Coevolution in sexually reproducing populations of predators and prey

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Abstract

The dynamics of coevolution is a spatio-temporal process that cannot be understood by mean field approximations, where populations are considered well mixed and interactions are random. This intrinsic characteristic makes comprehensive empirical studies difficult and computer simulations can help to understand the interplay between the many components of the interactions. Here we created an individual-based model to study the coevolution of sexually reproducing populations of prey and predators that engage in an arms race. The phenotype interface of the interaction is a defensive trait for the prey and a counter-defensive one for the predator, both having costs that decrease reproduction chances. The simulations captured several features of natural systems, such as oscillations of the phenotypes levels and abundances. More importantly, the simulations show that local depletion of prey by predators with high levels of counter-defenses followed by recolonization by less defensive prey is a key mechanism that regulates the arms race and the spatio-temporal distribution of phenotypes, creating mismatches similar to those observed in natural systems.

Keywords: antagonistic interaction, phenotype evolution, individual based model, trade-off

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1. Introduction

It has been long recognized that evolutionary processes take place in space and time and that simple mean field approximations, where space is ignored, are unable to describe important aspects of their dynamics [1]. A classic example is the phenomenon of pattern formation in host-parasite systems where the parasite can mutate, becoming more or less lethal. Whereas in a mean field approximation the dynamics would lead to the prevalence of the most lethal form and to the extinction of both hosts and parasites, in a spatial population only local patches of organisms disappear and are recolonized by hosts and less lethal forms of the parasite [2, 3, 4].

In coevolutionary systems the spatio-temporal character of the dynamics appears to be equally important. Empirical observations indicate that patches of locally coadapted populations are short lived, being prone to mismatches, to extinctions and to constant invasion by other such local populations [5, 6, 7, 8, 9].

Antagonistic interactions, such as predator-prey [10, 11] or host-parasite [12], are one of the principal forces of selection [13] and can produce adaptations and counter-adaptations on the populations, leading to an arms race.

Brodie Jr. and colleagues [14, 15, 16] studied a predator prey system in which newts of the genus *Taricha* produce a toxin (tetrodoxin - TTX) that can be ingested by snakes of the genus *Thamnophis*. The resistance of the snake is due to a genetic modification the sodium channel [17, 18, 19, 20]. Although the consequences of those modifications are not completely understood, studies [21, 19] suggest that there is a correlation between resistance to TTX and lower locomotion capability, which can be linked to the snake's chance to survive and reproduce [22]. That would indicate the existence of a trade-off between resistance to TTX and fitness, since it would decrease the snake's ability to escape from predators and reproduce. Although the mechanism by which TTX is produced by the newts is still unknown, there is evidence that newts also pay indirect costs according to their levels of TTX [23, 24]. The cost appears to be related to the resistance to the toxin the newts themselves need to have. The

species suffered parallel convergence, resulting on similar changes of the sodium channel [24].

The snakes-newts predator prey system is distributed over a large spatial area [16] and the correlation between the corresponding phenotypes (toxin and resistance levels) is not uniform. Whereas in many regions the phenotypes are closely balanced, in others there are significant mismatches. Interestingly, in all mismatched regions the predator counter defensive trait was ahead the prey defensive trait. This geographic pattern suggests an oscillatory dynamic on the evolution of phenotype traits on the predator prey interaction.

The idea of geographical mosaics of coevolutionary interactions is not new [25] and poses that different outcomes can evolve on different places of the same system depending of local conditions and also on the amount of migration between sites [26]. Aside the importance of spatial variation, time has a remarkable role in coevolutionary systems [12]. This multidimensionality of coevolutionary dynamics makes the assessment and study of this important process very difficult. Thus, the use of mathematical models and simulations becomes a important tool that can help understand the role of specific components of the process.

In this paper we developed an individual-based model to simulate the coevolutionary process in a predator-prey system using as inspiration the newt-snake system studied by Brodie and collaborators [10, 27, 16]. Although the model has many assumptions and parameters, it is still an oversimplified version of the natural newt-snake system to allow for direct comparison between the results of simulations and the empirical data. Our goal is to study the main qualitative features of the dynamics and, in particular, to understand the role of space in generating the phenotypic mismatches reported in [16].

We show that evolution in this system exhibits a complex spatio-temporal dynamics of local extinctions and colonizations. While local populations of prey and predators tend to engage in an arms race and evolve closely balanced phenotypes, they can also go extinct. Moreover, since the population of prey is much more abundant than that of predators, groups of prey may become temporar-

ily isolated from predators, decreasing the evolutionary pressure and lowering their toxic content. This, in turn, increase their reproductive ability, and make them potential colonizers of nearby extinct patches, leading to phenotypic mismatches.

