

Computer simulations of sympatric speciation in a simple food web

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Galapagos finches, have motivated much theoretical research aimed at understanding the processes associated with the formation of the species. Inspired by them, in this paper we investigate the process of sympatric speciation in a simple food web model. For that we modify the individual-based Penna model that has been widely used to study aging as well as other evolutionary processes. Initially, our web consists of a primary food source and a single herbivore species that feeds on this resource. Subsequently we introduce a predator that feeds on the herbivore. In both instances we manipulate directly a basal resource distribution and monitor the changes in the populations. Sympatric speciation is obtained for the top species in both cases, and our results suggest that the speciation velocity depends on how far up, in the food chain, the focus population is feeding. Simulations are done with three different sexual imprintinglike mechanisms, in order to discuss adaptation by natural selection.

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I. INTRODUCTION**A. Observations and measurements in nature**

Darwin Finches are a classical living example of evolution in action. They form a group of 13 finch species of the Galapagos Islands [1]. The beaks of each species are apparently specifically adapted to feed on a precise food type, running from seeds and cactus flowers to buds or insects. It is supposed that natural selection drove, and is indeed still driving, the beak morphology of each finch species. Detailed analyses of these birds have revealed that the changes in beak morphology can occur very quickly, even within the course of a single season [2].

The sexual imprintinglike mechanism is apparently ubiquitous in Darwin's finches and is present in some form in species of all orders of birds examined so far [3,4]. It has been shown that, as a consequence of beak evolution, there have been changes in the structure of finch vocal signals [5]. Patterns of correlated evolution among morphology and song are consistent with the hypothesis that beak morphology constrains vocal evolution. Different beak morphologies differentially limit a bird's ability to modulate vocal tract configurations during song production. Data [6,7] illustrate how morphological adaptation may drive signal evolution and reproductive isolation, and furthermore identify a possible cause for rapid speciation in Darwin's finches.

B. Theory

Traditionally, two main classes of models are used to explain speciation [8,9]. Allopatric speciation models assume

that the initial population is suddenly divided into two geographically separate subpopulations, which then diverge genetically until they become reproductively isolated. Sympatric speciation corresponds to the division of a single local population into two or more species without any geographical barrier. Here, we use a modified version of the Penna model to examine this process [10]. The model assumes that competition for resource and sexual selection are the dominant forces acting on the population.

II. MODEL DESCRIPTION**A. The original Penna model**

The Penna model is based entirely on Darwinian evolution. Originally focused on problems of biological aging, applications to several different evolutionary problems substantially increased its scope [11,12]. In the sexual version of the original Penna model, each individual is represented by an age-structured pair of bit-strings of 32 bits each, that are read in parallel. Each bit position corresponds to a period, say year, in the individual lifetime. In this way, each individual can live at most for 32 years. Deleterious mutations are represented by bits 1. If at a specific bit position, one of the two bit-strings has a bit zero and the other has a bit one, it affects the health of that individual if and only if this position is one for which the harmful allele (bit 1) is dominant. If the current number of deleterious mutations reaches some threshold T , the individual dies. If a female succeeds in surviving until the minimum reproduction age R , it chooses randomly a male with age R or above to mate with and produces b offspring, each having one of the father's gametes and one of the mother's gametes as its two bit-strings. The gametes (single bit-strings) are produced by random crossover and

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recombination of each bit-string pair, followed by one random mutation. The offsprings' sex is fixed randomly. There is also a competition for space and food given by the logistic Verhulst factor, which may kill the individual independently of its age or genome, and that prevents the exponential increase of the population. This completely random killing factor, present in the original Penna model, is going to be modified, as explained in the next section. The complete Fortran program of the original model is listed in Ref. [11].

B. Speciation model

In the first simulations using the Penna model to obtain sympatric speciation [13–15] it has been considered that competition for resources changes according to the ecology. In the present model the competition does not change, and fitness and mate choice depend on the same trait, that is, the beak morphology. This trait is represented by a new pair of nonage structured bit-strings, added to the original structured one, which suffers the same process of crossing and recombination described above. The phenotypic characteristic is measured by counting, in this new pair of bit-strings, the number of recessive bit positions (chosen as 16), where both bits are set to 1, plus the number of dominant positions with at least one of the two bits set. It will therefore be a number k between 0 and 32. We call M_F the mutation probability per locus of this trait.

