Effects of plant availability and habitat size on the coexistence of two competing parasitoids in a tri-trophic food web of canola, diamondback moth and parasitic wasps

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ABSTRACT

Using experiments and spatial modeling, we here show the conditions for two competing parasitoids to coexist under two levels of plant availability in a tri-trophic food web of canola, diamondback moth (*Plutella xylostella*) and two parasitic wasps (*Diadegma semiclausum* and *Cotesia vestalis*) that target the same life stage of the herbivore diamondback moth. Plant availability had a significant effect on both the abundances of parasitoids and the herbivore. However, parasitoid abundances were not different with or without the occurrence of other parasitoid species, suggesting no effect of parasitoid coexistence on their abundances. Using a three-species Lotka–Volterra model, we confirmed the competitive exclusion of species with low consumption rate (=initial population size × per capita consumption rate) in a well-mixed habitat patch. We further built a cellular automaton (CA) to explore the minimum habitat size that ensures the coexistence of these two parasitoids, assuming different searching efficiencies (i.e. different radiuses of searching area and movement abilities for locating the host). With the in-patch dynamics portrayed by the three-species Lotka–Volterra model, the CA model demonstrated the possibility for the two parasitoids to coexist when the number of habitat patches reached a certain number. This research thus highlights the importance of both plant availability and habitat size to the dynamics and stability of the tri-trophic food web.

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1. Introduction

Plants can indirectly affect the natural enemies (e.g. parasitoids and predators) of herbivores by directly regulating the density of the herbivores (known as the density-mediated indirect interaction; Werner and Peacor, 2003). For instance, the nutrient content in plants can affect herbivore vitality and leads to cascaded effects on the dynamics and coexistence of the herbivore's natural enemies (Bottrell et al., 1998). The density regulation could be specifically strong if the herbivore is a specialist or if the plants are rare and patchily distributed. Indeed, this indirect interaction has been a main driver of ecological variation in many communities (Ohgushi, 2007). Plant density, diversity and patch size have been identified as factors that can directly regulate herbivore density and thus indirectly regulate the dynamics of parasitoids and predators. However, the effect of plant patch size on herbivore density has yielded

inconsistent results in literature (Bach, 1988). Systematic analysis is also lacking on the indirect interactions between plant availability and the parasitoids of herbivores, as well as the stability and coexistence of this tri-trophic system. It is even more difficult to forecast whether these indirect interactions will enhance or reduce the population size of herbivores and parasitoids, which is especially relevant when the focal species is a direct target of biological control.

Competition between multiple parasitoids is common in such tri-trophic systems (McGlade, 1999; Schoener, 1982; Walls, 1990). Classical competition theory predicts the exclusion of particular parasitoids when they compete for a single resource (Chesson and Case, 1986); that is, competing species cannot coexist unless mechanisms exist to allow the resource being partitioned (Bonsall et al., 2002). Many mechanisms have been identified to promote the coexistence of two parasitoids when feeding on a single host, such as temporal and spatial partitioning of resource (Comins and Hassell, 1996) and differences in attack rate and emergence rate, as well as differences in searching and dispersal abilities (Amarasekare, 2007; Hastings, 1980). These mechanisms of niche

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Fig. 1. Spatial arrangement of experimental potted plants in cages in which three insect species, the herbivore (*Plutella xylostella*), parasitoid *P* (*Diadegma semiclausum*) and parasitoid *Q* (*Cotesia vestalis*) coexist with canola plants for 8–9 herbivore generations (25 weeks) under fixed environmental conditions.

differentiation and partition can be considered as stabilizing forces to ensure the long-term coexistence of multiple competing species (Adler et al., 2007).