2. Models and Definitions

The model description follows closely the ODD (overview, design concepts, details) protocol [28, 29]. Along all the description the index 1 will be assign to prey and 2 for predator. Many features of the present model were based on a previous spatially explicit model by de Aguiar et al [30], which was adapted here to describe two species interacting through a single additive trait.

2.1. Purpose

The purpose of the model is to understand the geographical and phenotypical distribution of coevolving populations of prey and predators. The model is inspired in the system of snakes and newts that inhabits the west coast of North America and which shows, in some areas, a mismatch between the prey defenses and predator resistance.

2.2. Entities, state variables and scales

Entities consist of prey and predator individuals and the state variables are their spatial positions (located on a 2-dimensional grid) and their genomes, a haploid string with biallelic loci assuming the values zero or one.

$$i = (i_1, i_2, \ldots, B_f). \tag{1}$$

The genome determines the phenotype of the individual, which measures the amount of toxin produced by prey (as a means to protect it from being eaten by predators) or the amount of resistance to the toxin possessed by a predator. Phenotypes are attributed to the individuals at their birth and are modeled as

an additive trait:

$$f(i) = \sum_{k=1}^{B_f} i_k. \tag{2}$$

Therefore, the number of ones on the genome is the amount of toxin (for prey) or the amount of resistance (for predators).

The phenotype also determines the reproduction rate for each individual. In the model we assume the existence of a trade-off between the phenotype character and the cost of producing it. We further assume that the functional form of the cost is similar for both predator and prey, although the parameters controlling the function may differ for each group. We model the reproductive rates by the function (fig. 1):

$$r_{(1,2)}(i) = r_{(max1,max2)} \frac{1 + e^{-\alpha_{(1,2)}}}{1 + e^{-\alpha_{(1,2)}(1 - f_{(1,2)}(i)/\delta_{(1,2)})}}, \tag{3}$$

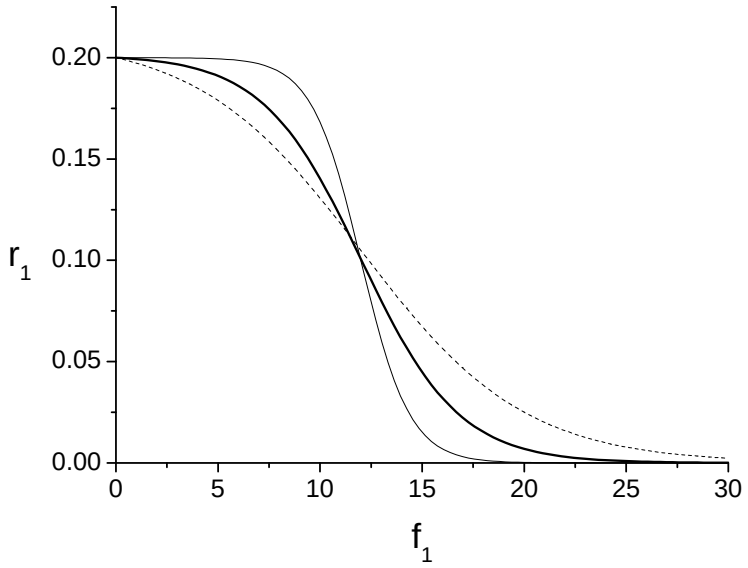


Figure 1: Probability of reproduction as a function of the level of toxin for $r_{max1} = 0.2$, $\delta = 12$ and for $\alpha = 3$ (dashed curve), 5 (thick curve) and 10 (thin curve). The decrease in the chances of reproduction reflects the costs associate with the level of toxin.

The environment is described by a rectangular 2D grid where cells can be available for occupation or represent an inhospitable site (a barrier). Available cells can be occupied by a prey, a predator or be empty. Except for the barriers, the environment is homogeneous, so that every available grid cell is as good for survival as any other. Barrier cells cannot be occupied by individuals and are located in the center of the lower half of the rectangle (fig. 2, first panel). The purpose of the barrier is twofold: first it is inspired in the snakes-newts system, whose environment has a horseshoe shape because of the inhospitable area occupied by the San Joaquim valley. Second, it allows us to analyze the role of corridors in the dynamics.

2.3. Process overview and scheduling

Prey individuals can die or reproduce and predators can die, eat a prey and, if they succeed in eating, they can reproduce. The mortality rates, d_1 for prey and d_2 for predators, are fixed numbers between 0 and 1 giving the probability that individuals die per time step.