The death probability by intraspecific competition, for extremal phenotype, is given by the following modified Verhulst factor:

$$V_{1(2)}(k, t) = \frac{P_{1(2)}(k, t) + P_m(k, t)}{F(k, t)}, \quad (1)$$

where $P_{1(2)}(t)$ accounts for the population with phenotype $k < 16$ ($k > 16$), respectively, and P_m accounts for the population with phenotype $k=16$, and $F(k, t)$ is the carrying capacity of the environment as seen by each individual, since it depends on the number k . The Verhulst factor for intermediate (m) phenotype is

$$V_m(k, t) = \frac{P_m(k, t) + 0.5[P_1(k, t) + P_2(k, t)]}{F(k, t)}. \quad (2)$$

At every time step, and for each individual, a random number is generated; if this number is smaller than V , the individual dies. In both cases presented in the next section, $F(k, t)$ is the basal resource species of a food chain. It may, for instance, represent plants with a given size distribution. Individuals with extremal phenotype (P_1, P_2) compete for small/large plants among the individuals with its same extremal phenotype, and also with the whole intermediate population [Eq. (1)]. Individuals with intermediate phenotype (P_m) compete among themselves and also with half of each population presenting an extremal phenotype [Eq. (2)].

Finally, we refer to mating selectiveness, we introduce into each genome a locus that codes for this selectiveness, also obeying the general rules of the Penna model for genetic heritage and mutation. If it is set to 0, the individual is not selective in mating (panmictic mating). It is selective (assor-

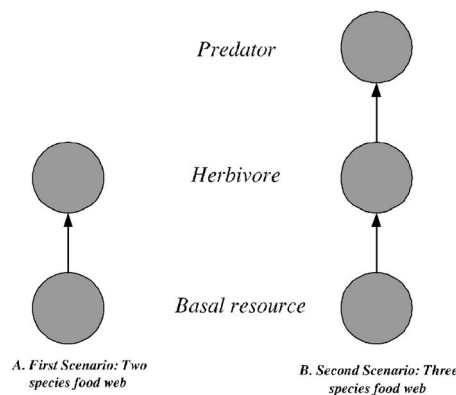


FIG. 1. The two different simple food web scenarios explored in this paper; we study the sympatric speciation for the top species of each food web.

tative mating) if this locus is set to 1. At the beginning of the simulations all females are nonselective. The mutation probability for this locus is set to 0.001 in both directions ($0 \rightarrow 1$ and $1 \rightarrow 0$). Females that are selective choose mating partners according to one of the following mating strategies:

Mating strategy 1: If a female has phenotype $k < 16$ (≥ 16) it mates with the first randomly chosen male that has its same phenotype $k < 16$ (≥ 16).

Mating strategy 2: In this case a female chooses, among six males, the one with the smallest difference between its phenotype k_F and the male's phenotype k_M .

Mate strategy 3: The mating of a pair occurs with probability $P=(k_F-k_M)/32$, where k_F is the female phenotype and k_M is the male phenotype. The female tries to mate for at most six times; if it does not find a proper male, than it mates randomly.

III. RESULTS AND DISCUSSION

A. Two species food web

In our first scenario we have a two species food web with a basal resource and a consumer that feeds on this resource (Fig. 1). Here, the consumer (herbivore) has genetic properties and evolves for 250 generations with a constant food distribution, called *Before* in Eq. (3). Suppose for instance, that during a given season this food distribution consists of plants which sizes favor the individuals of the second species presenting medium phenotypes. Suddenly, due to a new different rainfall regime, the first species distribution changes into a bimodal one, now favoring herbivores with extremal phenotypes:

$$F(k, t) = 2 \times 10^5 \begin{cases} 1.0 - \frac{|16 - k|}{20.0} & \text{Before} \\ 0.1 + \frac{|16 - k|}{20.0} & \text{After.} \end{cases} \quad (3)$$

For the mating strategies 1 and 2 the second species phenotypic distributions are the same, shown in Fig. 2(a). This is an interesting result since for strategy 1 the female knows the drift direction of the ecological change and it is easy to un-

