

Prey selection can cause novel coevolutionary patterns

2018-09-24

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Abstract

Many theoretical models have been formulated to better understand the coevolutionary patterns that emerge from antagonistic interactions. In most of these models it is assumed that the attacks by the exploiters are random, so that the effect of victim selection by exploiters on coevolutionary patterns remains unexplored. Here we study an individual-based model for the coevolution of predators and prey in which every individual predator can attack only a small number of prey any given time. We investigate coevolutionary patterns that result from two scenarios: (i) predation occurs at random; (ii) predators select prey according to phenotype matching. We show that both scenarios result in well known similar coevolutionary patterns if population sizes are sufficiently high: symmetrical coevolutionary branching and symmetrical coevolutionary cycling (Red Queen dynamics). However, for small population sizes prey selection can cause other coevolutionary patterns that have not yet been reported. One is the breaking of symmetry of the coevolutionary pattern, where the phenotypes evolve towards one of two evolutionarily stable patterns. As population size increases, the phenotypes oscillate between these two values in a novel form of Red Queen dynamics, the episodic reversal between the two stable patterns. Thus, prey selection causes prey phenotypes to evolve towards more extreme values, which reduces the fitness of both predators and prey, increasing the likelihood of extinction. An analytical approach allows us to show the robustness of our results.

Keywords

coevolution, predator-prey, matching phenotype, predator strategy, predator choice, prey selection

1 Introduction

Antagonistic interactions are an ubiquitous phenomenon in nature, in which one species gains resources at the expense of another. Victim-exploiter relationships encompass a range of interspecific interaction modes such as plant-herbivore, prey-predator and host-pathogen interactions. These interactions can exert reciprocal selective pressures resulting in genetic changes in populations; what is defined as coevolution (Janzen 1980). In the last decades, many theories have been formulated to explain and better understand how interacting species affect the evolution of others (eg. in Thompson (2005) and Abrams (2000)).

One of the most influential hypotheses in coevolution is the evolutionary arms-race (Ehrlich and Raven 1964), which proposes that species must constantly adapt as a response to the unceasing adaptations of the organisms with which it interacts. As the fitness of the exploited species is reduced, selection will favor those organisms with a better capability of defending themselves or evading exploiters, whereas exploiters will be selected to evolve countermeasures (Hochberg and van Baalen 1998). Many empirical examples and systems that attain such dynamics are already well known and studied, as between birds and avian brood parasites (Avilés et al. 2006; Martín-Gálvez et al. 2006; Refsnider and Janzen 2010; Noh et al. 2018) and between herbivorous insects and their host plants (Chew 1977; Ehrlich and Raven 1964; Merrill et al. 2013; Nylin et al. 2005).

Theoretical models have predicted different evolutionary dynamics for these interactions. These dynamics may be a result of different combinations of contexts in which coevolutionary interactions occur (Thompson 2005). Two frequent ingredients present in evolutionary antagonistic models are stabilizing selection and interaction strength. Stabilizing selection is the outcome of all selective pressures not explicitly modeled and favors an optimum phenotype (here we call it as external optimum phenotype) that the population phenotypes would evolve towards in absence of the interaction strength. The interaction strength can be directional or not; when it is not, the fitness benefit for the

exploiter (or the fitness loss for the victim) is generally determined by the similarity of the interacting species' phenotypes - phenotype matching (Brown and Vincent 1992; Berenbaum and Zangerl 1998; Gomulkiewicz et al. 2000; Abrams 2000; Gandon and Michalakis 2002; Nuismer and Thompson 2006; Calcagno et al. 2010; Yoder and Nuismer 2010; Gokhale et al. 2013). As consequence prey have a "bidirectional axis of vulnerability" (term used by Abrams (2000)), which means that its phenotype can evolve to values below or above the phenotype predators aim at . When stabilizing selection and non-directional interaction strength are combined, the reported temporal population phenotype distributions are symmetrical with respect to the external optimum phenotype, resulting in *symmetrical coevolutionary branching* (Brown and Vincent 1992; Abrams 2000; Calcagno et al. 2010; Yoder and Nuismer 2010) or *symmetrical coevolutionary cycling* (Gomulkiewicz et al. 2000; Abrams 2000; Dieckmann et al. 1995). In the former the population phenotypes evolve towards stable phenotypes, but all stable phenotypes are equally far from the external optimum phenotype while in the latter the phenotypes oscillate around the external optimum phenotype. On the other hand, when the interaction strength is directional (for example when the outcome of the interaction is determined by phenotype differences among interacting species), prey has a "unidirectional axis of vulnerability" (Abrams 2000) and there is a preferential evolution pathway (Abrams 2000). As consequence the symmetry is broken (this is clearly presented in a study by Yoder and Nuismer (2010)).

The use of theoretical predictions allows a better interpretation of mechanism associated to empirical studies. The study of Duffy et al. (2008) with *Daphnia* and parasite, for example, showed that *Daphnia* evolved to a bimodal phenotype distributions (*coevolutionary branching*) during a parasite epidemic, which can be associated to a mechanism where the host had a bidirectional axis of vulnerability. Bidirectional axis of vulnerability could also be associated to host egg coloration subject to avian brood parasitism, where the host phenotypes showed to be bimodal (Yang et al. 2010) and also on ongoing arms race (*coevolutionary cycling*) (Spottiswoode and Stevens 2013) . Unidirectional axis of vulnerability would be associated to directional selection, as for example the

interaction between garter snake, of the genus *Thamnophis*, and its toxic salamander prey, of the genus *Taricha* (Brodie III and Brodie Jr 1990), where the snake has evolved resistance to tetrodotoxin (TTX) in response to the toxicity of the salamander.

In particular, an exploiter can increase its fitness if it can choose the victim that maximizes its chances of success if it is presented with a range of possible victims. Brood parasites, known to coevolve with their hosts (Rothstein 1990), can choose to parasitize the host nest according to egg colour matching (Avilés et al. 2006; Soler et al. 2014). The choice of host has consequences for offspring success and therefore it is subject to strong selection (Resetarits 1996; Refsnider and Janzen 2010). There is also a vast literature on insect oviposition patterns suggesting that host plant preference and selection has a significant role in the coevolutionary history of these species (Chew 1977; Jorge et al. 2014; Nylin et al. 2005; Merrill et al. 2013). Non-random oviposition-site choice is also documented in fish, amphibians and reptiles (Refsnider and Janzen 2010).

That sigmoid functional responses can contribute to ecosystem persistence is textbook knowledge, and it was realized early on that such sigmoid functional responses result quite readily from optimal switching between different prey types Stephens and Krebs (1986). This insight gave rise to an extensive literature that attempted to elucidate the ecological consequences of prey switching (see e.g., Murdoch, 1969; May, 1974; Hutson, 1984; Matsuda, 1985; Gleeson and Wilson, 1986; Gendron, 1987; Fryxell and Lundberg, 1994; Abrams and Kawecki, 1998; van Baalen et al., 2001). The models that were used to study these questions were usually multi-prey variants of the standard Lotka-Volterra predator-prey model. As the Lotka-Volterra setup assumes homogeneous spatial distributions, all exploiters encounter the same distribution of victim types, and many differences in victim selection strategies (or preferences) are selectively neutral (Matsuda, 1985). If the victims are inhomogeneously distributed, however, individual exploiters will encounter different subsets of victim types and any preference they might have will have immediate ecological and evolutionary consequences. To our knowledge, however, few studies have addressed the potential consequences of

victim choice in simultaneously encountered prey. Berec (2000) identified the issue and made a first step in modeling it using a spatially explicit approach, but with the limiting assumption of fixed victim densities. We will not consider a fully explicit spatial model, but the novel aspect is that individual exploiters will have to make an actual choice in the victim they will attack.