Reproduction is sexual and local. It involves the focal individual and a mate, to be found in a local circular neighborhood of radius $S_{(1,2)}$ around the focal individual. The offspring is produced by crossing over the bit strings representing the genomes of the parents. After the offspring's genome is constructed each locus can mutate from 0 to 1 or from 1 to 0 with a fixed probability $\mu_{(1,2)}$.

Predators can eat a prey only if the prey is within its local neighbourhood and if it has enough resistance to survive the toxin of the prey.

The dynamics proceeds as follows:

An individual, prey or predator, is selected. If the individual is a prey it dies with probability d_1. If it does not die it reproduces if there is another prey individual to mate with within its local neighbourhood and if there is an empty site in the same neighbourhood to place the offspring.

If the individual selected is a predator, it dies with probability d_2. If it does not die it chooses a prey at random within its local neighbourhood. Predation is successful if the predator resistance is high enough compared to the toxicity

of the chosen prey:

$$f_2 \geq f_1 - R, \tag{4}$$

where R is the 'internal resistance' of the predator, that allows it to eat some of the prey even if $f_2 < f_1$. We used $R = 1$ in most of our simulations, giving the predators a slight advantage over the prey. Increasing R decreases the selection pressure on the coevolving trait, since for large R the predators can eat almost any prey. If the predator cannot eat it dies. If it does eat it has a chance of reproducing. Reproduction happens if there is another predator individual to mate with within its local neighbourhood and if there is an empty site in the same neighbourhood to place the offspring.

The dynamics is discrete and in one time step all individuals of the population will have a chance to act (die or reproduce for prey, die, eat or reproduce for predators).

2.4. Design concepts

The *basic principles* on which the model is constructed are that coevolution is dependent on space and time [31, 12, 16], and that there is a phenotype driving the coevolutionary interaction [32, 14]. In the model these basic principles are implemented as follows: (i) the interactions between predators and prey are mediated by a single phenotype that is encoded genetically and subjected to random mutations; (ii) the environment is spatially explicit and interactions occur only between sufficiently close individuals; (iii) reproduction is sexual and individuals are haploid and hermaphrodites. Predators can only hunt prey or reproduce with other predators in a circular area of radius S2 centered on the individual. Similarly, prey can only reproduce or be hunted by individuals in a circular area of radius S1.

Phenotype distribution and abundances are *emergent properties* of the system and will be monitored in space and time.

The *adaptive* trait of each population is the phenotype value, defense and resistance, which are coupled by predation and by the trade-off between trait

value and reproductive capability. In a predator-prey interaction, if the phenotype value of a prey is higher than that of the predator the prey will not be eaten and the predator dies, while if the opposite the prey will be eaten and the predator then can reproduce. A prey with high value of toxin may not be eaten but will have low chances of reproducing.

The *interactions* between the agents are given by direct encounters of individuals of the same group (for reproduction) or of different groups (for predation). Interactions also occur indirectly by competition for space, given that two individuals cannot occupy the same site, and an empty site is needed to reproduce.

Stochasticity is present during death and reproduction, which are controlled by the probability parameters ($d_{(1,2)}$, $r_{(1,2)}$) and when choosing the partner to reproduce, a conspecific chosen at random within the neighbourhood $S_{(1,2)}$. The offspring is also generated from the parents genomes with a single crossover at a random point plus mutations with rates $\mu_{(1,2)}$. Finally, predation also involves the choice of a random prey in the predator vicinity.

As output the genome and the location of every individual is saved, from which we can compute the total abundance of each group as well as the geographical and phenotype distributions.

2.5. Initialization

At the start of the simulation all alleles are set to zero for all individuals. The predators and prey begin in the regions (C) and (D) (fig. 2, first panel). In this regions, the probability that a site is initially occupied by a prey or a predator was random assigned with probabilities $P_{(1,2)}$. With probability $1 - P_1 - P_2$ the site remained empty.