Here, using a laboratory experiment and an extended lattice model, we demonstrate how two parasitoids compete and coexist on potted plants in cages, even when the coexistence on a single patch (e.g. a leaf) is predicted unfeasible. We hypothesize that the coexistence of the two parasitoids is made possible because the plants and also leaves are patchily distributed at micro scales. The patchy habitat formed by different levels of plant availability could provide conditions for coexistence. We demonstrate this hypothesis using cellular automata (CA). Our study is a joint research of both greenhouse trials and mathematical modeling that support the observed coexistence due to the spatial partition of hosts. Given the importance of maintaining high biodiversity and enhancing the guild functionality of parasitoids in food webs, our research highlights how changes in plant availability could cause periodic starvations to the herbivores and, therefore, indirectly affect the dynamics, stability, and spatial distributions of the two parasitoids attacking the common host.

2. Methods

2.1. Study species

Our system comprises a guild of two parasitic wasps, the specialist *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae) and the oligophagous *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae), and a specialist herbivore, the diamondback moth (DBM), *P. xylostella* (L.) (Lepidoptera: Plutellidae) that feeds on the host plants of a canola cultivar (*Brassica napus* cv. SLM₀₄₆). Both wasps are solitary, koinobiont and endoparasitoids of DBMs; they oviposit into the larvae of all four instars of DBMs (Talekar and Yang, 1993).

2.2. Experimental design

A canola cultivar, SLM₀₄₆, was used in greenhouse trials. It is the most suitable host for DBM amongst 10 tested canola cultivars (Soufbaef et al., 2010). Seeds were collected from the Seed and Plant Improvement Institute (Karaj, Iran) and used for raising plants in field soil without the use of any fertilizers under greenhouse

conditions ($25 \pm 5^\circ\text{C}$, $60 \pm 10\%$ RH, and LD 16:8 h). The DBM larvae and pupae were originally collected from cabbages grown in the horticulture fields at Tehran University. The colonies of *D. semiclausum* and *C. vestalis* were introduced to DBM larvae in ventilated Perspex cages (30 cm $\times$ 30 cm $\times$ 30 cm) in the laboratory at $25 \pm 2^\circ\text{C}$, and the 4th generation adult parasitoids were used in further treatments.

A cage experiment on the effect of resource limitation on population dynamics was implemented using the canola cultivar under two different levels of availability: a low resource availability (plant limited treatment), where new plants were provided in each cage every 8 days, and a high resource availability (plant unlimited treatment), where new plants were put in cages before the complete consumption of all leaves by DBM larvae (usually every 3 days in high herbivore densities). For each plant treatment three scenarios of natural enemies were established: DBM + *D. semiclausum*, DBM + *C. vestalis* and DBM + both parasitoids, and each scenario was then replicated four times. Each experiment started with 5 pairs (male and female) of 1-day-old DBM adults; with pots each containing two 4-week-old plants and aqueous sugar solution (10%) in each cage. One pot was used for plant limited treatment, and two pots for plant unlimited treatment (Fig. 1). After 20 days when DBMs of all stages have established (DBM has overlapping generations), two 2-day-old mated females of each parasitoid with one respective male were released to each parasitoid treatment cage. The cages (80 cm $\times$ 80 cm $\times$ 100 cm) were maintained at constant environmental conditions ($25 \pm 1^\circ\text{C}$; $60 \pm 5\%$ RH; L:D 16:8 h). The experiment was run for 25 weeks, which equals nearly 8–9 completed generations of DBM. Populations were monitored weekly by counting live adults in each cage. It was evident that, when the density of DBMs is high in the limited plant treatment, individuals can consume all the leaves a few days before replacement; that is, the specialist herbivores suffered a short starvation period mimicking food scarcity after canola harvest season or when multicultural crops are planted.

2.3. Statistical analysis

Multivariate general linear models with estimated marginal means (EMMEANS) were used to assess the effects of plant availability and parasitoid coexistence (i.e. the three establishment scenarios of natural enemies) on both herbivore

Table 1
Description and values of model parameters.