To investigate the effects of prey selection in the coevolutionary dynamics of antagonistic populations, we approach the evolutionary predator-prey system by proposing an individual-based model where the individual phenotypes related to the interaction are explicitly modeled and can evolve subject to both the interaction (phenotype matching) and a stabilizing pressure. We explore the coevolutionary outcomes in phenotypic evolution considering two scenarios: (i) Predation occurs at random; (ii) predators select which prey to attack among those present in the predator's 'attack neighborhood', according to phenotype matching. We also analyze a simplified version of the model to study the effect of attack strategy and carrying capacity on ensuing coevolutionary patterns.

2 Methods

2.1 Model Description

We use an individual-based model (IBM) to simulate the phenotypic evolution of two populations that interact antagonistically. We will refer to these as prey and predators, but they also stand for herbivores and food plants, or for parasites or parasitoids and their hosts. The phenotype of each individual i in a given generation is represented by a real number, u_i (v_i), where i identifies the individual and u (v) the prey (resp. predator) species. For simplicity, the model considers synchronized events; in a given generation, the members of both populations first interact and then reproduce to form the next generation. Space is not modeled explicitly, but we assume that each predator i can attack only a subset of n_i individuals of the prey population chosen at random. We

assume that the number of prey in a predator's predation neighborhood, n_i can vary over the predator population following a binomial distribution:

$$B(n_i, M_X, \frac{1}{M_Y}) = \binom{M_X}{n_i} \frac{1}{M_Y^{n_i}} \left(1 - \frac{1}{M_Y}\right)^{M_X - n_i}, \quad (1)$$

where

$$\binom{M_X}{n_i} = \frac{M_X!}{n_i!(M_X - n_i)!} \quad (2)$$

is the binomial coefficient and M_X (M_Y) represents the number of prey (predators) in a given generation. This binomial implies that, on average, the predation neighborhood is given by the predator and prey population ratio (M_Y/M_X). Each predation neighborhood is set randomly and independently, so that one prey can be in more than one predation neighborhood. In the limit where M_X goes to infinity, this binomial distribution converges to a Poisson distribution,

$$P(n_i) = \frac{\bar{n}^{n_i} \exp(-\bar{n})}{n_i!}.$$

We compare two different attack strategies: (i) *Without prey selection*: the predators attack their prey at random; (ii) *With prey selection*: the predators sort their attacks according to phenotype matching, prioritizing the lowest values of $|u - v|$. In both scenarios the attacks occur until the first attack is successful or after the predator has tried to attack all prey in its neighborhood. We assume that the success of an attack only depends on the matching of predator and prey phenotypes, according to

$$f(u_i, v_i) = \exp[-\alpha(u_i - v_i)^2], \quad (3)$$

where α is a positive value that defines the specificity of the attack as a function of the predator and

prey phenotypes (the higher α , the lower the probability of successful attack for imperfect matching). Predation success increases with the similarity of phenotypes, which means that it can promote a "bidirectional axis of vulnerability" (Abrams 2000). If an attack is successful, the prey dies and the predator will have an opportunity to produce an offspring. This process also resembles the interaction between hosts and parasitoids where parasitoids attempt to deposit eggs inside their hosts, but hosts may defend themselves, e.g., by encapsulating the parasitoid egg (Bartlett and Ball 1966), whereas the successful development of the parasitoid results in the death of the prey. During the simulations we first set all predation neighborhoods and then the interactions occur in a random sequence. A prey can only be successfully attacked once, and if it occurs, the prey is removed from the other predation neighborhoods into which it pertains.

Only surviving prey M'_X and successful predators M'_Y will reproduce, and their probability of having one offspring is defined as

$$\begin{aligned} E(u_i) &= g(M'_X) \exp[-\gamma_u(u_i - u_{opt})^2] , \\ E(v_i) &= \exp[-\gamma_v(v_i - v_{opt})^2] , \end{aligned} \tag{4}$$

where γ_u (γ_v) is the strength and u_{opt} (v_{opt}) the static optimum phenotype imposed on prey (predator) population by stabilizing selection. The function $g(M'_X)$ is an intraspecific competition term that puts an upper bound to the size of the prey population, with

$$g(M'_X) = \frac{1}{1 + \rho(M'_X - 1)} , \tag{5}$$

where ρ is a parameter that controls the strength of competition. In absence of competition, $g(M'_X =$

1) = 1, and as the population grows $g(M'_X)$ goes to zero. Also note that $M'_X \geq 1$, otherwise the population is assumed to be extinct. Predator population size is indirectly limited by the size of the prey population. Observe that the selection imposed by Eqs. (4) favors the evolution of the phenotype towards the static optimum values.

The model also imposes that each prey (predator) individual has F_x (F_y) chances of producing an offspring. The intensity of prey intraspecific competition ρ can then be written in terms of K and F_X , by assuming absence of predators, $M''_X = M'_X = M_X = K$ (M''_X designates the prey's next generation population size) and that the prey are well adapted to the external pressure. From

$$M''_X = F_X \sum_{i=1}^{M'_X} E(u_i)$$

we obtain

$$K = \frac{F_X K}{1 + \rho(K - 1)},$$

so that a given carrying capacity K implies a density dependence factor

$$\rho = \frac{F_X - 1}{K - 1}.$$

For simplicity we consider asexual reproduction only; an offspring possesses the same phenotype as its parent plus a normally distributed mutational variation δ_s , with

$$P(\delta_s) = \frac{1}{\sigma_s \sqrt{2\pi}} \exp \left[-\frac{\delta_s^2}{2\sigma_s^2} \right], \quad (6)$$

where σ_s is the standard deviation. The new generation replaces the previous generation ($M' = M''$), a new set of interactions occurs, the surviving prey and fed predators have offspring, and the cycle restarts. A list of all parameters involved in the model is shown in Table (1).

Table 1: List of all parameters involved in the model, their values utilized in the simulations and a short description of their meaning

parameter	value	short meaning
α	$\{1,2,4,6,8,10,12\}$	Intensity of selection imposed by the interaction
$\gamma_u; \gamma_v$	1	Intensity of stabilizing selection pressure
$u_{opt}; v_{opt}$	0	Optimum phenotype imposed by the stabilizing selection
$F_X; F_Y$	$\{2, 4, 6, 8, 10, 12\}$	Fecundity
K	$\{500, 2000, 5000, 10000, 50000\}$	Prey carrying capacity
$\sigma_u; \sigma_v$	$\{0.01, 0.02\}$	Standard deviation that defines the mutation amplitude

2.2 Scenarios

We investigated the coevolutionary patterns (phenotype distributions over the generations) and population sizes for both models (*with prey selection* and *without prey selection*) considering different parameter combinations (see Table1) but we fixed the strength of stabilizing selection and the optimum phenotype favored in absence of the interaction ($\gamma_u = \gamma_v = 1$; $u_{opt} = v_{opt} = 0$). For all simulations the initial condition corresponded to one thousand individuals of each trophic level and phenotype values were equal to the optimum phenotype imposed by the stabilizing selection, plus a normally distributed variation (as in Eq.6). Each simulation was iterated over ten thousand generations.