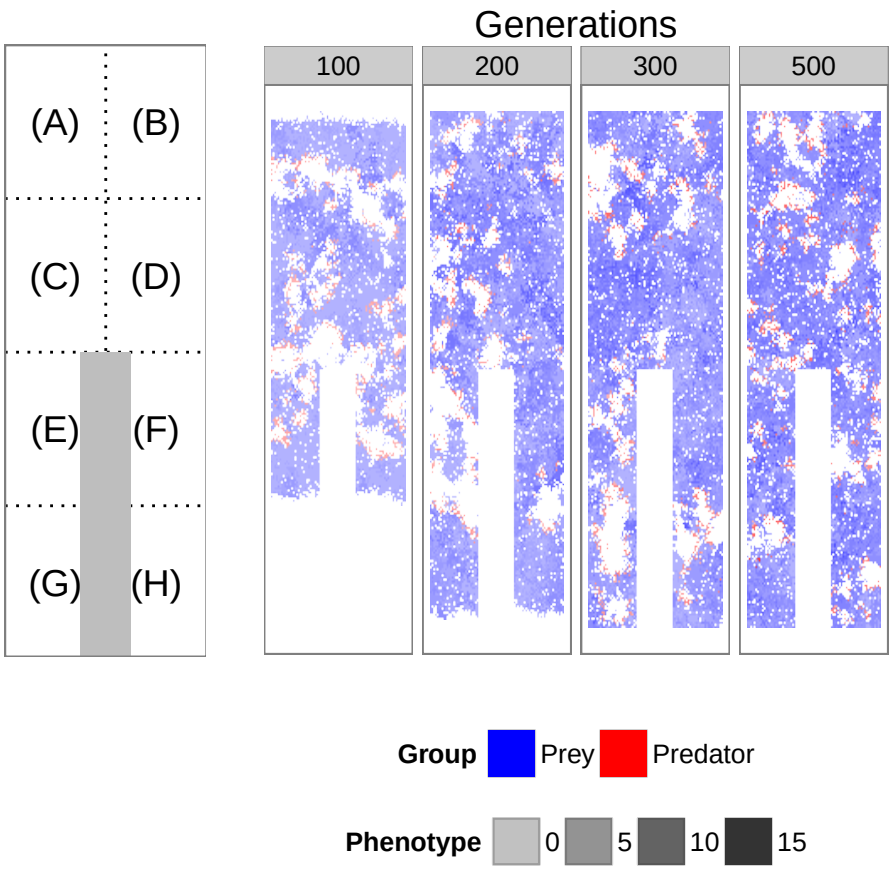


Figure 2: The first panel is the representation of the regions created, a rectangular area of sizes 80×250. The grey area represents a barrier which the individuals cannot cross. The others panels show examples of one simulation on generations 100, 200, 300 and 500. Red dots represent predators and blue dots represent prey. The tone of the color is set according to the phenotype value.

2.6. Input data

The input data consists of the dimensions of the 2D grid, the barrier cells and the parameters specifying the probabilities related to dying, eating and reproducing for the prey and predators (see table 1). In the case a simulation is continued from a previous run, the input also contains the spatial position and genomes of the individuals at the end of the last simulation.

Table 1: Table with the input names and the description.

Name	Description
T	time - number of generations of simulation
$L_{(x,y)}$	size of x and y values of the lattice world
$P_{(1,2)}$	probability of placing a prey or a predator at the beginning of the simulation
$d_{(1,2)}$	prey and predator death rates
$r_{max1,max2}$	prey and predator maximum reproduction rates
$S_{(1,2)}$	prey and predator spatial radius for interaction
$Bf_{(1,2)}$	size of the genome for prey and predator
$\mu_{(1,2)}$	prey and predator mutation rate per locus
$\alpha_{(1,2)}$	parameter that controls the smoothness of the fitness function
$\delta_{(1,2)}$	parameter that indicates the inflection point of the fitness function
R	value of the intrinsic resistance of the predator

2.7. Submodels

The algorithm has four basic modules: find-neighbors, fitness-calculus, prey-reproduction and predator-reproduction.

The find-neighbors submodel scans the neighbourhood of an individual and writes down a list with all the neighbours found: prey, predators and empty sites. The submodel has two parameters: the spatial position of the focal individual and the radius $S_{(1,2)}$ of its circular neighbourhood. The output are vectors with the locations of prey, predators and empty spaces in the neighbourhood.

The fitness-calculus submodel calculates the reproductive rate r_i of each individual according to equation (3) as illustrated in figure 1. The value of r_i depends on the individual's phenotype value f_i, equation 2. The parameter α specifies the smoothness of the curve and the value of δ the position of the inflection point.

The prey-reproduction submodel checks if the focal prey individual will reproduce according to its reproductive rate r_1, equation 3. If the individual is selected for reproduction it chooses a mate at random from its vicinity, which is obtained from the find-neighbours submodel. The parents genomes are then crossed-over to generate the offspring's genome. A single cross-over point k is chosen at random and two genomes are constructed by putting together the first k genes of the focal individual with the last $Bf - k$ genes of the mate and

vice-versa. One of the two is picked with equal probability and each gene is allowed to mutate from 0 to 1 or from 1 to 0 with probability μ. The resulting genome is assigned for the offspring.