Symbol	Description	Value	Source
r	Intrinsic growth rate of herbivore H	0.304 day ⁻¹	Soufbaf et al. (2010)
K	Carrying capacity of environment	Varied	This experiment
m_p	Death rate of parasitoid P	0.03 day ⁻¹	Soufbaf et al. (2012)
m_q	Death rate of parasitoid Q	0.078 day ⁻¹	Nofemela (2004)
γ_p	Attack rate of parasitoid P	4 h ⁻¹	Wang and Keller (2002)
γ_q	Attack rate of parasitoid Q	2.5 h ⁻¹	Wang and Keller (2002)
μ_p	Handling time of parasitoid P	0.003 day	Hemerik (2007)
μ_q	Handling time of parasitoid Q	0.032 day	Mitsunaga et al. (2004)
α_{pq}	Competition coefficient from parasitoid Q on P	0.42	This experiment
α_{qp}	Competition coefficient from parasitoid P on Q	0.58	This experiment
e_p	Emigration coefficient of parasitoid P	0.01	Estimated from Wang and Keller (2002)
e_q	Emigration coefficient of parasitoid Q	0.02	Estimated from Wang and Keller (2002)
n_p	Number of neighbors for parasitoid P	8	Estimated from Wang and Keller (2002)
n_q	Number of neighbors for parasitoid Q	4	Estimated from Wang and Keller (2002)

and parasitoid abundances. Correlations were conducted using Pearson product-moment coefficient (r) with a significance level of $\alpha = 0.05$, to identify relationships between two parasitoids densities within different simulated habitats. All statistical analyses were conducted using SPSS 16 (SPSS, 2008).

2.4. The model

Since the host–parasitoid system has overlapping generations, we analyzed the population dynamics of this tri-trophic system using the following three-species Lotka–Volterra model based on ordinary differential equations (ODE) that incorporate Holling's (1959) type II functional response (Amarasekare, 2002):

$$\begin{aligned} \frac{dH}{dT} &= rH \left(1 - \frac{H}{K(R)} \right) - \frac{\gamma_p PH}{1 + \gamma_p \mu_p H} - \frac{\gamma_q QH}{1 + \gamma_q \mu_q H} \\ \frac{dP}{dT} &= \frac{\gamma_p PH}{1 + \gamma_p \mu_p H} - m_p P - \alpha_{pq} QP \\ \frac{dQ}{dT} &= \frac{\gamma_q QH}{1 + \gamma_q \mu_q H} - m_q Q - \alpha_{qp} PQ \end{aligned} \quad (1)$$

where r stands for the intrinsic rate of increase and $K(R)$ stands for the carrying capacity of herbivores under different plant resource availabilities (R). Subscripts (p and q) indicate parameters associated with specific species (*D. semiclausum* and *C. vestalis*, respectively). The values of all parameters were estimated either from our experiments or taken from literature (Table 1). To check for the sensitivity to initial conditions, we solved the above ODEs numerically with the initial population size of each species assigned from 0 to 1 with a step size of 0.05.

To examine how the number of patches (leaves) affects the coexistence and spatial distribution of the two parasitoids, we developed a stochastic cellular automaton (CA) under different numbers of patches on a two dimensional habitat with a periodic boundary condition (Hui and Li, 2003, 2004; Ramanantoanina et al., 2011):

$$\begin{aligned} H_{t+1}[i, j] &= H_t[i, j] + \varepsilon \times \frac{\partial H_t[i, j]}{\partial t} \\ P_{t+1}[i, j] &= P_t[i, j] + \varepsilon \times \frac{\partial P_t[i, j]}{\partial t} - e_p P_t[i, j] + \frac{e_p}{n_p} \sum_{(x, y) \in \Omega_p} P_t[x, y] \\ Q_{t+1}[i, j] &= Q_t[i, j] + \varepsilon \times \frac{\partial Q_t[i, j]}{\partial t} - e_q Q_t[i, j] + \frac{e_q}{n_q} \sum_{(x, y) \in \Omega_q} P_t[x, y] \end{aligned} \quad (2)$$

where ε represents the Euler coefficient for calculating the numerical solutions to the full system (Eq. (1)) ($\varepsilon = 0.1$); Ω_p indicates the neighboring patches of patch (x, y) for parasitoid P and Ω_q for Q ; e and n stand for the emigration rate and the movement range (the number of patches the parasitoid can move during one time

step) for specific parasitoid. The ODEs and CAs were solved numerically using *Mathematica* 8.0 (Wolfram Research Inc.). The in-patch dynamics (the derivative terms above) was governed by the ODEs in Eq. (1), and the movement of DBM between patches was ignored.