3 Results

Here we first present the results of the simulation for both versions of the models and in the subsequent subsection we develop an analytical approach that explains the outcomes found in the models.

3.1 Simulation results

Both models were sensitive to the interaction strength (α) and the carrying capacity (K) (Figures 1 and 2). Higher values of α lead to a more intense selection in the predator population whose

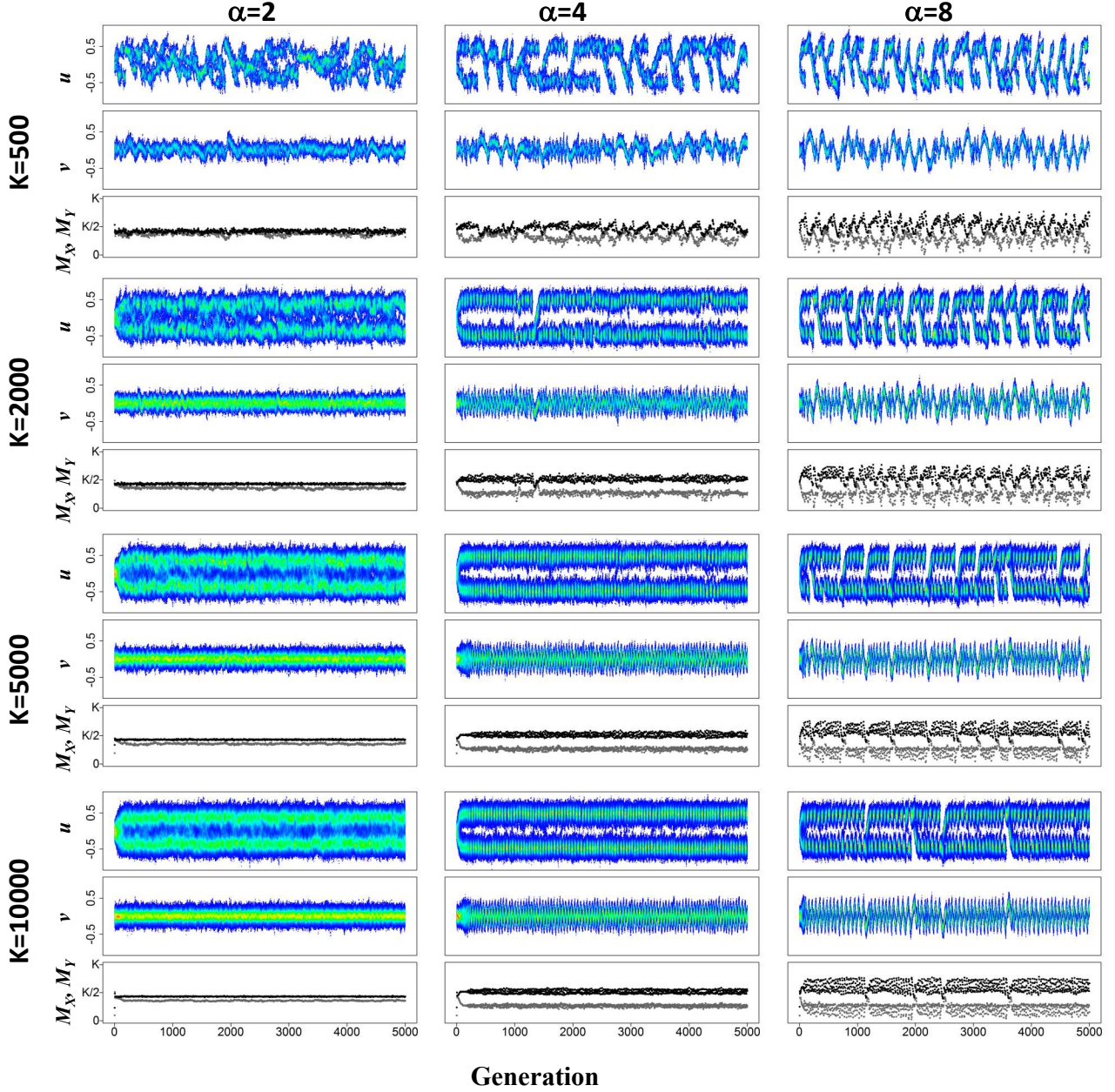


Figure 1: Coevolutionary temporal patterns for the model *without prey selection* and with different intensities of interaction strength (α , in columns) and carrying capacity (K , in rows). The first two graphs of each set of three sequential graphs shows prey (u) and predator (v) phenotype temporal evolution, respectively. The color scale is proportional to the number of individuals with a given phenotype (from blue to red meaning low to high frequencies). The bottom graph shows the prey (black) and predator (gray) population size over time. Only the last three values of K correspond to the same parameter values present in Figure 2. Parameters: $\gamma = 1$, $u_{opt} = v_{opt} = 0$, $F_X = 2$, $F_Y = 8$, $\sigma_u = \sigma_v = 0.02$.

