence in predator-prey interactions has received special attention in response to evidence that indicates an ecological balance between cannibalism and the predation frequently observed in IGP systems (Polis 1981). Multiple factors can induce individuals to exhibit cannibalism,

namely, limitations in the amount or quality of food, high population density, age, parasitism, or even abiotic factors. However, the presence of intense cannibalism in a population can lead to low densities and, consequently, to the risk of local extinction.

Taking into account the possibility of simultaneous occurrence of the above-mentioned types of interaction, the presence of different predator species in a community can result in an interplay among species, and the effects of two or more species on one another can induce additive effects (the impact of the addition of a predator species to the system on community structure) and non-additive effects (the interaction strengths among species can be greater than the sum of the effects observed between pairs) (Morin 1995; Otto et al. 2008).

In this study, we aimed to quantify the interplay between additive and non-additive effects emerging from interactions between predator species as well as the direct and indirect components of non-additive effects using a small food web in which different types of predation interactions (parasitism, IGP and cannibalism) are present. Cannibalism, IGP and parasitism frequently occur simultaneously in communities of necrophagous insects, particularly blowflies and their parasitoids. Among blowflies, IGP has commonly been observed during the larval phase of *Chrysomya albiceps* (Wiedman), in interactions with other blowfly species such as *Chrysomya megacephala* (Fabricius) (Faria et al. 1999; Reigada and Godoy 2005). In addition to exhibiting IGP, *C. albiceps* is cannibalistic during its larval phase (Faria et al. 2004; Shiao and Yeh 2008) and both of blowfly species are commonly attacked by parasitoids (Whiting 1967).

An exploratory study involving the simultaneous effect sizes of these interactions would be valuable in enhancing the global comprehension of this system and serving as a basis for application inference in other studies involving complex trophic interactions. Two general ecological questions arise from this scenario: (i) what is the impact on the local persistence of interacting species when IGP, cannibalism and parasitism act simultaneously; and (ii) is there a dominant interactive mechanism in the system that can modulate the effects that are produced by the other interactions? In the attempt to answer these questions, laboratory experiments and ecological modeling were used to investigate the effects of trophic interactions on the persistence dynamics of blowflies, considering the simultaneous and additive effects of cannibalism, intraguild predation (IGP), and parasitism (Fig. 1). The ecological modeling was conducted to project the short-term consequences of the interactions that were studied on a long-term time series.

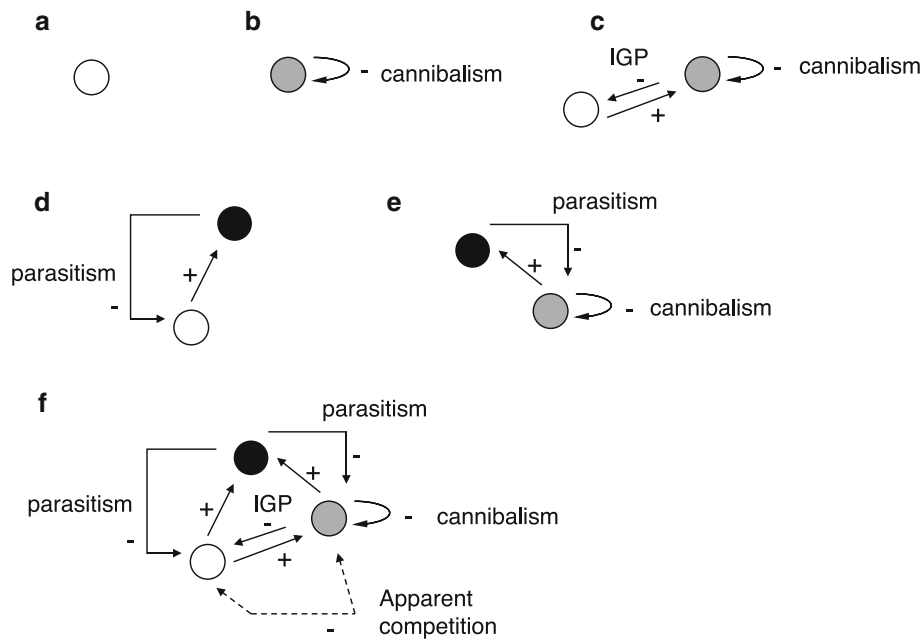


Fig. 1 Steps for the additivity of ecological interaction effects considered in this study to estimate the impact of enemies on their respective preys. **a** IG-prey in absence of IG-predator and parasitoid, **b** IG-predator in absence of IG-prey and parasitoid (cannibalism effects), **c** IG-prey + IG-predator (IGP/cannibalism effects), **d** IG-

prey + parasitoid (parasitism effects) **e** IG-predator + parasitoid (cannibalism/parasitism effects) and **f** IG-prey + IG-predator + parasitoid (cannibalism/IGP/parasitism effects). White, gray and black circles represent IG-prey, IG-predator and parasitoid, respectively. Solid arrows represent direct effects and dashed arrows represent indirect effects

Materials and methods

Study species

Blowflies

Chrysomya megacephala, and *C. albiceps* (Diptera: Calliphoridae) are necrophagous blowfly species. Their reproduction is conditioned to the presence of carrion, where their larvae can feed until they leave and become pupae. Resources are generally scarce due to the high abundance and diversity of flies present (Carvalho et al. 2004). As a consequence of food scarcity, the larvae of both species must efficiently consume the largest amount of food during the shortest period of time possible to reach the minimum weight required to pupate (Goodbrod and Goff 1990). This condition often induces competition among larvae; where *C. albiceps* larvae are present, both intraguild predation (IGP) and cannibalism can be observed.

Parasitoid

Nasonia vitripennis (Hymenoptera: Pteromalidae) is a generalist parasitoid wasp that is commonly associated with necrophagous dipterans, utilizing the pupae of blowflies for both feeding and reproduction (Whiting 1967; Rueda and Axtell 1985; Grassberger and Frank 2004). *Nasonia vitripennis* is a gregarious species, laying a large

number of eggs per pupa. Its population can increase rapidly when high host densities are available, which is an important characteristic that can result in the decrease or extinction of local blowfly populations (Whiting 1967; Rueda and Axtell 1985).

Short-term experimental study

We used laboratory experiments to test the consequences of different interactions (cannibalism, IGP and parasitism) on the survival and behavior of three trophic levels of interacting species. The lowest trophic level was represented by *C. megacephala* (IG-prey). The intermediate trophic level was represented by *C. albiceps* (IG-predator and/or cannibal). The highest trophic level was represented by a parasitoid of pupal blowflies, *N. vitripennis*.

The experiments were designed to simulate the natural scenario in which adult blowflies lay eggs, which hatch to produce larvae. Blowflies exhibit three larval instars. Two types of interactions were expected to occur primarily during the third larval instar: cannibalism within *C. albiceps* and IGP on *C. megacephala* by *C. albiceps*. The blowflies that survive the larval interactions become pupae, at which stage they are susceptible to parasitism by *N. vitripennis*.

To quantify the effects of species presence and the effects causing by their presence on other species interactions in the system when all interacting species are present

in the experimental arenas (Fig. 1f), a protocol consisting of nine treatments was designed (Table 1). The results allowed us to estimate the impacts of enemies on prey (pair-wise interaction strengths) and their interference effects on other interacting species. These effects were classified and quantified, contrasting the simplest cases in which the species were reared alone in the experimental arena with cases in which two or more species were reared in the same experimental arena. When present, the number of IG-predators was lower than the number of IG-prey (Table 1) to ensure that some IG-prey survive and reach the pupal stage at which parasitism occurs. Three densities of parasitoids, including zero, were used to estimate the potential impact of parasitoids on blowfly species.

IG-predator effects on IG-prey survival were quantified by comparing the survival rates among treatments 1 and 4. The IGP, cannibalism and IG-prey effects on IG-predator survival were quantified by comparison between treatments 4 and 7. To compare and quantify the effects of parasitism and parasitoid presence on blowfly species after different larval interactions, tests were conducted among the nine treatments to quantify each type of species interaction and the simultaneous effects of species presence, parasitism, cannibalism and IGP on the survival of both blowfly species (Table 1).