2.5. Parameterization

This experiment was the last part of three consecutive experiments. The intrinsic population growth rate (r) of the herbivore in the absence of parasitoid was estimated from the first experiment (Soufbaf et al., 2010), and the mortality of parasitoid P (m_p) was estimated from the second experiment (Soufbaf et al., 2012). The carrying capacity (K) and the per capita effects of each parasitoid on the other (α_{pq} , and α_{qp}) were estimated from the last experiment (this study). The carrying capacity has two different levels: K_{limited} (with a mean of 43.5 plants and a mean number of 54.9 DBM adults found per cage) and $K_{\text{unlimited}}$ (with a mean of 215 plants and a mean of 101.2 DBM per cage). The following removal matrix, formerly was described as interaction strength (I_{ij}) between competitors by Paine (1992), was used to define the values of α_{pq} for our experimental data:

$$\alpha_{pq} = \frac{N_{PQ} - N_{PQ-}}{N_{PQ} - N_Q} \quad (3)$$

where N_{PQ} is the abundance of P (target) when the agent (Q) is present, N_{PQ-} is the abundance of the target when the agent is absent, and N_Q is the abundance of the agent in absence of the target.

Values of parameters were then assigned to the ODEs (Eq. (1)) to derive the conditions for coexistence and the dynamic behaviors of the system. In case the two parasitoids cannot coexist due to competitive exclusion, we further analyzed the stability of the degraded system (i.e. one parasitoid system). The CA simulation was then used to analyze whether there is a minimum number of patches to ensure the coexistence of these two parasitoids and how the parasitoids distribute spatially in the lattices. Specifically, Wang and Keller (2002) have studied the movement of these two parasitoids, based on which we set the movement abilities as $e_p = 0.01$ and $e_q = 0.02$, and the searching areas as $n_p = 8$ (Moore neighborhood) and $n_q = 4$ (von Neumann neighborhood) (Hoekstra et al., 2010; Hui and Li, 2004) (Table 1). It is worth noting that setting the parameters to these values does not affect the overall results of spatial coexistence.

We ran this CA model on 70×70 lattices for 400 time steps to generate the spatial distribution of these three species (densities in patches). Each lattice in the CA model represents a patch of an average leaf size ($\sim 40 \text{ cm}^2$) and thus has $6.3 \text{ cm} \times 6.3 \text{ cm}$ in dimension. Considering the three-dimensional structure of canola (with 11 leaves per plant on average), a number of 5×5 lattices should

Table 2
Results from the multivariate general linear model analysis of the abundances of herbivore *H* and parasitoids *P* (*D. semiclausum*), and the herbivore *H* and parasitoid *Q* (*C. vestalis*) under two levels of plant availability (i.e. limited and unlimited) and two coexistence situations (i.e. coexisting or not).

Source	Dependent variables	Type III sum of squares	df	F
<i>D. semiclausum</i>				
Intercept	<i>P</i>	12360.99	1	206.757***
	<i>H</i>	104186.93	1	1.712E3***
Coexistence	<i>P</i>	27.46	1	0.459 ^{ns}
	<i>H</i>	109.41	1	1.798 ^{ns}
Plant	<i>P</i>	924.16	1	15.458**
	<i>H</i>	12800.66	1	210.396***
Coexistence × Plant	<i>P</i>	3.31	1	0.055 ^{ns}
	<i>H</i>	428.49	1	7.043*
<i>C. vestalis</i>				
Intercept	<i>Q</i>	11259.33	1	92.843***
	<i>H</i>	84791.62	1	1.012E3***
Coexistence	<i>Q</i>	146.17	1	1.205 ^{ns}
	<i>H</i>	446.48	1	5.330*
Plant	<i>Q</i>	642.62	1	5.299*
	<i>H</i>	7791.59	1	93.022***
Coexistence × Plant	<i>Q</i>	2.47	1	0.020 ^{ns}
	<i>H</i>	17.39	1	0.208 ^{ns}