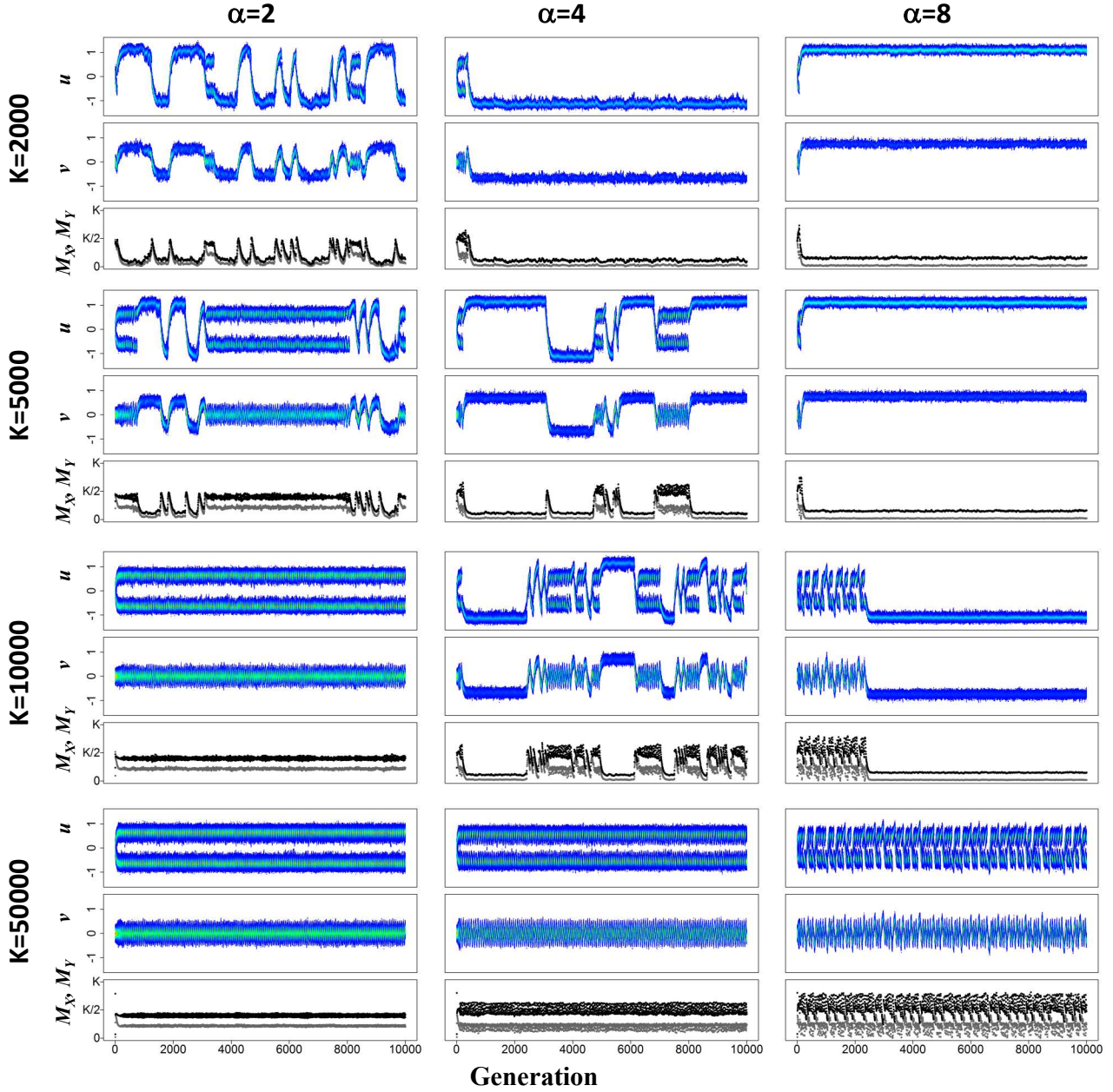


Figure 2: Coevolutionary temporal patterns for the model *with prey selection* and considering different intensities of interaction (α , in columns) and carrying capacity (K , in rows). The first two graphs of each set of three sequential graphs shows prey (u) and predator (v) phenotype temporal evolution, respectively. The color scale is proportional to the number of individuals with a given phenotype (from blue to red meaning low to high frequencies). The bottom graph shows the prey (black) and predator (gray) population size over time. Only the first three values of K correspond to the same parameter values present in Fig. 1. Parameters: $\gamma = 1$, $u_{opt} = v_{opt} = 0$, $F_X = 2$, $F_Y = 8$, $\sigma_u = \sigma_v = 0.02$.

phenotypes better matches their prey phenotypes. From the prey point of view, the pressure results in the differentiation of their phenotypes from the predator population. The carrying capacity is also an important parameter for the evolutionary outcomes since smaller populations are more vulnerable to extinction (Figs. 1 and 2).

We qualitatively classify three different patterns for the population phenotype distribution across the generations: *symmetrical coevolutionary oscillations*, *symmetrical coevolutionary branching* and *asymmetrical branching*. The term "symmetry" means that phenotype temporal distribution occupied both regions (with equal amplitude) delimited by the optimum phenotype (here, above and below zero). In *symmetrical coevolutionary oscillations*, prey and predator phenotypes oscillate around the respective optimum values in absence of the interaction (as an example see Fig.1 when $K = 500$ and $\alpha = 8$ and Fig. 2 when $K = 2000$ and $\alpha = 2$). In this scenario, neither population reaches an equilibrium phenotype distribution. Occasionally a bifurcation in the distribution of the prey phenotype appears that lasts for a few generations but that will eventually disappear again when one of the branches goes extinct. In the *symmetrical coevolutionary branching* pattern, prey phenotypes bifurcate between two lineages with phenotype values symmetric in relation to the optimum phenotype imposed by the stabilizing pressure, while the predator phenotypes assume values between both lineages and around v_{opt} (as an example see Figs.1 when $K = 10000$ and $\alpha = \{2, 4\}$ and 2 when $K = 50000$ and $\alpha = \{2, 4\}$). Finally, the *asymmetrical branching* pattern was observed exclusively in the model with prey selection (we have tested this prediction for other 400 simulations, changing parameters combinations, see Robustness section below). Both prey and predator phenotypes evolve to values above or below the static optimum phenotype imposed by stabilizing pressure but without tallying up; predator phenotypes stay between the prey phenotype and the optimum phenotype imposed by the external pressure (see Fig. 2 when $(K; \alpha) = \{(2000; 4), (2000; 8), (5000; 8), (10000; 8)\}$). Predators that can selectively attack a preferred prey can lock the prey phenotype in one of the two stable phenotypes. Any prey mutant that tries to cross towards the other stable phenotype becomes

the preferred prey, which minimize its reproductive success. When the attack is random (without prey selection) that mutant prey will never be preferentially attacked. (We study this phenomenon in more detail in the section "Analytical insight").

If we consider a given interaction strength $\alpha > 0$ and observe the patterns as a function of K , we first have extinction of predators or of both populations (not shown in Figs. 1 and 2, as it occurs with lower values of K than presented). As population densities increase, predator and prey populations coexist going through the following patterns: *asymmetrical branching* (only in the model with prey selection), *coevolutionary oscillation* and finally *symmetrical branching* (as an example see Fig.2 when $\alpha = 4$). In the transitions between these patterns we may have combinations of them, for instance with populations that oscillate, bifurcate and have lineages that go extinct and emerge again (see Fig.1 when $K = 500$ and $\alpha = 4$ and Fig. 2 when $K = 10000$ and $\alpha = 4$, for example). A similar sequence of coevolutionary patterns occurs if we consider a given value K and decrease α .

In addition to the asymmetrical pattern, prey selection produces more extreme evolutionary dynamics compared to the random predation model: the phenotypes evolve to values further from the optimum set by stabilizing pressure, decreasing the fitness of both populations. As a consequence, extinction is more likely to happen when predators attack with prey selection under low prey carrying capacity. For example, when $K = 500$ either predators or both predator and prey populations become extinct for any value of α , while in the model without prey selection we observe coevolutionary oscillation (see Fig.1 when $K = 500$). Coevolutionary oscillation also appears in the model with prey selection for higher values of K , resulting in oscillations with higher amplitude and periods (compare Fig.1 when $K = 500$ and $\alpha = 2$ to Fig.2 when $K = 2000$ and $\alpha = 2$).

Population size fluctuations arise in particular under non-equilibrium dynamics of phenotype evolution (coevolutionary oscillation and in the transition between patterns) while a more constant population size was associated with stable phenotype evolutionary patterns (asymmetrical and symmetrical branching) (Fig. 1 and 2). Although asymmetrical branching leads to a constant population

size, predator population size was lowest in these cases, making it more vulnerable to extinction (by increasing the interaction strength or imposing a perturbation). We also computed the mean size of the predation neighborhood, $\langle n \rangle = \langle M_X / M_Y \rangle$ and mean relative population densities, $\langle M_X \rangle / K$ and $\langle M_Y \rangle / K$, calculated from the last 6000 generations of each simulation (Fig. 3). Both population densities tend to converge for a given interaction strength (α), as the carrying capacity increases. Prey populations remain sensitive to the intensity of interaction regardless of the predators' strategy, whereas predator populations are sensitive only if they attack at random; if predators attack preferentially certain prey, their density seems to converge to the same point independently of α . Consequently, the predation neighborhood increases with the intensity of the interaction. For high values of K , prey selection leads to a slightly larger mean predation neighborhood. For low values of K , where the asymmetrical branching occurs, both population densities are reduced, but the predator population diminishes more drastically. In compensation, the predation neighborhood increases so that the few predators have more prey to choose from (see the highlighted dots in Fig. 3).