All experimental treatments were set up in vials (20 cm in height \times 15 cm in diameter) containing blowfly larvae reared in an excess of ground beef (4 g of meat per larva), wood shavings to allow for pupation, and one of three parasitoid densities (0, 1, or 10 females), maintained at laboratory-controlled conditions (25 °C, 70 % relative humidity, 12: 12 light: dark cycle). The specified amount of food (4 g of meat per larva) is enough to significantly reduce the effects of competition for food in blowflies (Godoy et al. 1996), ensuring the minimization of the density-dependence effects of competition on focused interactions.

Female parasitoids, which were introduced into the system at the beginning of the experiment, received honey

and water ad libitum. These 10-day-old females were nulliparous and originally reared in laboratory conditions. After the larval and pupal interactions, closed parasitized blowfly pupae were individually placed in capsules, and the number of parasitized pupae was counted after 35 days. Ten replicates were set up for each treatment.

Statistical analysis

The proportions of flies surviving IGP, cannibalism, or parasitism were analyzed by fitting mixed logistic regression models considering vials as a random effect factor whereas treatments and other covariates such as final densities were considered fixed-effect quantitative factors (Faraway 2006). The mixed-effect model suits this analysis because each vial is an experimental unit. The random effects model introduces a covariance structure that takes into account possible correlations between individual responses within the same vial in addition to accounting for extra variability between vials under the same treatment. Linear predictors were fit to the logit link function $\log(P_i/(1-P_i))$, where P_i is the (prey or predator) probability of surviving (as larvae or pupae) in vial i . Thus, the fitted survival probabilities are given by $\exp(\text{linear predictor})/(1 + \exp(\text{linear predictor}))$.

We used the 'lmer' function from the 'lme4' package of the R statistical program (The R Foundation for Statistical Computing; <http://www.R-project.org>) to fit the models. Wald tests were used to test the hypothesis of nullity of each fixed effect in the model.

Survival after larval phase interactions

IG-prey Larval Survival—a mixed logistic regression model was fitted to explore the effect of IG-predator presence/absence as well as the linear effect of larval interaction effects (Interaction Strength—IS), given by the final IG-predator density (when predator was present), on the probability of larval prey survival. Thus, high final

Table 1 Experimental conditions designed to estimate the effects of ecological interactions on blowfly survival: IGP and cannibalism during larval interactions and parasitism during pupal phases

Experimental condition	Density			Interaction effect acting upon species survival		
	Prey	Predator	Parasitoid	IGP	Parasitism	Cannibalism
1	300	0	0	No	No	No
2	300	0	1	No	Yes	No
3	300	0	10	No	Yes	No
4	300	100	0	Yes	No	Yes
5	300	100	1	Yes	Yes	Yes
6	300	100	10	Yes	Yes	Yes
7	0	100	0	No	No	Yes
8	0	100	1	No	Yes	Yes
9	0	100	10	No	Yes	Yes

IG-predator densities were assumed to be the result of a decrease in cannibalism due to the presence of prey.

IG-predator Larval Survival- Similar models were fitted to the surviving proportion of IG-predator larvae as a response variable. The larval interaction effects (IS) on predator larvae survival, given by the final IG-prey densities, were assumed to be the consequences of IGP effects on the IG-prey population. Thus, low final IG-prey densities were interpreted as the result of high IGP effects during the larval interaction phase.

During interspecific larval interactions, the numbers of both IG-prey and IG-predator larvae are expected to decrease as a result of IGP and cannibalism, meaning that the initial numbers of larvae will not remain constant during the period of larval-phase interactions. However, we assumed that IS is controlled by the density of larval species present during the larval interactions. In this way, the proportions of surviving individuals (represented by variables final number of prey/predator, respectively) may indicate the intensity of the effects of larval interactions that each species underwent during that period.

Survival after pupal-phase interactions

IG-prey Pupal Survival—the probability of IG-prey pupae survival was investigated as a function of the presence/absence of IG-predators and the number of parasitoids. The number of parasitoids (+0.05) was transformed on the log10 scale to fit a more parsimonious model. Linear and quadratic effects of parasitoid density and the interaction effect between IG-predators and parasitoids (IS) were included in the logistic model.

IG-predator Pupal Survival—the probability of IG-predator survival was investigated as a function of IG-prey presence/absence, the density of prey pupae, and parasitoid density (with the same transformation as above). Interactions among all terms and the quadratic effect of parasitoid density (IS) were included in the logistic model. The prey pupa densities used for this analysis were the numbers of surviving prey individuals at the end of the larval interaction period.

The analyses of the pupal phase allowed us to gather information about how the pupal abundances of the host species under shared parasitism can affect the persistence and/or coexistence times of both blowfly species.

Results

Short-term experimental study

The species presence and interaction effects (IS) in the system studied were evaluated for two different blowfly phases: the larval and pupal phases. The effects of

cannibalism and IGP appeared earlier than parasitism in the blowfly populations, and the effect of parasitism was dependent on the survival of blowflies during the larval interaction period. In IG-prey populations, parasitism had a strong effect when parasitoids were the only enemies present (Fig. 2a), resulting in the reduction of pupal prey population density from 85.5 to 73.7 and 34.5 % when 1 and 10 parasitoids were present, respectively. However, the impact of IG-predators on IG-prey was stronger than the effect of parasitoids when IG-predators were the only enemies, resulting in the reduction of the prey population in the larval phase to 7.76 % of its original value (Fig. 2b). When parasitoids were also present, only 26.23 and 4.62 % of the original number of prey pupae were available for parasitization with 1 and 10 parasitoids, respectively (Fig. 2b). Consequently, the mortality of IG-prey pupae caused by parasitoids was decreased to 4.5 and 1.86 %, respectively.

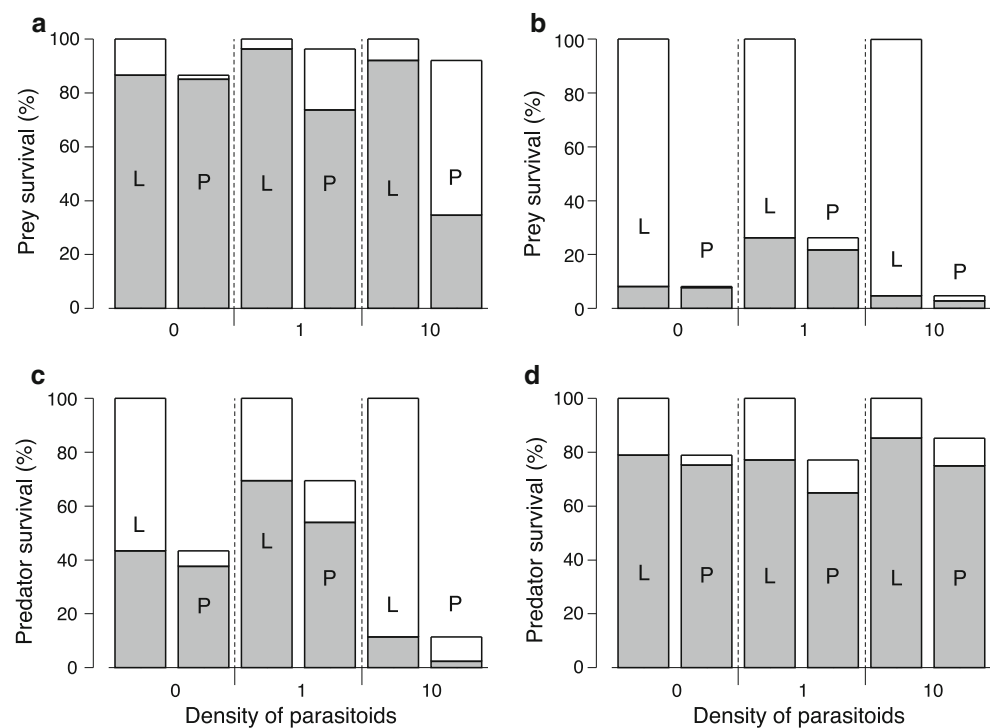
IG-predator populations exhibited high mortality in the absence of prey due to a high rate of cannibalism, with only 37.6 % of the population surviving (Fig. 2c). Cannibalism also reduced the number of IG-predator pupae available to parasitoids. The effects of parasitoids on IG-predator pupae were consequently weaker compared with the effects of the IG-prey population, causing 15.5 and 5 % of IG-predator mortality with 1 and 10 parasitoids, respectively (Fig. 2c). However, in the presence of IG-prey, predator survival in the absence of parasitoids increased to 75.2 %, but where parasitoids were present, the survival was 64.9 and 75 % with 1 and 10 parasitoid densities, respectively (Fig. 2d). In summary, the IG-predator population was benefited and the IG-prey population dramatically reduced by short-term tri-trophic interactions.