The newborn will be placed on a empty site in the neighbourhood of radius S_1 around the focal individual. If there is no empty site near the focal individual the reproduction will not occur. The input for this submodel is the focal individual and the list of neighbours generated by the find-neighbors submodel. As output it returns the site and the genome of the offspring.

The predator-reproduction is similar to the prey-reproduction submodel, except that before verifying if the focal predator will reproduce it checks if it can find a prey it can eat. First, a prey is randomly selected from the vicinity of the focal predator; if the prey has a phenotype value less than that of the predator then the predation is successful: the prey dies and the predator reproduces. If predation is not successful the predator dies without reproducing.

2.8. Scenarios

We first studied the range of parameters where coexistence of prey and predators were possible. To do that we simulated the dynamics in various scenarios. The parameter set for these scenarios were:

δ_1 and $\delta_2 = \{10, 15\}$,

α_1 and $\alpha_2 = \{3, 6\}$,

$R = \{1, 2, 3\}$ and

r_{max1} and $r_{max2} = \{0.1, 0.2, \ldots, 1\}$.

Each scenario was simulated 10 times for 5000 generations.

Based on these simulations we fixed the parameters with the values:

$r_{max1} = 0.6$, $d_1 = 0.2$, $\alpha_1 = 3$, $\delta_1 = 10$, $r_{max2} = 0.3$, $d_2 = 0.08$, $\alpha_2 = 6$, $\delta_2 = 10$, $S_{(1,2)} = 2$, $Bf_{(1,2)} = 20$, $\mu_{(1,2)} = 10^{-3}$. We simulated for 1500 generations.

The world regions A-H were used to study the phenotypes of both predators and prey in the different areas around the barrier. The phenotypes were

measured by comparing the difference of the predator phenotype with the mean value of the prey nearby.

3. Results

3.1. Coexistence and extinctions

In our simulations the coexistence of predators and prey was achieved only for a small set of parameters, occurring especially when the reproductive rate of prey was larger in comparison to that of predators ($r_{max1} > r_{max2}$) and also when the selective pressure on the prey was greater ($\delta_1 \leq \delta_2$ and $\alpha_1 \leq \alpha_2$), as shown in fig. 3 for $R = 1$. Increasing the predator internal resistance makes the parameter set that allow coexistence even more restrict (see supplementary information for all set of internal resistance fig. S1 - S3).

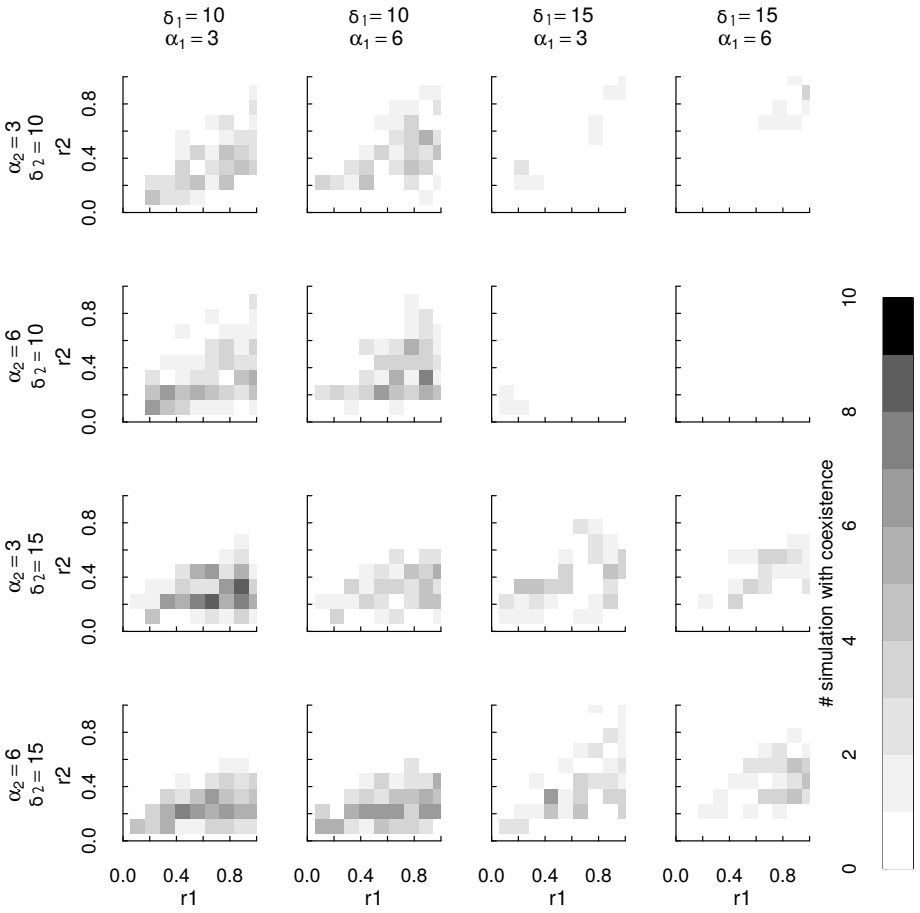


Figure 3: Coexistence of predator and prey, for $R = 1$. For each set of parameters there is a plot with values of $r_{(max1,max2)}$ varying from 0 to 1. The quantity of simulations that achieve the coexistence is marked by the color, with the darkest ones being those with more coexistence.