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

^{ns} $p > 0.05$.

represent all leaves of the two plants in a single pot and thus have a physical size of 31.5 cm × 31.5 cm in the experiment, i.e. a width of 6.3 cm (=31.5/5) per patch. Consequently, the width of each lattice in the model is equal to 6.3 cm both in terms of leaf and pot dimensions, and the 70 × 70 lattices thus equal a habitat size of 14 × 14 pots (or 28 × 28 plants). We also ran the CA model with different number of lattices (from 1 × 1 to 15 × 15) to assess whether the coexistence of parasitoids can be affected by the habitat size (i.e. the number of patches). Each run started with randomly assigned initial values, and the proportion of the three scenarios (i.e. *P* excluded, *Q* excluded and the coexistence of *P* and *Q*) were then estimated from 100 runs.

3. Results

The effects of plant availability on the equilibrium abundances of DBM and both parasitoids were significant but the coexistence of parasitoids (*P* + *Q*) did not affect the abundance of parasitoids significantly (Table 2). There was also a significant effect of parasitoid coexistence on the herbivore abundance if parasitoid *Q* (*C. vestalis*) remained from the competitive exclusion (Table 2).

According to the theory of limiting resources (MacArthur and Levins, 1964; Tilman, 1982), this tri-trophic system (Eq. (1)) does not have any positive stable equilibrium, meaning that the two parasitoids (*P* and *Q*) cannot coexist theoretically. The outcome of competitive exclusion relies on the following condition:

$$\frac{P_0}{Q_0} > \frac{\gamma_q/(1 + \gamma_q\mu_qH)}{\gamma_p/(1 + \gamma_p\mu_pH)}, \quad (4)$$

where P_0 and Q_0 are the initial population sizes of the two parasitoids. The right hand side of the above inequality stands for the ratio of the functional response of parasitoid *Q* per herbivore ($\gamma_q/(1 + \gamma_q\mu_qH)$), i.e. the consumption rate of *H* by *Q* to the functional response of parasitoid *P* per herbivore ($\gamma_p/(1 + \gamma_p\mu_pH)$), i.e. the consumption rate of *H* by *P*. If this inequality holds, parasitoid *P* will expel parasitoid *Q*; otherwise, parasitoid *Q* will expel *P*. This suggests that the survivor from the parasitoid competition will entirely depend on the initial population consumption rate (=initial population size × per capita consumption rate). Apparently, competitive exclusion does not depend on the resource levels of plants (*R*). Numerical simulations support this proposition that the above ratio (Eq. (4)) forms a divide in the phase plane (Fig. 2a and b).

Evidently, the ratio on the right hand of the above inequality is not really sensitive to the abundance of herbivores in our experiment (i.e. for the full range of *H*, the ratio remains around 0.58) (Fig. 2a and b).

Competitive exclusion of one parasitoid leads to a degraded system between the herbivore (*H*) and the remaining parasitoid (Fig. 2c and d). For instance, for the degraded system that consists of herbivore *H* and parasitoid *Q*, we have the following ODEs:

$$\begin{aligned} \frac{1}{H} \frac{dH}{dt} &= r \left(1 - \frac{H}{K(R)} \right) - \frac{\gamma_q Q}{1 + \gamma_q \mu_q H} \\ \frac{1}{Q} \frac{dQ}{dt} &= \frac{\gamma_q H}{1 + \gamma_q \mu_q H} - m_q \end{aligned} \quad (5)$$

This degraded system only has a single non-negative equilibrium (H^* , Q^*):

$$\left(\frac{m_q}{\gamma_q(1 - \mu_q m_q)}, \frac{r(1 - H^*/K)}{\gamma_q(1 - \mu_q m_q)} \right) \quad (6)$$