Our overall results clearly show that species survival was not explained by the simple presence or absence of individual species. The changes caused by species presence on interaction effects of other species played an important role in the system. Because of this, we included the interaction terms (given by IS) to analyze each period of blowfly life to quantify the effects of the species interaction strength on blowfly species survival.

Larval phase interactions

IG-prey Larval Survival—the predator's presence in the system had a very strong and negative effect on prey population. The IS quantified by the remaining density of predators also had a significant negative effect on the proportion of surviving prey (Table 2a). The interaction effect (IS) can be visualized by the observed and estimated marginal proportions of prey larvae as a function of the final number of predator survivors (Fig. 3a). The relatively large final density of predators may be the result of a low

Fig. 2 Survival rates (mean) of blowfly survival (gray bars) for different parasitoid densities. **a** IG-prey survival in absence of IG-predators, **b** IG-prey survival in presence of IG-predators, **c** IG-predator survival in absence of IG-prey and **d** IG-predator survival in presence of IG-prey. The letters *L* and *P* represent respectively number of blowfly larvae and pupae. The white bars correspond to the percentage of dead individuals in larval and pupal phases



cannibalism rate followed by a high predation rate that substantially reduced prey density.

IG-predator Larval Survival—the effect of prey presence on predator surviving numbers was highly significant and positive, whereas the interaction effect (IS) exhibited a negative effect (Table 2b). Although the presence of heterospecific prey ensured low rates of cannibalism, reducing cannibalism's effects on the IG-predator population, the observed and estimated marginal proportions of predator larvae as a function of the final number of prey survivors (Fig. 3b) indicates that the relatively low final density of prey may be the result of low IGP rates and a high cannibalism rate among predators, decreasing the probability of predator survival.

Pupal phase interactions

IG-prey Pupal Survival—the effects of increasing the density of parasitoids on pupae were distinct when compared to the effects of the presence/absence of the IG-predator (interaction effects, in the statistical sense, Fig. 2a, b). When parasitoids were the sole enemy acting on an IG-prey population, the higher parasitoid density led to lower survival of prey pupae (Figs. 2a, 4a). However, parasitoid density exhibited very weak effects on IG-prey pupa survival in the presence of IG-predators (Figs. 2b, 4b). The estimated IG-prey survival probabilities for the experimental conditions are presented in Table 2c. The significance of the interaction term between IG-predator and parasitoid presence indicated

that the survival of IG-prey pupa is not explained only by the simple presence or absence of individual species. The influence of the indirect effects of the IG-predator on parasitism rates due to the sharing of parasitism between both blowfly host species should also be considered when interpreting the survival rate of prey in the tri-trophic interaction. A high parasitoid density increased the mortality of IG-prey pupae when the IG-predator was absent (Fig. 4a). However, the presence of predators at the high parasitoid density had a significant positive effect on IG-prey survival. After a severe decrease in prey population due to IGP, the presence of the IG-predator pupae prevented the low abundance of IG-prey individuals from becoming extinct due to parasitism effects (Fig. 2b).

IG-predator Pupal Survival—an increase in parasitoid density had negative effects on the IG-predator population in the absence of IG-prey (Fig. 2c). The estimated IG-predator survival probabilities for the experimental conditions are presented in Table 2d. However, the effects of parasitism should be considered in the context of previous cannibalism, which reduces the number of available predator pupae for parasitoids. When prey was present, IGP effects (the number of prey pupae available to parasitoids) should also be considered, as suggested by Fig. 2c and d.

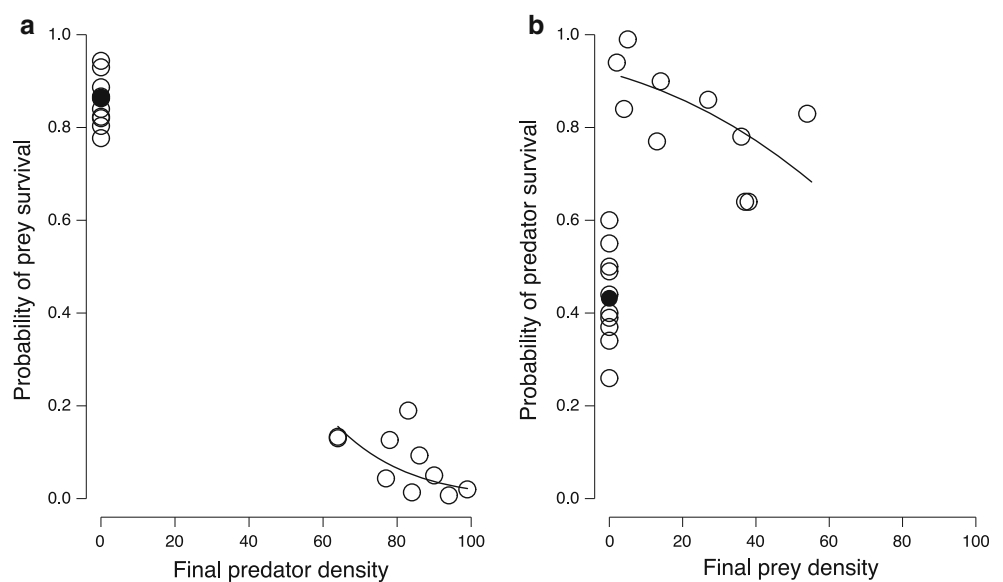
When IG-prey was absent, a higher parasitoid density reduced the probability of survival for IG-predator pupae (Figs. 2c, 5a). The presence of prey at the higher parasitoid density had significant and positive effects on IG-predator survival. The density of IG-prey pupae (the larvae

Table 2 Estimates of the parameters of the mixed logistic regression models for IG-prey (*Chrysomya megacephala*) and IG-predator (*C. albiceps*) survival proportions under IGP, cannibalism (larval interactions), and pupal parasitism by *Nasonia vitripennis*

Response	Species interaction	Treatment conditions*	Explanatory factors	Parameter estimate (SE)	P value
(a) Prey survival density (larvae)	IGP	1 & 4	Intercept	1.85 (± 0.20)	<0.0001
	Cannibalism		Predator presence (X_1)	-4.62 (± 0.29)	<0.0001
			IS (X_2)	-0.06 (± 0.02)	0.0016
(b) Predator survival density (larvae)	IGP	4 & 7	Intercept	-0.28 (± 0.18)	0.0990
	Cannibalism		Prey presence (X_1)	1.96 (± 0.25)	<0.0001
			IS (X_2)	-0.03 (± 0.01)	0.0034
(c) Prey survival density (pupae)	Parasitism	1, 2, 3, 4, 5 & 6	Intercept	2.23 (± 0.26)	<0.0001
			Predator presence (X_1)	-0.62 (± 0.39)	0.1111
			Parasitoid density (X_2)	-1.59 (± 0.18)	<0.0001
			IS (X_2^2)	-1.16 (± 0.24)	<0.0001
			IS ($X_1 \times X_2$)	1.07 (± 0.32)	0.0008
			IS ($X_1 \times X_2^2$)	1.66 (± 0.40)	<0.0001
(d) Predator survival density (larvae)	Parasitism	4, 5, 6, 7, 8 & 9	Intercept	0.84 (± 0.25)	0.0006
			Prey presence (X_1)	0.52 (± 0.37)	0.1598
			Parasitoid density (X_2)	-1.69 (± 0.29)	<0.0001
			Prey pupae density (X_3)	0.01 (± 0.01)	0.0159
			IS (X_2^2)	-0.62 (± 0.30)	0.0384
			IS ($X_1 \times X_2$)	1.86 (± 0.35)	<0.0001
			IS ($X_1 \times X_2^2$)	1.50 (± 0.41)	0.0003

* Treatment conditions are defined in Table 1 and used for fitting the model. IS represents Interaction Strength effect on blowfly species for each period of their life cycle

Fig. 3 Observed (circles) and estimated marginal (line) probabilities of **a** IG-prey survival as a function of final IG-predator density and **b** IG-predator survival as a function of final IG-prey density. The empty circle at 0 larval density represents the observed probability of survival in the absence of heterospecific larvae. The filled circle represents the fitted marginal probability in the absence of heterospecifics, and the line is the fitted marginal probability as a function of the number of heterospecific larvae when they are present



surviving IGP) had a positive and significant effect on IG-predator survival (Table 2d). In the presence of parasitoids, a high abundance of prey pupae increased the survival of IG-predator pupae (Fig. 5b).