3.2. Arms race

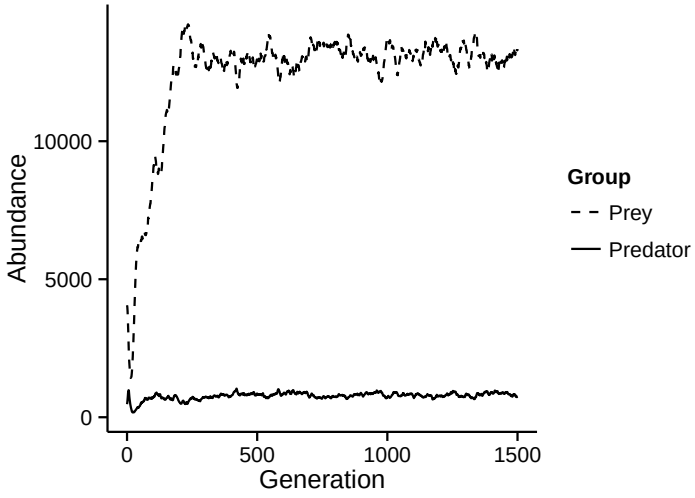
To study the co-evolution of toxicity and resistance we first considered the dynamics of a population of prey without predators (dotted line in fig. 4(b)). Because of random mutations, the toxin level does not remain zero, but stabilizes at a low value. When predators are present the arms race starts immediately, but only between prey and predators that are in contact. We observed intensive local co-evolution that lead to a decrease in the reproductive abilities of both predators and prey. Predators typically deplete the local resources and move

towards less toxic prey, creating a wave of predation. The resulting depleted areas caused by local extinctions of prey is rapidly recolonized by less defensive ones (fig. 2, for full simulation see movie simpop.avi). This dynamic of extinction and recolonization also occur for the predator, but the recolonization was considerable slower.

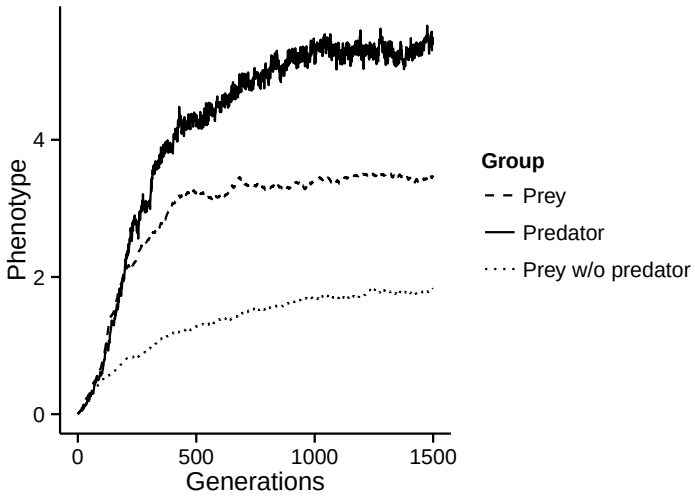
The population abundances showed the typical oscillatory behavior of a predator-prey system. After a short transient period, the prey population increased and maintained a large abundance, whereas the predators kept a low abundance (fig. 4(a), for the dynamic on each region see fig. S4 and the phase diagram see fig. S5).

The phenotypes of predators and prey also oscillated over time. When both predators and prey are present the mean prey phenotype increases very fast in the earlier generations but is eventually surpassed by the predators, that stay ahead for the rest of the simulation (fig. 4(b), for the dynamic on each region see fig. S6).

The increase in the predators and prey phenotypes in the first generations is very similar, displaying a classic arms race. However, after about 200 generations the evolution of the predator counter-defense is faster than the evolution of the prey toxin. Finally the prey's and predator's phenotypes stabilized at about 3.5 and 5, respectively (fig. 4(b), for the whole phenotype trajectory see fig. S7). It might seem intriguing that the predators are more resistent than needed, especially considering that they have an internal resistance of $R = 1$. This higher difference between the average phenotypes can be understood when the spatial character of the dynamics is taken into account (see below).