Robustness

To assess the robustness of our results we analyzed some modifications in the model. The modifications and results are outlined below (and detailed in the supplementary material)

We modeled the antagonistic interaction by promoting a fitness benefit for the exploiter and a fitness prejudice for victim instead of death due to interaction. The benefit and prejudice are controlled by two independent parameters, which allows to analyze the effect of different impact on each trophic level. For simplicity, the population size of each trophic level remained constant, then the contribution of each individual to the next generation population was proportional to its individual fitness. The number of victim in a exploiter's attack neighborhood was a fixed parameter and the interaction occurs only with one individual. As in the original model, we investigate two scenarios: (i) attack occurs at random; (ii) exploiters can select a victim according to phenotype matching.

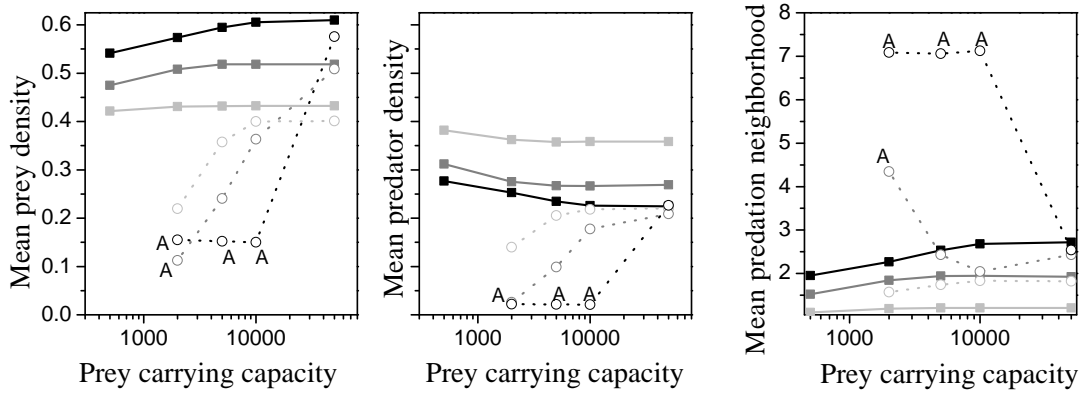


Figure 3: From left to right: Prey and predator population densities, $\langle M_X \rangle / K$ and $\langle M_Y \rangle / K$, and mean size of the predation neighborhood, $\langle n \rangle = \langle M_X / M_Y \rangle$, as function of prey carrying capacity, K . The filled squares refer to the scenario where predators attack at random (without prey selection) while the open circles to the scenario with prey selection (the first point, $K = 500$, is not plotted for the case with prey selection because predator and prey do not coexist). These averages were computed considering the last 6000 of 10000 generations. The colors, light gray, gray and black correspond to α equal to 2, 4 and 8, respectively. The letter "A" highlight the parameter combinations where the asymmetrical pattern occurs.

We ran simulations for 400 combinations of parameters for each scenario (with and without prey selection): we qualitatively predict the same coevolutionary patterns observed originally, including the exclusivity of the asymmetrical pattern for the second scenario (See TableS1, in the supplementary material).

3.2 Analytical insights

The stable *symmetrical coevolutionary branching* pattern has already been well discussed and analytically explained by Brown and Vincent (1992). Such symmetry is expected when the predators do not impose directional selection along the axis of vulnerability (Abrams 2000). This theory, however, cannot explain the stable asymmetrical pattern that we observed with selective predators. To better understand this pattern we analyse a simplified version of the model. Although the model can seem to be simple when compared to natural populations, it turned out complicated when we

tried to analyze it with mean field equations and looking for its Evolutionary Stable Solutions (Brown and Vincent 1992; TAYLOR and JONKER 1978). As the model modifications that we considered show that the asymmetrical branching does not depend on the size of the predation neighborhood (see section 3.1-Robustness), we simplify our analysis to a fixed predation neighborhood. Besides, given that the simulated results are also independent of the temporal variation of population size, we analyze only the fitness components related to the phenotype adaptations, that is, the probability of an individual producing an offspring after interacting with the members of the other trophic level. Although very restricted, we show below that these simplifications allowed us to identify that the asymmetrical branching can be an evolutionary stable pattern and that the prey selection is the crucial mechanism that causes it.

Asymmetrical branching stability

We first consider a scenario in which one prey and one predator population with given phenotypes interact. To start, suppose that each predator has only one prey in its neighborhood which it will therefore always attack. The interest of considering only one prey in a predation neighborhood is that we do not need to impose any selection strategy: both models, with and without prey selection, become equivalent. We will use this as a starting point to assess the consequences of prey selection.

When a prey and a predator interact, their respective payoffs (the probability of winning the interaction and produce an offspring) can be written as

$$P_v(u, v) = fh_v, \quad (7)$$

$$P_u(u, v) = (1 - f)gh_u, \quad (8)$$

where $f = \exp[-\alpha(u - v)^2]$ is the probability of a successful attack (Eq. 3), and $h_s = \exp[-\gamma s^2]$ is the cost function that centers the optimum at 0 (for both prey and predators) in absence of

interactions. The parameter g is the prey competition term (Eq. 5) which does not depend on the phenotypes and can be assumed to be given. If we look for the phenotypes (u and v) that simultaneously maximize these payoffs, the following conditions must be satisfied: $\frac{\partial P_s}{\partial s} = 0$ and $\frac{\partial^2 P_s}{\partial s^2} \Big|_{u^*;v^*} < 0$. The first condition is equivalent to

$$\begin{aligned} \{ \gamma + \alpha(u - v) - \gamma \exp[-\alpha(u - v)^2] \} \exp[-\alpha(u - v)^2 - \gamma u^2] &= 0, \\ [\alpha(u - v) - \gamma v] \exp[-\alpha(u - v)^2 - \gamma u^2] &= 0. \end{aligned}$$

One potential solution is $u = v = 0$. However, as the second derivative of the prey payoff is positive,

$$\frac{\partial^2 P_u}{\partial u^2} \Big|_{u^*=0;v^*=0} = 2\alpha > 0,$$

$u = 0$ is not an optimum. Assuming $|u - v| < 1$, and deriving the Taylor expansion to the second order of $(u - v)$ we have $\exp[-\alpha(u - v)^2] \approx 1 + \alpha(u - v)^2$, obtaining the approximate pair of solutions

$$u^* = \pm \frac{\sqrt{\alpha + \gamma}}{\gamma}; \quad v^* = \pm \frac{\alpha}{\gamma\sqrt{\alpha + \gamma}}.$$

Observe that $u^* - v^* = \pm 1/(\alpha + \gamma)$ so that the condition $|u^* - v^*| < 1$ is satisfied if $\alpha + \gamma > 1$. The second assumption, $\frac{\partial^2 P_s}{\partial s^2} \Big|_{u^*;v^*} < 0$, shows that this asymmetrical scenario is stable. The prey outcome, when $v = v^*$, has also another maximum at $u^{**} \approx \mp \frac{1}{\sqrt{\alpha + \gamma}}$, meaning that prey population could split in two lineages. However, $\{u^{**}, v^*\}$ is not a stable solution (Fig S1 in supplementary material shows the plots for $P_v(u^*, v)$ and $P_u(u, v^*)$).