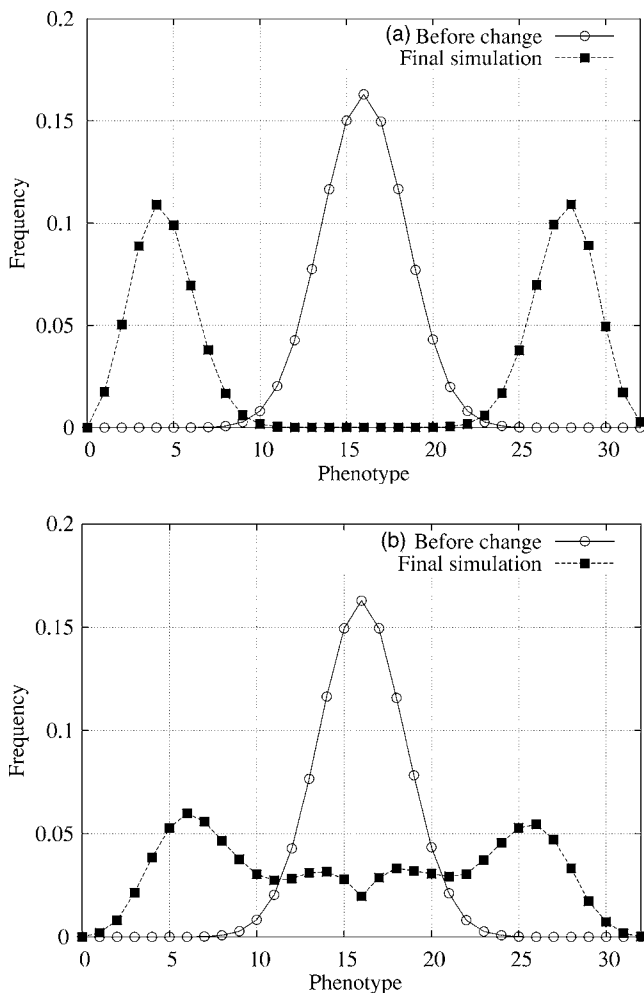


FIG. 2. Phenotype distributions of the herbivores in the first food web scenario, before and after the sudden change of the basal resource species distribution. (a) For mating strategy 1 or 2 and (b) for mating strategy 3. Parameters: $T=10$, $b=2$, $M_F=0.5$, and $R=10$.

derstand why the final population presents two substantially different phenotypes and how reproductive isolation between them has driven the elimination of all intermediate phenotypes. Females with mating strategy 2 do not know this direction and, even so, the ecological change drives their preferences in the same way as with choice 1.

For the mating strategy 3, Fig. 2(b), there is no correlation between ecological changes and female preferences, and the intermediate phenotypes are not totally eliminated. However, this strategy is more realistic than strategy 2, since the female's preference is subject to the males availability.

B. Three species food web

The consumer (a predator) feeds solely on the herbivore and has genetic properties. The herbivore also has genetic properties, but no mating preference, and evolves for 250 generations with the same initial basal resource distribution of the first food web scenario [Eq. (3)]. Now, when the basal resource distribution suddenly changes, the phenotype distri-

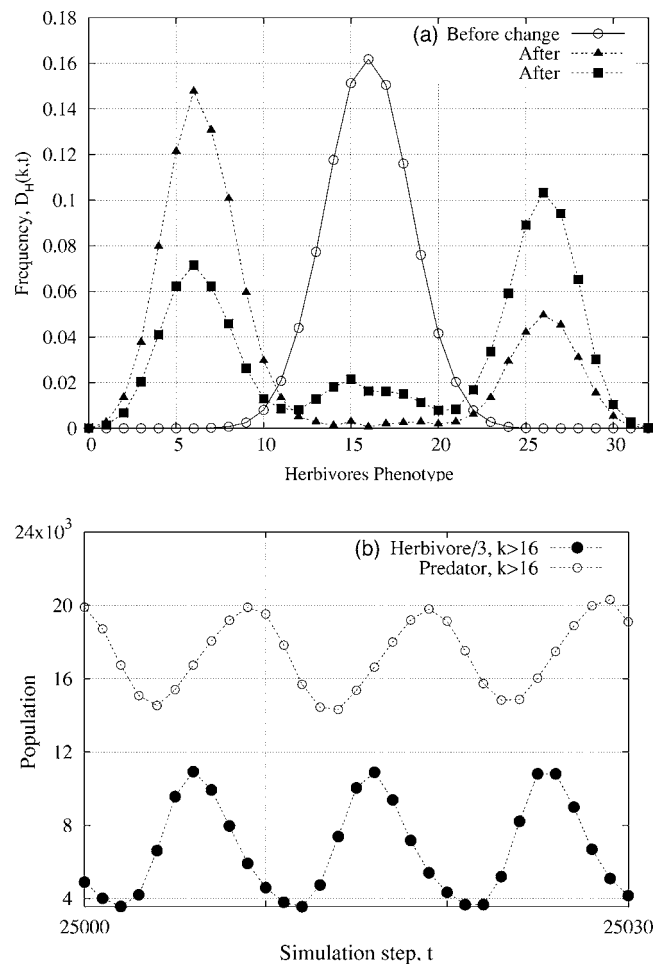


FIG. 3. Second food web scenario. (a) Phenotype distribution of the herbivores; there is no sexual selection for this species and its corresponding parameters are: $T=1$, $b=10$, $M_F=0.8$, and $R=9$. (b) Oscillations of the populations with extremal phenotypes after the ecological change: open circles for predators and filled circles for herbivores. Notice that the amplitude of the herbivores oscillations is divided by three in the figure. Notice also that there is a phase difference of three time steps between them.