(a) Population abundance



(b) Mean phenotype

Figure 4: Temporal variation of predators (solid line) and prey (dashed line) on: (a) population abundance and (b) mean phenotype of all individuals of each group. On (b) the dotted line is the simulation without predators.

3.3. Geographic features and phenotype mismatches

The role of space in the dynamics is to promote local interactions between prey and predators, as opposed to random interactions obtained in mean field

models. The arms race, therefore, happens for all predators, but only for part of the prey. Because prey are much more abundant, groups of prey away from the predators will lower their toxin levels, increasing their reproductive rates. As a consequence, the mean phenotype value of the predator population is much greater than the prey phenotype (fig. 4(b) and fig. 5 green line). However, comparing the phenotype value of the predators only with the nearby prey, the difference becomes considerably smaller (fig. 5 red curve and black dots and fig. S8). A match between-defensive and counter defensive traits can be observed most of the time in most areas. When a mismatch occurred it was usually in favor of the predator but it would not last long, returning to matched values after a few generations. It can also be observed that the prey can be ahead in the arms race for very short periods.

The effect of the barrier was also important, as it decreased the available area leading to a decrease in the predator population (black dots on fig. 5). This, in turn, generated local extinctions in some regions (for instance region F around generation 250) and increased the fluctuations.

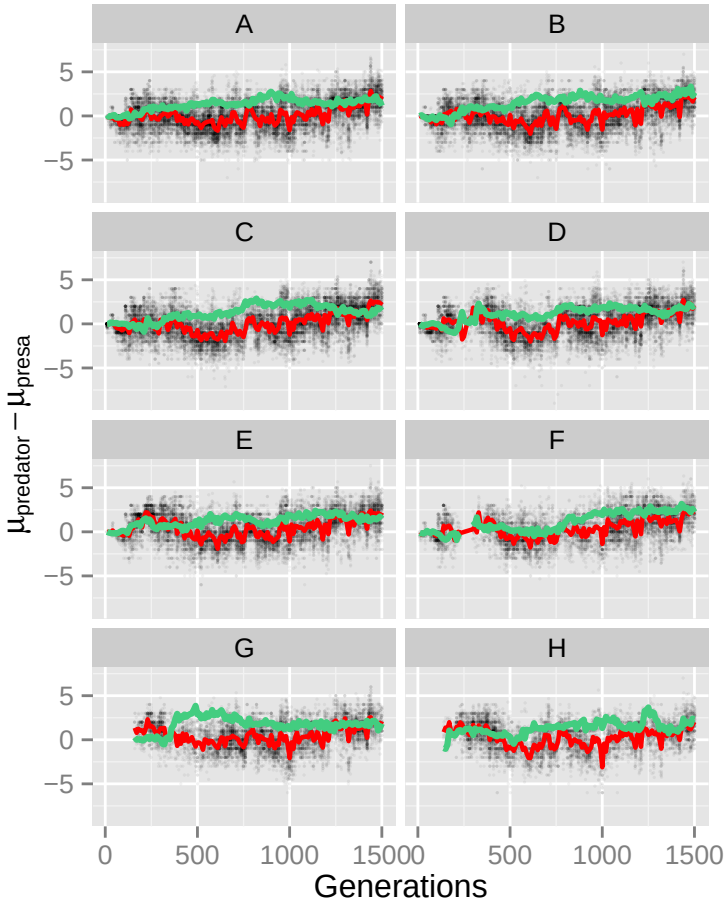


Figure 5: Difference of the predators phenotype and the mean of the prey, near them, over time for each region. The red line represents the mean value for each generation and the black dots are the values of the difference for each predator. The green line shows the average phenotype difference taking into account all prey in the each region.

4. Discussion

Coevolutionary predator-prey systems are known to display important space-time dynamics [25, 26, 12, 16], making comprehensive empirical studies difficult and challenging. In this context, mathematical models and simulations have proved useful to help understand the interplay between the many parameters of the system. Our model displayed qualitative features that were similar to the

natural system of *Taricha* newts and *Thamnophis* snakes [15, 16], on which it was inspired. In particular, we observed oscillatory dynamics of the phenotypes and populations of both groups, with local coevolutionary hotspots and places showing mismatches between the traits of predators and prey, characterizing an escape from the arms-race [25, 26, 12, 16].

The coexistence of predators and prey occurred only when the trade-off between the phenotype and reproduction rate was more costly to the prey than to the predator, showing a coevolutionary asymmetry. In our model this asymmetry was necessary to the stability of the system. This is consistent with observations in nature of higher selective pressure over the prey than on the predator [33, 10], indicating that systems where this trend is reversed are probably unstable, leading to the extinction of the predator or of both species [34].