Now consider the case where predators have two prey in their neighborhoods. If the prey population is monomorphic not much changes except that the predators have now two chances to attack

a prey. As we have seen, if prey evolve and the predators are selective, this may have profound evolutionary consequences.

Suppose prey and predator phenotypes have evolved to u^* and v^* , respectively, and let a new prey phenotype u^m appear. In accordance with custom in adaptive dynamics theory we will call the dominant phenotype u^* the “resident”, and u^m the “mutant” (Metz et al. 1992). We consider now that there are two prey in a given predation neighborhood; a resident and a mutant. The fate of the mutant will depend on the predator’s strategy. If the predator attacks randomly, the mutant has a 50% chance of being attacked first. However if the predator is selective it depends whether the mutant is the most preferred prey or not. That is, if u^m is closer to v^* than u^* the predator will attack it; on the other hand, if u^m is further away than u^* the predator will consider it as the second option. Thus, the fitness of the mutant depends not only on its own phenotype, but also on that of its conspecifics as well as the predators’ strategies. If predators attack at random, the payoff of the mutant prey is thus given by

$$P_{\text{random}}^m(u^*, u^m, v^*) = \frac{1}{2} [f + (1 - f)(1 - f^m) + (1 - f^m)] gh^m, \quad (9)$$

where $f^m = \exp[-\alpha(u^m - v^*)^2]$ and $h^m = \exp[-\gamma(u^m)^2]$ are respectively the probability of a successful attack and the stabilizing selection on the mutant. The term $1/2$ refers to the probability of one of the any two prey being attacked first. If the resident is attacked first, the mutant can escape from successful predation with probability $f + (1 - f)(1 - f^m)$, which means that the resident can be successfully attacked (f) or, if it not ($1 - f$), the attack on the mutant is not successful ($1 - f^m$). If the mutant is attacked first, its fitness will be proportional to $(1 - f^m)$, the last sum in the Eq.(9).

If predators attack selectively, however, the mutant prey’s payoff depends in a discontinuous fashion on its strategy, depending on whether it is preferred by the predator or not,

$$P_{\text{prey selection}}^m(u^*, u^m, v^*) = \begin{cases} (1 - f^m) gh^m & \text{if } |u^m - v^*| \leq |u^* - v^*| \\ [f + (1 - f)(1 - f^m)] gh^m & \text{if } |u^m - v^*| > |u^* - v^*| \end{cases} \quad (10)$$

so if the mutant is less preferred it only risks an attack if the predator failed the attack on the preferred prey. Payoff functions for the predator and the resident prey could be constructed in a similar fashion, but here we only will use mutant payoff in order to demonstrate how its fitness varies with its strategy.

The consequences of predators preferring certain prey is that in a homogeneous resident prey population, mutant prey that are slightly farther away from the ‘focus’ of the predator are better protected. In the situation depicted in Fig. (4) the phenotype combination (v^*, u^*) is unilaterally optimal (i.e., a Nash equilibrium) and thus an ESS candidate. To the prey it does not pay to reduce costs by reducing u^m , as they would immediately attacked preferentially, to the predators it does not pay to focus on larger prey because of the balancing selection. There is a higher optimum for the prey, but this cannot be reached by small mutation steps without crossing the adaptive valley. Only when u^* and v^* are close, mutations may arise that ‘jump’ the valley and thus break the asymmetric pattern. In larger populations, the symmetric pattern is likely to result then, but in smaller, stochastic population, the asymmetric pattern may just switch to the other side.

Symmetrical branching stability

Assume now a situation where there is one predator population, with phenotype v , and two different prey resident populations, with phenotypes u_1 and u_2 . As before, we will look for the stable solution when there is only one prey (u_1 or u_2) in a given predation neighborhood, and then we do not need to impose any selection strategy. The probabilities that prey and predators win the interaction and produce an offspring can be written as

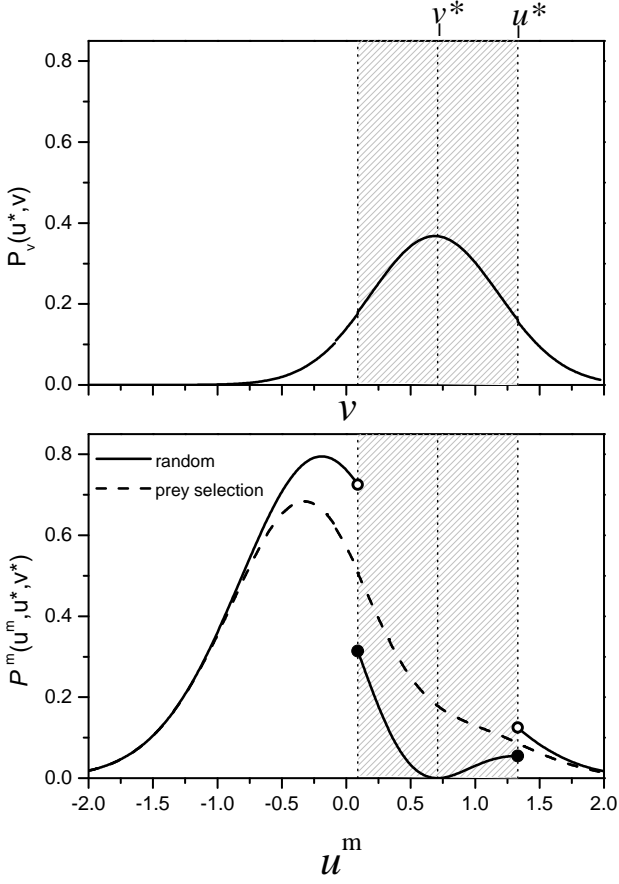


Figure 4: Payoffs for predator and prey considering one prey resident population. The upper panel shows predator payoff as a function of its phenotype and setting the prey phenotype at its optimum value, $P_v(u = u^*, v)$, Eq. (7). The maximum of this function refers to the optimum predator phenotype (v^*). The lower panel shows prey mutant payoff as a function of its phenotype, setting the prey resident and predator phenotypes at their optimum values. The dashed line refers to mutant payoff with non-selective (random) predation, $P_{\text{random}}^m(u^*, u^m, v^*)$ (Eq.9); the solid line represents predation with prey selection, $P_{\text{prey selection}}^m(u^*, u^m, v^*)$, Eq.(10). The gray area shows the predator's preferred phenotype range, where $|u^m - v^*| < |u^* - v^*|$. If we consider a mutant prey whose phenotype is similar to the resident one, the evolutionary outcome will be totally dependent on the predation strategy: The curve for $P_{\text{random}}^m(u^*, u^m, v^*)$ shows that the mutant phenotype will evolve towards the maximum payoff and then will break the asymmetrical branching; the curve for $P_{\text{prey selection}}^m(u^*, u^m, v^*)$ has two maxima (one when $u^m = u^*$ and a higher one around -0.4), however there is a valley when $u^m = v^*$ and the higher peak cannot be attained with small mutation steps (if some mutations do, oscillatory evolutionary dynamics that we observed in some simulations may result). Parameters $g = \gamma = \alpha = 1$.