Long-term theoretical study

A theoretical model based on the experimental data was developed to evaluate the consequences of the simultaneous

Fig. 4 Observed and estimated marginal (line) probabilities of prey pupa survival as a function of initial parasitoid density in the **a** absence and **b** presence of IG-predators

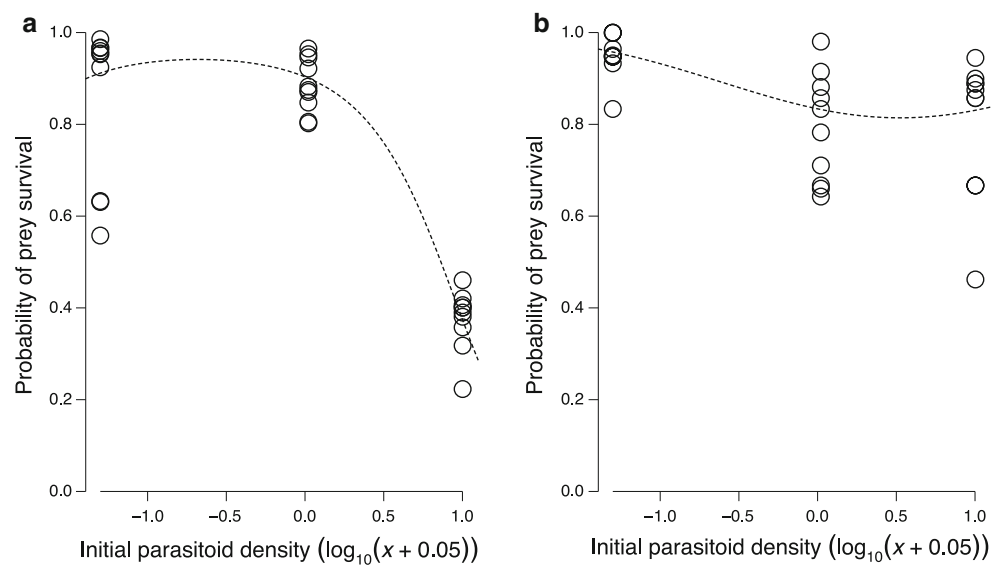
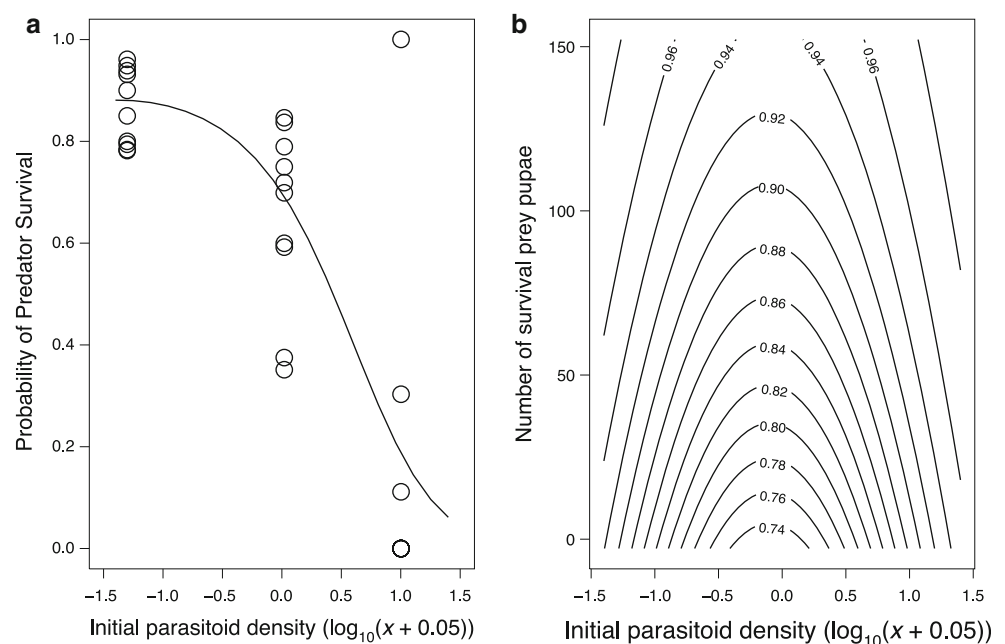


Fig. 5 **a** Observed (circles) and estimated marginal (line) probabilities of predator pupa survival as a function of initial parasitoid density in the absence of IG-prey. **b** Estimated marginal (line) probabilities of predator pupa survival as a function of the initial parasitoid density in the presence of IG-prey and prey pupae abundance



effects of cannibalism, IGP and parasitism for the persistence of the two blowfly species in our closed experimental system. This model is presented as a useful tool for the understanding and exploration of the consequences of studied ecological processes, making it possible to make predictions about blowfly dynamics using the interaction effect sizes derived from our experimental results.

Species interactions were described by a discrete-time model in which the time step (m) was set to one day. The blowfly life cycle (n) is completed every 15 days. Simulations started ($m = 1$) with blowflies in egg phase ($n = 1$).

When simulations complete 15 days, $m = n = 15$. However when $m = 16$, a new blowfly generation arises and $n = 1$. A detailed description of the steps necessary to model the complete blowfly life cycle is provided in Table 3.

The labels (*meg*) and (*alb*) were used to refer to *C. megacephala* and *C. albiceps*, respectively, and the label (*W*) referred to the female wasp parasitoid (Table 3). The model considers that adult female blowflies lay their eggs during the first day of each cycle of interaction. After larvae hatching adult blowflies cannot use the same resource to lay more eggs. The model aims to describe the blowfly population

Table 3 Description map for complete blowfly life cycle: egg (*E*); larva (*L*); pupa (*P*); and adult (*A*)

(a) $n < n_e$	(b) $n = n_e$	(c) $n_e < n < n_e + n_{L1}$	(d) $n_e + n_{L1} < n < n_e + n_{L1} + n_L$	(e) $n = n_e + n_{L1} + n_L$
$E_{meg}^{n+1} = E_{meg}^n$	$E_{meg}^{n+1} = 0$	$E_{meg}^{n+1} = 0$	$E_{meg}^{n+1} = 0$	$E_{meg}^{n+1} = 0$
$E_{alb}^{n+1} = E_{alb}^n$	$E_{alb}^{n+1} = 0$	$E_{alb}^{n+1} = 0$	$E_{alb}^{n+1} = 0$	$E_{alb}^{n+1} = 0$
$L_{meg}^{n+1} = 0$	$L_{meg}^{n+1} = E_{meg}^n$	$L_{meg}^{n+1} = (1 - \delta_{Lmeg})L_{meg}^n$	$L_{meg}^{n+1} = (1 - \delta_{Lmeg})L_{meg}^n f_1^n$	$L_1^{n+1} = 0$
$L_{alb}^{n+1} = 0$	$L_{alb}^{n+1} = E_{alb}^n$	$L_{alb}^{n+1} = (1 - \delta_{Lalb})L_{alb}^n$	$L_{alb}^{n+1} = (1 - \delta_{Lalb})L_{alb}^n f_2^n$	$L_2^{n+1} = 0$
$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = L_{meg}^n$
$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = L_{alb}^n$
$A_{meg}^{n+1} = 0$	$A_{meg}^{n+1} = 0$	$A_{meg}^{n+1} = 0$	$A_{meg}^{n+1} = 0$	$A_{meg}^{n+1} = 0$
$A_{alb}^{n+1} = 0$	$A_{alb}^{n+1} = 0$	$A_{alb}^{n+1} = 0$	$A_{alb}^{n+1} = 0$	$A_{alb}^{n+1} = 0$
(f) $n_e + n_{L1} + n_L < n < n_e + n_{L1} + n_L + n_P$	(g) $n = n_e + n_{L1} + n_L + n_P$	(h) $n_e + n_{L1} + n_L + n_P < n < n_e + n_{L1} + n_L + n_P + n_A$	(i) $n = n_e + n_{L1} + n_L + n_P + n_A$	
$E_{meg}^{n+1} = 0$	$E_{meg}^{n+1} = 0$	$E_{meg}^{n+1} = 0$	$E_{meg}^0 = \gamma_{meg} A_{meg}^n / 2$	
$E_{alb}^{n+1} = 0$	$E_{alb}^{n+1} = 0$	$E_{alb}^{n+1} = 0$	$E_{alb}^0 = \gamma_{alb} A_{alb}^n / 2$	
$L_{meg}^{n+1} = 0$	$L_{meg}^{n+1} = 0$	$L_{meg}^{n+1} = 0$	$L_{meg}^{n+1} = 0$	
$L_{alb}^{n+1} = 0$	$L_{alb}^{n+1} = 0$	$L_{alb}^{n+1} = 0$	$L_{alb}^{n+1} = 0$	
$P_{meg}^{n+1} = (1 - \delta_{Pmeg})P_{meg}^n - P_{meg}^n W_m g / (P_{meg}^n + P_{alb}^n)^*$	$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = 0$	$P_{meg}^{n+1} = 0$	
$P_{alb}^{n+1} = (1 - \delta_{Palb})P_{alb}^n - P_{alb}^n W_m g / (P_{meg}^n + P_{alb}^n)^*$	$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = 0$	$P_{alb}^{n+1} = 0$	
$A_{meg}^{n+1} = 0$	$A_{meg}^{n+1} = P_{meg}^n$	$A_{meg}^{n+1} = (1 - \delta_{Ameg})A_{meg}^n$	$A_{meg}^{n+1} = 0$	
$A_{alb}^{n+1} = 0$	$A_{alb}^{n+1} = P_{alb}^n$	$A_{alb}^{n+1} = (1 - \delta_{Aalb})A_{alb}^n$	$A_{alb}^{n+1} = 0$	
(j) $W_{m+1} = (1 - \delta_{PA})W_m + ch_{m+1-k}W_{m+1-k}^{**}$				