One of the conditions for the stability of predator-prey system is that when the prey abundance is low, the selection acting on the prey to increase their abundance must be stronger than the selection on the predator to reduce it [34]. One way to achieve this condition is to have prey evolving faster than the predators [35]. In our model, the individual mutation rate for both groups is equal, but two effects combine in favor of the prey, namely, higher prey abundance and spatial distribution. Indeed, the larger prey population allows mutations to take place more often, increasing the mutation rate for the population. Moreover, part of the prey population is not in contact with predators all the time, allowing them to lower their defenses and increase their reproductive rates.

The simulations showed very clearly the escalation of the prey's phenotype generated by the presence of the predator. Natural selection acts in favor of more defensive prey than what would be expected in the absence of predators (fig. 4(b)). This phenotype escalation was also observed in other predator-prey systems, such as the predation of the Japanese camellia (*Camellia japonica*) by its seed predator, the camellia weevil (*Curculio camelia*) [11]. It was also observed in the escalation of toxicity of the European weed (*Pastinaca sativa*) on presence of the parnsnip webworm (*Depressaria pastinacella*) [36] and others [27, 37, 38].

Studies have shown that species interactions play a very important role in the organization of biodiversity [31, 39, 40] and that these interactions can vary depending on the local species composition [26, 41]. In our model the coevolutionary dynamic occurred on a local scale, showing spatial correlation in the defensive and counter-defensive traits, characteristic of antagonistic coevolution [36, 27, 11, 38]. However, the correlation between the phenotypes fluctuated, with the predator usually ahead in the arms race, but with short periods when the prey' phenotype was stronger. As counter intuitive as it may seem, the higher pressure on prey lead to stronger predators. This, however, seems to be in agreement with the life-dinner principle [33], which suggests that in a predator-prey arms-race the group that can afford to invest more, on defensive or counter-defensive traits, has the advantage over the other player. Therefore, the group that can invest more will surpass the threshold of the other, causing a reduction in its investment and leading to cycles in the arms race.

Our simulations indicate a complementary mechanism resulting explicitly from the local interactions. The coevolution of phenotypes seems to be the result of two combined factors: first, when prey become too toxic, so that the cost is higher than the benefit, they stop having a selective advantage over the less defensive ones. The predators, which invest more in counter-defenses, can still eat these prey and extinguishing their local population. In this sense the predators act as a "cleaners" for the prey' gene pool. The predators, on the other hand, do not have cleaners, so they keep their phenotype at high values. Patterns of phenotype mismatch similar to those observed in the simulations were found in empirical studies, both temporally [12] and spatially [16].

The second factor affecting phenotype coevolution is the local character of the interaction. If we compare the phenotype of the predators with the phenotype of their nearby prey (fig. 5, red curve), a significant decrease in the mismatch is observed when compared to global averages (fig. 5, green curve). This emphasizes that not all the prey are under the predators' pressure, and that part of the prey population can escape this coevolutionary dynamic by some periods of time [26, 16]. This characteristic creates a pool of low defen-

sive and highly reproductive prey that can recolonize depleted areas very fast, keeping the average prey phenotype low.

Costs for toxin production and defense play a key role in the dynamics. When costs are eliminated two important effects take place: first, an escalation of both prey and predator phenotypes. Second, the subpopulations of prey that temporarily escape the predator's coevolutionary pressure no longer have an advantage over the highly toxic ones and the prey that have a high phenotype, near the predators, are selected. This leads to an increase in the average phenotype of the prey, causing the local mismatch to flip in favor of the prey, which represents a situation not found in real populations.

The size of available space is also an important factor, as can be inferred by the barrier at the lower part of the simulated area. The barrier acted as a constraint for the individuals, increasing their isolation and decreasing the predator population, making these regions more prone to stochasticity and fluctuations on abundances and local extinctions [42].

Our results show that computer models have the potential to contribute to the understanding of coevolutionary processes of predator-prey systems. Other important aspects of the problem, such as speciation of one or both species, can also be explored with simple extensions of the present model.

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Video caption

simpop.avi Simulation of the predator (red dots) and prey (blue dots) population. The strength of the color represent the value of counter-defensive and defensive phenotypes of predator and prey, respectively, the darker higher value of the phenotypes.

simreprphen.avi Representation of the mean difference of the predators and prey phenotypes on each region. The strength of the color represent higher deviation from one group. Red means higher values of predators phenotypes and blue higher values of prey phenotypes.