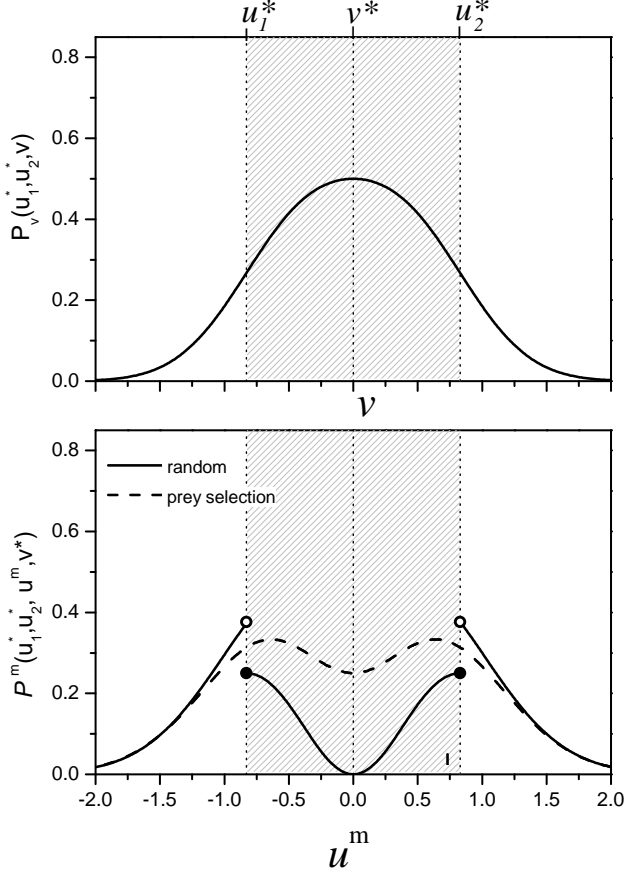


Figure 5: Payoffs for predator and prey considering two prey resident populations. The upper panel shows predator payoff as a function of its phenotype and setting the prey phenotypes at their optimum value, $P_v(u_1 = u_1^*, u_2 = u_2^*, v)$, Eq. (7). The maximum of this function refers to the optimum predator phenotype (v^*). The lower panel shows prey mutant payoff as a function of its phenotype, setting the two prey resident and predator phenotypes at their optimum values. The dashed line refers to mutant payoff with non-selective (random) predation, $P_{\text{random}}^m(u_1^*, u_2^*, u_i^m, v^*)$ (Eq.13); the solid line represents predation with prey selection, $P_{\text{prey selection}}^m(u_1^*, u_2^*, u^m, v^*)$, Eq.(14). The gray area shows the predator's preferred phenotype range, where $|u^m - v^*| < |u^* - v^*|$. Both payoff functions have two maxima which means that the symmetrical prey branching can be a stable pattern regardless of the predator strategy. However, when the predation occurs with preference there is a deeper valley minimizing the flux from one mode to the other. Parameters $g = \gamma = \alpha = 1$.

$$P_v(u_1, u_2, v) = \frac{1}{2} \{f_1 + f_2\} h_v, \quad (11)$$

$$P_{u_1}(u_1, v) = (1 - f_1) g h_{u_1},$$

$$P_{u_2}(u_2, v) = (1 - f_2) g h_{u_2}, \quad (12)$$

where $f_s = \exp[-\alpha(u_s - v^*)^2]$ and the term $1/2$ assume that prey populations occur with equal abundance. Analogous to the previous procedure (however without any approximation), the first and second derivatives allow us to calculate a possible solution

$$u_1^* = \pm \sqrt{\frac{1}{\alpha} \ln \left(\frac{\alpha + \gamma}{\gamma} \right)}; \quad u_2^* = -u_1^*; \quad v^* = 0,$$

that is evolutionarily stable (Fig. S2) when $(\alpha + \gamma) > 2\alpha \ln \left(\frac{\alpha + \gamma}{\gamma} \right)$ (if we assume $\gamma = 1$, for example, then the condition is $\alpha < 1.37$). (For greater values of α , $v^* = 0$ becomes a minimum point and two symmetrical maximum points emerges for $P_v(u_1^*, u_2^*, v)$, leading to divergence in the predator population (Vincent and Brown 1989)).

Regarding the stable symmetric pattern, where the phenotypes evolve to u_1^* , u_2^* and v^* , we approached the effect of another prey (mutant) in the predation neighborhood, whose phenotype is u^m . As before, consider now that a new mutant appearing in a given predation neighborhood. Then, there are two prey in this predation neighborhood; a resident (u_1^* or u_2^* with equal probability) and a mutant (u^m). The probability that the mutant prey is not attacked and produces offspring depends on their phenotypes and on the predator strategy. If predators attack at random,

$$P_{\text{random}}^m(u_1^*, u_2^*, u_i^m, v^*) = \frac{1}{2} \left\{ \frac{1}{2} [f_1 + f_2 + (2 - f_1 - f_2)(1 - f^m)] + (1 - f^m) \right\} g h^m, \quad (13)$$

otherwise,

$$P_{\text{prey selection}}^m(u_1^*, u_2^*, u^m, v^*) = \begin{cases} (1 - f_i) gh^m & \text{if } |u^m - v^*| \leq |u^* - v^*| \\ \frac{1}{2} [f_1 + f_2 + (2 - f_1 - f_2)(1 - u^m)] gh^m & \text{if } |u^m - v^*| > |u^* - v^*| \end{cases} \quad (14)$$

Both payoff functions have two maximum points (see Figure 5), which means that the symmetrical prey branching can be a stable pattern regardless of the predator strategy. However, if the predator attacks with prey selection, the two optimum phenotypes for the mutant coincide with the phenotypes of the residents while if the predation occurs randomly they are closer (the simulated results also show that, compare Figs. 1 and 2 when $K = 10000$ and $\alpha = 2$). Moreover, if the predator attacks selectively, the two prey lineages are well separated, $P_{\text{pref}}^m(u_1^*, u_2^*, u^m, v^*) = 0$, and then the flux from one lineage to the other occurs only by large mutations (see Fig.5). If one of the lineages goes extinct, selective predation will probably drive the phenotypic adaptations towards the asymmetrical pattern, while for random predation large mutations are not required for the extinct lineage to reemerge.

4 Discussion

We presented an individual-based model for the coevolutionary dynamics of predator-prey systems in which predators can choose which prey to attack in their immediate neighborhood. In the model the interaction between prey and predators is stabilizing and non-directional interaction strengths, only the difference between prey and predator phenotype determines predation success. However, next to a version in which predators encounter prey only randomly, we also allow them to select prey to attack from prey present in its predation neighbourhood, where they will preferentially attack prey with the closest match.. We compare the temporal population phenotype distributions – coevolutionary patterns – for a number of different parameter combinations that represent different

ecological settings. Our results support four main conclusions described below.