The subscripts (*meg*) and (*alb*) refer to IG-prey (*C. megacephala*) and IG-predator (*C. albiceps*) respectively. The variable n is the number of blowfly life cycles (1 cycle = 15 days) and m is the time in days since species interactions started. The relation between m and n is given by $n = m - 15 \times INT(m/15)$, where $INT()$ means the integer part of the fraction. The subscript k represents the length (days) of the parasitoid life cycle (egg to adult phases), that corresponds to 14 days inside the blowfly pupae

n_e , n_{L1} , n_L , n_P , and n_A are the number of days that blowfly species remain in egg, 1st and 2nd larval instar, 3rd larval instar, pupal and adult life stage, respectively. $\delta_{Lmeg} = \delta_{Lalb} = 0.1$; $\delta_{Pmeg} = \delta_{Palb} = 0.04$; $\delta_{Ameg} = \delta_{Aalb} = 0.1$; $\gamma_{meg} = 206$; $\gamma_{alb} = 203$; $\delta_{PA} = \delta_{PA} = 0.1$; $c = 80$

It is important to note that when f_1 , f_2 and g (Eqs. 1, 2 and 3) are undefined, these functions are multiplied by zero when $L_{meg}^n = 0$, $L_{alb}^n = 0$, and $W_m = 0$, ensuring respectively that $L_{meg}^{n+1} = 0$, $L_{alb}^{n+1} = 0$ and $W_{m+1} = 0$

* To avoid negative values, we impose that $P_x^{n+1} = 0$ if $(1 - \delta_{Px}) < W_m g / (P_{meg}^n + P_{alb}^n)$, which means that the wasp cannot parasitize more than the available pupae

** We impose $ch_{m+1-k} W_{m+1-k} = 0$ when $m < k$

development in a single resource. Every time that a blowfly life cycle is completed, a new resource is available for new adult females lay their eggs on it. The resource was considered not limited, supporting high number of larvae feed on it.

The species interactions took place in different periods: the IG-prey and IG-predator interacted with each other only as 3rd instar larvae, period correspondent to two days in their life cycle, when both cannibalism and IGP may occur. Parasitoids (*W*) interfered in the blowflies' life cycle dynamics, laying their eggs in the blowflies when (*meg*) and (*alb*) were in their pupal stages (during four days of each blowfly life cycle). As in the experiments, the model considered only synchronized events, meaning that both blowfly species were always at the same developmental age on the resource exploited. There is no generation overlapping in blowfly populations.

The parasitoid's life cycle is also assumed to be synchronous with those of the hosts: the new parasitoids emerged from parasitized pupae will interact with blowfly pupae in next generation, since they spent 14 days (k) inside of parasitized host pupae (egg, larval and pupal phases) before the adults emergence. In simulations, parasitoid generations can overlapping, depends on adult mortality rates.

Blowfly

The initial numbers of eggs were set at $E_{meg}^1 = 300$ and $E_{alb}^1 = 100$, as in the experiment. After hatching, IG-prey and IG-predator larvae started to interact. During the larval phase, a larval death rate ($\delta_{Lmeg} = \delta_{Lalb} = 0.1$) was considered, which may be associated with density-dependent effects of competition. However, the effects of IGP and cannibalism on the larval death rate were considered separately. The function f_1 describes IG-prey survival of IGP (effects of L_{alb} upon L_{meg}) and was modeled by an exponential decay:

$$f_1^n = \exp(-\alpha L_{alb}^n / L_{meg}^n). \quad (1)$$

The parameter α represents the intensity of IGP effects on the IG-prey population, meaning that the higher the ratio of L_{alb}/L_{meg} , the lower f_1 will be.

Cannibalism in L_{alb} , which was intense upon unavailability of IG-prey, was also modeled by an exponential function. The function describing the proportion of IG-predator that survived cannibalism is written as follows:

$$f_2^n = 1 - 0.5 \exp(-\beta L_{meg}^n / L_{alb}^n) \quad (2)$$

where β represents the intensity of the effects of cannibalism on the IG-predator population, i.e., the higher the ratio of L_{meg}/L_{alb} , the higher f_2 will be. The benefit to the predator from consuming the prey can be understood by considering Eqs. 1 and 2 simultaneously: f_1 shows that predation increases with the number of preys per predator, and f_2 shows that an increase in preys consumed per predator (which implies the occurrence of predation) results in a decrease in the predator mortality rate.

We performed two experiments aimed at finding reasonable values for α and β . First, five densities of IG-prey larvae (10, 20, 30, 40 and 50 individuals) were offered to single IG-predator larvae. Second, same densities of IG-prey larvae were offered to five IG-predator larvae to obtain the proportion of prey-predator survival for each combination of prey and predator larva densities. These experimental conditions were set up in Petri dishes (30 mm diameter) maintained at the previously described laboratory-controlled conditions. For each combination, 10 replicates were set up.

By adjusting IGP and cannibalism functions to our empirical data, we obtained the values $\alpha = 5.5$ and $\beta = 1.5$, respectively. The effects of increasing the intensity of IGP effects from $\alpha = 5.5$ to $\alpha = 9.0$ (Fig. 6a) and decreasing the effect of cannibalism on predator mortality from $\beta = 1.5$ to $\beta = 0.5$ (Fig. 6b) also were analyzed.

IG-prey and IG-predators that survived predation and cannibalism turned into pupae, becoming susceptible to parasitism. The pupal phase exhibits two kinds of mortality: the intrinsic death rate ($\delta_{pmeg} = \delta_{palb} = 0.04$) and parasitism. The factor W_g is the total number of pupae available for the wasps to parasitize, and $P_x^n / (P_{meg}^n + P_{alb}^n)$ designates that they have no preference between the different host pupae. The parasitism function,

$$g^n = g_0 \left[1 - \exp(-\lambda(P_{meg}^n + P_{alb}^n)) \right] \quad (3)$$

represents the number of pupae that was parasitized by each parasitoid and depends on the total number of pupae that were available. The constant g_0 (assumed to be 8) is the maximum number of pupae that one parasitoid can parasitize per day. The coefficient λ (assumed to be 0.2) is the attack rate of a parasitoid. The parasitism occurred during four days in each blowfly life cycle.