The herbivore equilibrium does not depend on its own vital parameters (*r* and *K*) that could potentially be affected by the plant resource levels but, rather, depends on the vital parameters of the parasitoid. This suggests that herbivore density is largely controlled by the parasitoid rather than by the level of plant availability. In contrast, the parasitoid equilibrium depends on both its own vital parameters and those of the herbivore that could be potentially affected by the level of plant availability. This indicates the existence of a bottom-up regulation of parasitoid density by the host plant.

Although the two parasitoids cannot coexist on a single herbivore population, the CA simulation demonstrated that they could spatially coexist, forming local clusters of degraded systems (Fig. 3). Both parasitoids exhibited spiral structures when the carrying capacity (*K*=50 and 100) and the population growth rate of DBM were high (*r*=0.304 and 0.6) (Fig. 3). Measured by Moran's *I* index with a negative exponential distance weight (see Appendix S1 in Hui et al., 2011), the level of patchiness in Fig. 3b increased significantly from 0.215 in plot 4 to 0.257 in plot 6, 0.271 in plot 8 and 0.337 in plot 10 ($t > 82.4$, $P < 0.001$); Moran's *I* index in Fig. 3c also significantly increased from 0.276 in plot 4 to 0.307 in plot 6, 0.319 in plot 8 and 0.32 in plot 10 ($t > 60.4$, $P < 0.001$). The densities of parasitoid *P* and *Q* in these patches showed a

Fig. 2. Phase plane and trajectories of stable spirals in the full model (numerical solutions to Eq. (1)). Plots (a) and (b) are the phase planes of the whole model; (c) and (d) are illustrations of trajectories from different initial conditions; (a) and (c) are results for plant limited treatment; (b) and (d) are results for plant unlimited treatment.

negative correlation (e.g. compare b9 with c9 in Fig. 3, $\ln(P)$ vs. $\ln(Q)$ for P and $Q > 0.0001$: $r = -0.837$, $P < 0.001$; similarly, compare b11 with c11: $r = -0.803$, $P < 0.001$). Two cases were further resized to demonstrate the details of the negative correlation in the distributions of P and Q (Fig. 3).

With an increase of the patch number, the proportions of the persistence of parasitoid P (and also Q) and the coexistence of P and Q reached 100% when the habitat consists of more than 9×9 patches (Fig. 4a). The periodic oscillation in degraded systems (Fig. 2c and d) also became damped oscillations (Fig. 4b).

4. Discussion

Evidently, the herbivore and both parasitoids had higher abundances under the unlimited plant treatment (i.e. high level of plant availability). Abundances of parasitoid P and Q when coexisting did not differ from the abundances when they were alone in the system, suggesting that the coexistence of these two parasitoids does not bring each other benefit or cost. Therefore, in contrast to

Amarasekare's (2002) assertion, there is no effect of interference on the competitive coexistence. The fact that parasitoid P and Q are able to coexist in a cage for at least 8–9 generations suggests mechanisms other than interference could be at work.

Heterogeneous habitat and temporal niche separation are potential mechanisms fostering coexistence of two specialist parasitoids on a single host (Hackett-Jones et al., 2009; Hassell et al., 1991). For instance, specialist parasitoids can coexist if they prefer different oviposition sites or if they have an additional relationship of intraguild predation (Borer, 2002; Borer et al., 2004). Our results showed that the two parasitoids with different searching efficiencies on the same host cannot coexist at a single location unless considering different movement abilities and search area sizes (e.g. Shi et al., 2004; Talekar and Yang, 1991; Wang and Keller, 2002). These two larval parasitoids can coexist in the CA simulation and form spatially non-overlapping distributions, especially when the vital parameters of DBM (r and K) are high. These non-overlapping distributions have been widely reported as from strong competition of ecologically similar species (e.g. MacArthur, 1958;