First, trait evolution is sensitive to the intensity of interaction strength and the populations' carrying capacity. For a given value of interaction strength, increasing the carrying capacity has the following effects: we first have extinction of predators or both populations; as population densities increase, they tend to coexist indefinitely, shifting through the following patterns: *asymmetrical branching* (which occurs only in the model with prey selection), *symmetrical coevolutionary oscillation* and finally *symmetrical branching*. The term "symmetry" means that phenotype temporal distribution occupied both regions (with equal amplitude) delimited by the optimum phenotype. In the transition between patterns these are combined with populations oscillating, bifurcating and forming lineages that go extinct and then evolving again. A similar sequence of coevolutionary patterns occurs with a fixed carrying capacity and decreasing interaction strength. With symmetrical branching, the prey evolves to a bimodal phenotype distribution, while the predator evolves to an intermediate phenotype which is equally effective with both prey lineages. The coevolutionary oscillatory pattern is related to Red Queen evolution (van Valen, 1973), where rare prey phenotypes are more likely to evade predation and thus phenotype frequencies in prey populations change continuously, while the predators keep evolving to specialize on the most common prey types (Dieckmann et al. 1995). It should be noted however, that the oscillatory pattern observed under prey selection is somewhat different, and results from the episodic reversal between two stable patterns. In contrast to van Valen's Red Queen dynamics, this oscillatory pattern strongly depends on population sizes, as it depends on the frequency of those rare mutations that manage to cross the adaptive valley driven by predators selectively attacking preferred prey.

Both stable and unstable patterns have been predicted by many theoretical models (Gomulkiewicz et al. 2000; Abrams 2000; Dieckmann et al. 1995; Levin and Udovic 1977; Thompson 2005; Brown and Vincent 1992; Calcagno et al. 2010), although empirical examples remain sparse. The presence of bimodal host phenotype distributions have been empirically observed in a natural *Daphnia* population

during a parasite epidemic (Duffy et al. 2008) and also in host egg coloration subject to avian brood parasitism (Yang et al. 2010). Empirical evidence of an oscillating pattern was again found in host egg colorations and their avian brood parasite by Spottiswoode and Stevens (2013) and in a herbivorous moth and its host plant (Berenbaum and Zangerl 1998). Frequency-dependent selection between populations have already been pointed by Levin and Udovic (1977) as an important driver in evolutionary history. In agreement with these authors, we verified that selective pressure in smaller populations can lead to different evolutionary effects from those expected in larger populations.

Second, both simulations and our analysis agree that prey selection causes prey phenotypes to evolve towards more extreme values than randomly attacking predators. When the resulting evolutionary pattern is oscillatory, its amplitude is higher and when prey phenotypes bifurcate, the stable phenotypes are more extreme. This result suggests that selective predation can facilitate speciation. This would be caused if phenotypic differentiation were followed by reproductive isolation (Dieckmann and Doebeli, 1999). The current model does not allow for this additional evolutionary step, as reproductive isolation makes no sense under the assumption of asexual reproduction. Future studies, expanding this model to include sexual reproduction and reproductive isolation could test the effect of the resource selection strategy on diversification rates in order to validate this prediction.

Third, prey selection makes predators more efficient which paradoxically, reduces at least the predator population size. Other models of exploitative interactions have found that enhancing a consumer's efficiency reduces its population density (Peterson 1984). In our model, for a sufficiently high carrying capacity, the predator strategy has no effect on prey density, or on the ensuing evolutionary pattern: in both behaviors the system converges to symmetrical branching at high carrying capacity (although the stable prey phenotypes are more divergent under selective predation). However, the predator density decreases when there is prey selection (see Fig. 3), and as a consequence, the predation neighborhood increases (since it is proportional to the ratio of prey and predator population sizes). Predator population size is reduced under selective versus random predation, probably be-

cause selective predation imposes a higher pressure on prey phenotype, which in turn exerts a higher pressure on predators. On the short term, for a given prey phenotype distribution, prey selection increases predator success, but in over evolutionary time it reduces the predator population benefit compared to random predation. At low values of carrying capacity, both populations are more vulnerable to extinction when predation is selective. This issue is particularly important regarding species that evolve in islands, in fragmented patches or that naturally occur in low abundance.

Fourth, an asymmetrical pattern can emerge in a totally different evolutionary dynamics than previously thought. Up to now, models showed that the definition of a symmetric or asymmetric phenotype distribution was determined exclusively by interaction strength type (when a stabilizing pressure that bounds the phenotype distribution around an optimum value is also considered): the expected mechanism that allows the species phenotypes to evolve in symmetry (oscillating or bifurcating in two or more lineages) is non-directional pressure; phenotype matching (promoting bidirectional axis of vulnerability, as approach by Abrams (2000)). For species phenotypes evolve in asymmetry, the mechanism would be directional pressure, phenotype difference, which promotes unidirectional axis of vulnerability (Abrams 2000). Here we showed that non-directional pressure (phenotype matching) associated to prey selection can limit prey phenotypes to an asymmetrical branching, which can only be broken if population densities increase. The analytical model shows the importance of sharp decrease in the probability of survival of the prey under prey preference, when the phenotype of the mutant is closer to the predator phenotype than the resident phenotype. This situation can occur when there is a slight difference between the prey phenotypes, and the predator prefers the phenotype that gives it the greatest fitness contribution, even if the difference is very small. This discontinuity may be not realistic, since in a predation neighborhood a small phenotypic variation may not be noticed by the predator. As a consequence, a mutant can no longer ‘hide’ behind more preferred prey, and the asymmetrical pattern would be broken more easily. However, we expect that the asymmetrical pattern persists, but less pronounced. Further study should

assess which level of differentiation by the predator is necessary to produce asymmetrical patterns.

Our study can shed light on currently observed evolutionary patterns, and a prime example is the evolution of egg morphology of cuckoo brood parasites and their hosts. This system presents the two elements we are highlighting : non-random host selection (parasite individuals choose the nest where they will lay eggs) and non-directional pressure (parasite success increases with phenotype matching) (Avilés et al. 2006; Soler et al. 2014). The study by Spottiswoode and Stevens (2013) compared the appearance (color and patterns) of cuckoo finch eggs with their hosts, the tawny-flanked prinia (*Prinia subflava*) from the same location in Zambia over 40 years. As mentioned before, they found that egg colors seem to be locked in an ongoing arms race (*symmetrical coevolutionary cycling*). However, part of the egg color pattern traits measured have been changing their mean values, accompanied by decreases in phenotypic variation, suggesting directional selection (evolving to an asymmetrical pattern which the authors interpreted as resulting from some undetected directional pressure which would drive this asymmetrical evolution). Our model provides an alternative explanation for this result, which requires no other pressure besides the host selection by brood parasites according to phenotypic matching; the observed pattern emerges directly from this non-random interaction.

In conclusion, our results bolster the conclusion that non-random interactions can have important ecological and evolutionary consequences. That prey selection strategies may have important ecological consequences was long known, but we show here that they may also have unexpected evolutionary consequences, such as generating striking asymmetrical (or cyclic) evolutionary outcomes. Our results are also a reminder to keep considering the ecological context, as our results are most pronounced under those ecological conditions where population sizes are relatively low. .

Acknowledgements

SBLA received research assistanships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), LRJ was supported by Fapesp scholarships (predoctoral grant #09/54806-0; post-doctoral grant #14/16082-9), and TML received CNPq productivity grant #311800/2015-7. SBLA, LRJ, TML and PRG thank the São Paulo Advanced School on Ecological Networks (supported by Fapesp grant #2010/51395-7) for promoting the collaboration of this work. MvB received support under the program 430 Investissements d’Avenir launched by the French Government and implemented by ANR with the 431 references ANR-10-LABX-54 MEMOLIFE and ANR-11-IDEX-0001-02 PSL Research 432 University.

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