For the pupae that have attained the adult phase, the following intrinsic death rates were assumed: $\delta_{Ameg} = \delta_{Aalb} = 0.1$. The number of eggs per adult in *C. megacephala* and *C. albiceps* were $\gamma_{meg} = 206$ and $\gamma_{alb} = 203$, respectively, according to studies on the fecundity of these blowfly species (Reigada and Godoy 2005; Riback and Godoy 2008). It was also assumed that half of the total adult blowfly population of the previous cycle was female,

and the number of eggs produced to initiate a new cycle (generation) was calculated.

Parasitoids

The parasitoid modeling was restricted to the description of female wasps. The length of the *N. vitripennis* life cycle (k) was 14 days (Nagel and Pimentel 1964). The number of female wasps at day $m + 1$ depended on the intrinsic death rate ($\delta_{PA} = 0.1$) and on the number of new adult female individuals that were alive k days earlier and parasitized the existing pupae (Table 3).

The value adopted for the numerical response of *N. vitripennis* is independent of host availability. It was assumed that a female wasp laid 10 eggs per pupae attacked ($c = 80$, maximum of 8 pupae with 10 parasitoids each). It was assumed that 10 eggs per pupae host represented a reasonable mean for the numerical response of *N. vitripennis*. Because *N. vitripennis* can modulate its progeny's sex ratio according to the number of pupae available per female parasitoid when eggs are laid, exhibiting female-biased sex ratios in favorable patches of exploitation (Grillenberger et al. 2009), the percentage of female eggs (h) was modeled for all of the eggs. Then, the sex ratio (t) between females and males was assumed to depend exponentially on the ratio $P_{meg}^n + P_{alb}^n / W_m$

$$t_m = t_0 \left[1 - \exp(-v(P_{meg}^n + P_{alb}^n) / W_m) \right], \quad (4)$$

where $t_0 = 4.8$ represents the maximal proportion of female progeny per male in parasitoid progeny (Nagel and Pimentel 1964). At a low density of pupae, this value decreased considerably. If t is the sex ratio between females and males, then the percentage of females relative to females and males is $h_m = t_m / (1 + t_m)$. The coefficients of the functions t were set to $v = 0.2$. Simulations were initiated considering only one parasitoid to investigate the effect of a low parasitoid density. This procedure was adopted to ascertain the minimum conditions for blowfly population persistence. The presence of more than one parasitoid resulted in a very short blowfly persistence time.

Simulation results

Parasitism effects

For this portion of the model, each host species interacted with two densities of parasitoid (1 and 10), as in the experimental study. *Nasonia vitripennis* always drove its hosts to extinction (Fig. 7). Of the two host blowfly species, the IG-predator species was the most negatively influenced, as both parasitism and cannibalism played roles

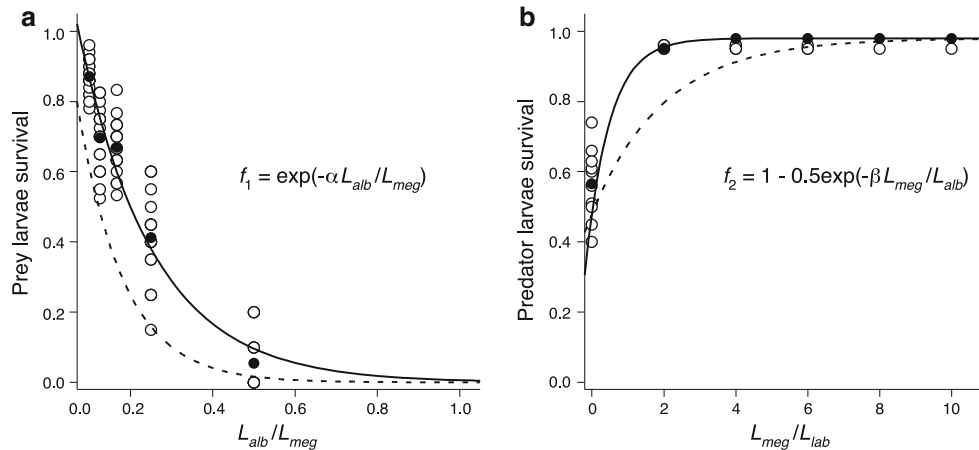


Fig. 6 Fitted curves to the experimental results on blowfly larvae survival under the effects of IGP and cannibalism. *Open dots* represent the experimental data ($n = 10$) and *filled circles* the average obtained from experimental data for surviving **a** IG-prey and **b** IG-predator larvae, respectively. In **a**, the *solid line* represents the proportion of prey larvae surviving the IGP intensity from the

experimental data ($\alpha = 5.5$) and the *broken line* the theoretical survival, given an IGP intensity of $\alpha = 9.0$; In **b**, the *solid line* represents the proportion of surviving predator larvae given the cannibalism intensity from the experimental data ($\beta = 1.5$), and the *broken line* represents the theoretical survival given a cannibalism intensity of $\beta = 0.5$

in its population decline (Fig. 7c, d). As suggested by the experimental results (Fig. 2c), model simulations showed that the IG-predator, in the absence of IG-prey and interacting with 10 parasitoids, could become locally extinct in the first cycle of interaction.

Parasitoids interacting with IG-prey exhibited high population sizes because parasitism was the only mortality factor in the system. Consequently, the high number of available pupae facilitated a large increase in the parasitoid population (Fig. 7a, b). In the experimental study, the effects of parasitism on the system were weak due to the previous effects of IGP and cannibalism, but the simulations showed that over the long term, the effects of parasitism increased, causing the extinction of both blowfly species (Fig. 7).

Cannibalism and IGP effects

The effects of cannibalism and IGP in the absence of the parasitoid were also explored. Under both high and low cannibalism and IGP intensities, the IG-prey died out and IG-predators persisted in the system (Fig. 8). Prey populations under high IGP intensity persisted for two cycles. In these cases, the increase in the intensity of cannibalism did not benefit the prey population (Fig. 8a, b).

Prey populations under low IGP intensity showed high persistence and high population sizes (Fig. 8c, d). The increase in the effects of cannibalism on the IG-predator population was not sufficient to increase the persistence time of IG-prey. However, when IG-predators were subject to high cannibalism intensity, IG-prey exhibited a higher population size before becoming extinct (Fig. 8c). The

effects of cannibalism among IG-predators, as suggested by the experimental results, showed weak positive effects on the IG-prey population persistence time. For predators, a larger increase in population was observed for simulations in which the IGP effect was high and the cannibalism effect was low (Fig. 8a).

Tri-trophic interaction

In this section, cannibalism, IGP, and parasitism as well as indirect effects derived from the effects of species presence on the persistence times of the blowfly host species were explored. For prey populations interacting with parasitoids, the presence of predators decreased persistence time (compare Fig. 7a with Fig. 9). However, the presence of prey was beneficial to the persistence of predators under parasitoid attack (compare Fig. 7c with Fig. 9).

Under high IGP intensity, the increase in cannibalism effects did not produce a beneficial effect for prey, which was always driven extinct by predators in the larval phase of the second cycle (Fig. 9a, b). In these simulations, the effects of low or high intensity cannibalism on the predator population after the exclusion of prey drove them to extinction in the third cycle of interaction (Fig. 9a, b).