Fig. 3. Spatial patterns of the tri-trophic system in 70×70 lattices at the 400th time step, with the initial population sizes in each patch randomly assigned. Cellular automata were run for three values of carrying capacity ($K_1 = 10$, $K_2 = 50$, and $K_3 = 100$) and four values of intrinsic growth rate r_m ($r_1 = 0.1$, $r_2 = 0.2$, $r_3 = 0.304$ and $r_4 = 0.6$). (a), (b) and (c) represent spatial patterns for herbivore, parasitoid P and parasitoid Q , respectively. Resized plots show details of non-overlapping distributions of the two parasitoids. The width of each lattice equals 6.3 cm, and the 70×70 lattices represent a habitat size of 14×14 pots (or 28×28 plants).

Schoener, 1974; Wilson, 1984). Therefore, there could be a local density-dependent regulation by both parasitoids, consistent with the pattern of percent parasitism in Hassell et al. (1991).

It is worth noting that the outcome of the competitive exclusion depends on the functional response ratio of the two parasitoids (Eq. (4)). This ratio consists of attack rates and handling times of two parasitoids, suggesting that bottom-up forces (plant availability) which contribute to the fitness of the herbivore (r and K) do not affect the outcome of parasitoid competition especially in a local habitat patch. However, the statistical analysis indicated a significant effect of plant availability on the abundance of both herbivore and parasitoids (Table 2), suggesting that the bottom-up force (plant availability) only affects the material flow but not the topological structure of this tri-trophic food web.

The model suggests that the coexistence of multiple parasitoids on one host is locally impossible but spatially feasible. In comparison to other models of the same sort, we further identified a few factors that could potentially intensify the competitive exclusion. Firstly, Hackett-Jones et al. (2009) have demonstrated a destabilizing effect of the type II functional response in a Nicholson–Bailey model which can lead to the competitive exclusion of one parasitoid species. Briggs (1993) has analyzed a similar system using stage-structured delay differential equations with a type I functional response and found similar results that either parasitoid P

or Q may expel the other depending on initial conditions. However, using a similar model with the type I functional response, Amarasekare (2002) has demonstrated the coexistence of two consumers on a single resource and attributes the coexistence to the potential beneficial interference between the two consumers. This suggests that the forms of functional responses might not be the real reason for competitive exclusion. Clearly, more investigation is needed to clarify the role of functional responses in the stability and structure of food webs.

Secondly, both non-stage and stage-structured Lotka–Volterra models of homogenous populations have exhibited competitive exclusion of species by the most efficient competitors (Briggs, 1993; Mills and Getz, 1996). Our results support that spatial heterogeneity induced by both the patch habitat and the patchily distributed DBMs in the CA simulation as a promotor of competitive coexistence. It is further evident that there exists a minimum habitat size to ensure species persistence and coexistence (Fig. 4a), consistent with the observation from Zhao et al. (2012). Evidently, damped oscillations in Fig. 4b indicated that large habitat size with multiple patches can further stabilize the dynamics of the system and promote the coexistence of these two competing parasitoids. The effects of environmental and spatial heterogeneity formed by both host plants and herbivores on the coexistence of parasitoids at the third-trophic level warrants further investigation.

Fig. 4. (a) The probability of different cases at the 400th time step as a function of the number of cells (patches) in the cellular automaton, with initial population sizes randomly assigned. Coexistence can be guaranteed when the number of cells is about 9×9 . (b) Damped oscillations of population sizes on a habitat of 15×15 lattices.

Overall, our results support that *D. semiclausum* is a more effective parasitoid than *C. vestalis* (Wang and Keller, 2002; but see Shi et al., 2004). Moreover, the competitive coexistence and exclusion of parasitoids is sensitive to the initial population sizes, functional response per herbivore and the patchiness of plant and herbivores, but not the level of plant availability. Other bottom up factors, such as the availability of refuge and the complexity of plant morphology that could potentially affect the persistence and coexistence of DBM parasitoids need to be examined in future studies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2012.06.033>.

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