Under low IGP intensity, larval prey survived to the second cycle of interactions, but during the pupal phase, parasitoids drove them to extinction (Fig. 9c, d). In these simulations, the effect of cannibalism on the predator population was important. Under low-intensity cannibalism, predator persistence was higher because the presence of prey during the pupal phase in the second cycle decreased the parasitism rate for the predator population,

Fig. 7 Densities of blowfly species long to generation times. **a** IG-prey under interaction with one parasitoid and **b** with 10 parasitoids; **c** IG-predator under interaction with one parasitoid and **d** with 10 parasitoids. Gray bars represent density of blowfly species in larval and pupal phases in each generation. White bars correspond to density of dead individuals in each life stage. Black lines represent parasitoid populations. Letters *L* and *P* represent respectively number of blowfly species in larval and pupal phases. The initial number of blowflies are: $L_{meg} = 300$ and $L_{alb} = 100$

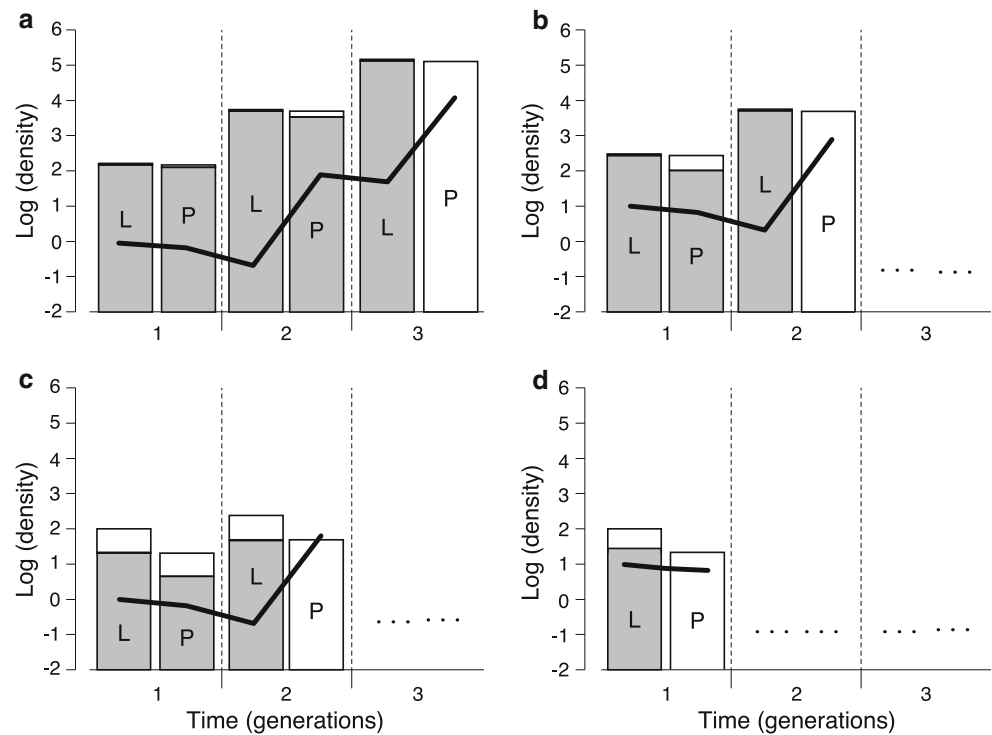
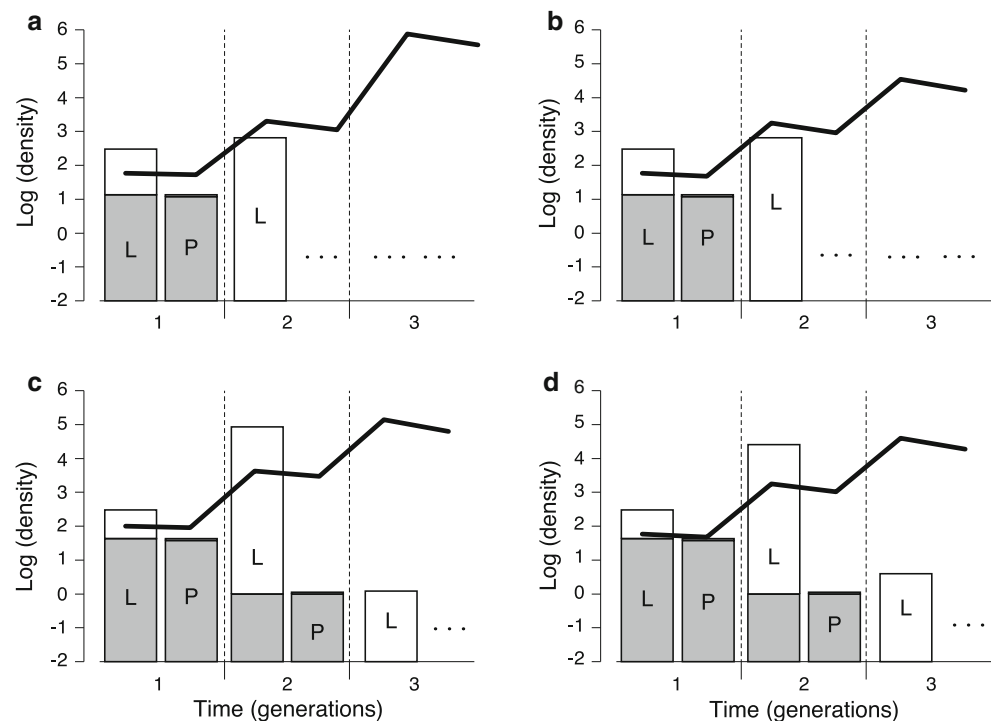


Fig. 8 Densities of IG-prey (bars) and IG-predator (black lines) interacting during larval period under different levels of IGP and cannibalism effects in absence of parasitoids. **a** $\alpha = 9.0$, $\beta = 1.5$ (high IGP and low cannibalism); **b** $\alpha = 9.0$, $\beta = 0.5$ (high IGP and high cannibalism); **c** $\alpha = 5.5$, $\beta = 1.5$ (low IGP and low cannibalism); and **d** $\alpha = 5.5$, $\beta = 0.5$ (low IGP and high cannibalism). Gray bars represent density of surviving IG-prey and white bars correspond to density of IG-prey dead in larval interaction phase long to generations. Letters *L* and *P* represent respectively number of IG-prey larvae and pupae. The initial numbers of blowflies are $L_{meg} = 300$ and $L_{alb} = 100$



allowing them to persist to the third cycle. However, when predators were the sole host species for parasitoids, they became extinct (Fig. 9c). With high-intensity cannibalism, predators became extinct in the larval phase of the third cycle (Fig. 9d).

The extinction times of IG-prey and IG-predators in the system were primarily related to the consequences of larval interactions for population sizes, corroborating the experimental results. The IGP effect was the most influential factor in the persistence of species in the tri-trophic system,

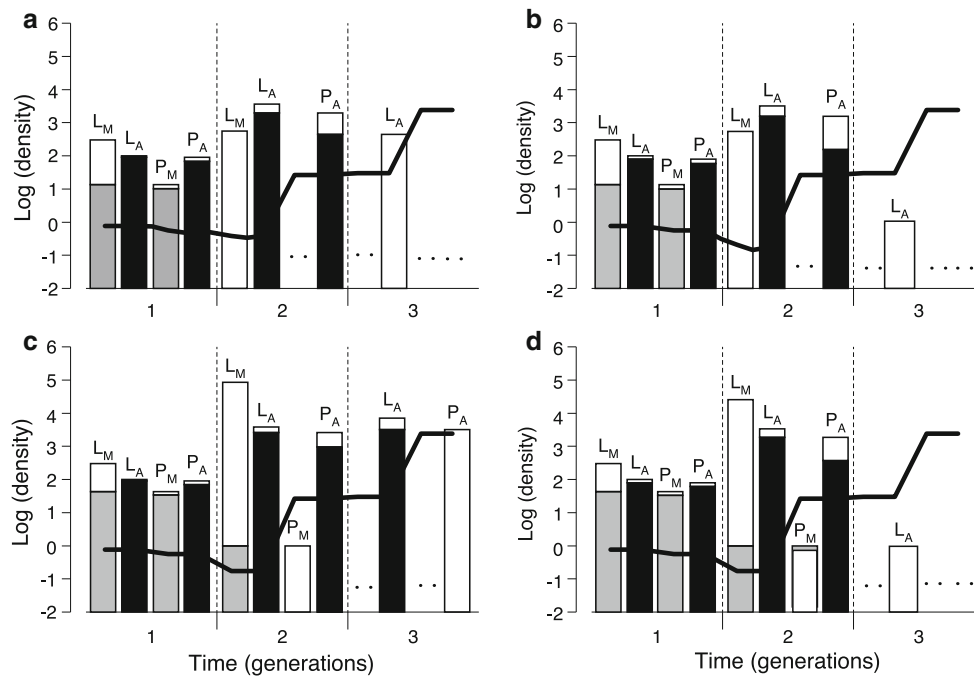


Fig. 9 Densities of surviving IG-prey (gray bars), surviving IG-predator (black bars) and parasitoids (black line) interacting under different levels of IGP and cannibalism effects. **a** $\alpha = 9.0$, $\beta = 1.5$ (high IGP and low cannibalism); **b** $\alpha = 9.0$, $\beta = 0.5$ (high IGP and high cannibalism); **c** $\alpha = 5.5$, $\beta = 1.5$ (low IGP and low cannibalism); and **d** $\alpha = 5.5$, $\beta = 0.5$ (low IGP and high cannibalism). White

bars correspond to density of blowfly species dead in larval and pupal interaction phase long to generations. Letters L_M , L_A , P_M and P_A represent respectively number of IG-prey, IG-predator larvae and pupae. The initial numbers of blowflies were $L_{meg} = 300$ and $L_{alb} = 100$, and the initial number of parasitoids was $W = 1$

as this interaction defined the presence of host species during parasitoid attacks. When both blowfly species were present in the pupa phase, IG-predators benefited and exhibited high persistence due to sharing parasitoid attacks with the prey population.

Discussion

Short-term impacts and additivity of interactions

Our experimental results demonstrate that the effects of species presence on the system were strong, affecting the abundance of blowfly populations. The addition of interactions among species also played an important role on survival rates.

The presence of IGP exerted a strong positive effect on cannibalistic behavior among predators. Our results showed that the absence of this interaction could alter the abundance of species, as IGP drastically reduced the IG-prey population and increased the success of the IG-predator by attenuating the effects of cannibalism. IGP also exhibited very important effects for parasitoids because their success relies upon the proportion of pupae surviving larval predation. Our experimental short-term results showed that the impacts of species presence and

interactions among species were modulated by IGP, which was the predominant ecological process in the experimental system.

The presence of parasitoids had only moderate effects on the presence of the two blowfly species because of the dependence on previous effects. When preys were absent, a high density of parasitoids intensified the mortality rates of predator larvae. This magnification of the effect of cannibalism may be due to the indirect effects produced by parasitoid presence on host larvae, which tend to spend more time in the larval phase and avoid developing into pupae in the presence of parasitoids, thus increasing the encounter rates among cannibalistic larvae (Reigada and Godoy 2012). The effects of parasitoid presence on hosts before the period in which parasitism has a direct effect illustrated how wide the influence of a species in a complex food web can be, in which the presence of one species can provoke changes in the behavior of others even when contact between species occurs in non-susceptible periods of interaction (Reigada and Godoy 2012).

During the pupa phase, it was observed that the attack behavior of the parasitoid changed according to blowfly host species presence and abundance in a tri-trophic system. The rate of parasitism on the prey population was reduced due to the small number of surviving larvae to the pupa stage as a result of IGP. The presence of a generalist

parasitoid relaxed the total impact of the mesopredator population in tritrophic interactions, making it possible for the IG-prey population to persist. Our results suggest that the presence of *N. vitripennis* in natural communities can help other blowfly species coexist with *C. albiceps* in a patch by creating spatial refuges for IGP prey when they are rare (Abrams and Chen 2002).

Long-term impacts and the additivity of interactions

The theoretical results produced by extrapolating the short-term experimental results enabled an understanding of the consequences of additivity interaction effects for blowfly species persistence. Our results showed that the variability caused by species-specific effects on blowfly species populations can have different impacts; however, IG-predators were the dominant influences in the system, defining the persistence time of prey and the number of cycles in which predator and prey could share the burden of parasitism.

The blowflies \times *N. vitripennis* interactions were extinction-prone in long-term simulations; however, depending on the intensity of the IGP and cannibalism effects on blowfly populations, their persistence times changed. In long-term interactions, IGP was able to modulate the dynamics of the system, thereby influencing its outcome and defining the persistence time of blowfly populations. Cannibalism exhibited a weak influence on the IG-prey population in terms of persistence time in the system. However, for the IG-predator, cannibalism exerted a higher influence on persistence time under tri-trophic interactions. In this case, low cannibalism and low IGP intensities increased the persistence of IG-prey and consequently decreased parasitism rates on IG-predator population due to sharing parasitism with the prey population.

Blowflies have been used as a laboratory model to study population ecology because of the interesting ecological patterns exhibited, including cyclic or chaotic fluctuations, which are frequently investigated in studies involving mathematical modeling (Gurney et al. 1980; Godoy et al. 2001). As suggested in this study, these complex patterns may be quantitatively or qualitatively modified in response to intra- or interspecific interactions.

The performance of *C. albiceps* as a simple competitor, especially in intraspecific cultures, has been considered to be poor (Rosa et al. 2006). Under conditions of intraspecific competition, *C. albiceps* exhibits low survival, most likely due to its cannibalistic habits (Faria et al. 2004, 2007; Rosa et al. 2006). However, the presence of heterospecific prey and IGP effects reduced this negative effect. Our results indicated that IGP is an essential mechanism to increase the survival of *C. albiceps*, playing an important role in communities of necrophagous dipterans because

several blowfly species that are able to share resources in carcasses are also prone to predation by *C. albiceps* (Faria et al. 1999, 2007). However, although IGP and cannibalism have been previously documented in *C. albiceps* (Faria et al. 1999, 2004), the role of IGP in compensating for the effects of cannibalism or the low efficiency of this species as an intraspecific competitor was elucidated for the first time in this study.

Studies have indicated that ecological interactions such as cannibalism and IGP may cause changes in predator–prey dynamics (Holyoak and Sachdev 1998; Rudolf 2007a, b). The presence of heterospecific prey can reduce cannibalism rates and causes long-term indirect effects, decreasing top-down forces in trophic cascades and stabilizing predator–prey dynamics (Rudolf 2007b). In nature, the patterns produced by the simultaneous action of IGP and cannibalism can explain the coexistence of IG predators and prey within a food substrate (Rudolf 2007a).

The impact of parasitism on the short-term persistence of blowflies was not particularly evident in our experimental results. However, our simulations showed that with an increase in the abundance of available hosts, the numerical response of parasitoids and the parasitism rate also increase in subsequent generations, leading to the extinction of the host species. However, our experimental and theoretical results showed that the interference of larval interactions at the system level could delay parasitoid population growth and increase the persistence time of the hosts.

The reproductive success of parasitoids is directly related to host abundance and to the way in which hosts are exploited (Godfray 1994). Several factors can influence a parasitoid's attack behavior towards its hosts, such as host quality, defense, and density (Godfray 1994). With respect to *C. albiceps* and *C. megacephala* acting as hosts, no study has yet compared the preference of *N. vitripennis* between these two blowfly species. However, the reduction of attacks on *C. albiceps* in the presence of *C. megacephala* suggests that both species are attractive for *N. vitripennis*, confirming the low specificity of this parasitoid. This result suggests that density is an important factor for *N. vitripennis* with respect to parasitism rates on host species and that the parasitoid changes parasitism rates according to the available host density. This distribution of parasitism between multiple host species can increase the persistence time of host species when they have low population sizes (Abrams and Chen 2002).

Species diversity is known to significantly influence the stability of systems by changing the strength of interactions among species (McCann et al. 1998). However, many studies concerning the effects of species diversity on complex food webs do not incorporate the non-additive interaction effects among species because they are restricted to analyses of the community structure in which

species constitute part of the studied food web rather than a full factorial manipulation of all species (Otto et al. 2008). Many studies also have tried to understand how ecological processes such as competition, predation, parasitism, and other indirect interactions structure natural communities (McCann et al. 1998; Van Veen et al. 2006; Rudolf 2007b). Some of these studies have shown that all of the above processes are mediated not only by changes in species density but also by changes in behavior and other traits among species (Van Veen et al. 2006), indicating the importance of indirect effects for ecological assemblages.

Knowledge of these factors is essential for a general understanding of community complexity and the link between biodiversity and ecosystem function. In a community, each particular species contributes directly or indirectly to particular processes within a food web. We showed both empirically and theoretically that the additivity of species and consequent interaction effects can affect the impacts of enemies on an ecological system; these indirect effects were mediated both trophically and behaviorally. The study of this simple food web revealed that changes in species composition in an ecological system can increase or decrease the persistence and coexistence time of species in accordance with the ecological processes operating on the food web. This investigation illustrated the value of examining the additivity of interactions for understanding the processes of community structuring as well as gaining a better understanding of when and how the simultaneous effects of traits can significantly affect community dynamics.

Acknowledgments We are grateful by comments and suggestion of anonymous referees. The work by CR was supported by scholarships from FAPESP and CAPES (PDEE); SBLA was supported by CAPES/PRODOC No 0004428/2010, FAPESP and the Consortium of the Americas for Interdisciplinary Science; MAMA and WACG were partially supported by CNPq; and PRGJ was supported by FAPESP.

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