bution of the herbivores, as a consequence, also changes [Fig. 3(a)]. In this figure the initial distribution represented by circles is stationary but those represented by squares and triangles are not; sometimes there are more individuals with one of the extremal phenotypes than the other—see the oscillations in Fig. 3(b), filled circles. This oscillatory polymorphism depends on the initial random seed as well as on the value of M_F .

Also, this polymorphism can be stable or unstable; in the latter case, the distribution may oscillate during a huge number of time steps and finally decay into a unimodal distribution (no polymorphism). The stable oscillatory polymorphism appears more frequently for small values of M_F , see Table I. The reason is that the higher the value of M_F , the larger the fluctuations in the phenotypes of the populations. The period of the stable oscillations is equal to the minimum reproduction age, R . Notice that the age zero is also counted.

In the first scenario (only two species) the sympatric speciation for the herbivores (top species) is always obtained. In

TABLE I. Results of 10 simulations (different initial random seeds) for different phenotype mutations, after the ecological change. Unimodal distribution corresponds to the case where no polymorphism occurred, the distribution is a Gaussian peaked at $k = 16$; Unstable distribution corresponds to the case where the distribution stays bimodal for a long time before decaying into a unimodal one.

M_F	Maxima of bimodal distributions	Phenotype distributions
0.8	6 and 26	2 bimodal, 7 unimodal, and 1 unstable
0.5	4 and 28	3 bimodal and 8 unimodal
0.1	1 and 31	10 bimodal
0.01	0 and 32	10 bimodal

this second scenario, however, speciation is not always obtained for the predators (top species). For them to speciate, Fig. 4(a), it is necessary to obtain the herbivores' polymorphism, but not sufficient; even for small values of the predators M_F (e.g., 0.01), this oscillatory behavior of the herbivores polymorphism produces extra fluctuations in the predators populations.

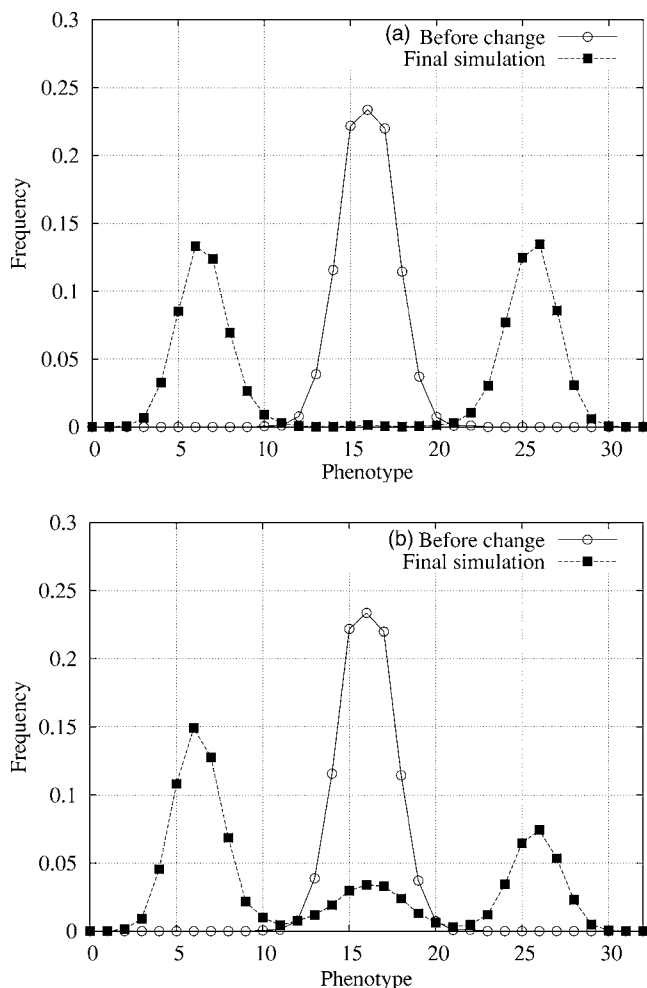


FIG. 4. Second food web scenario; Phenotype distributions for the predators, (a) using mating strategies 1 or 2 and (b) using mating strategy 3. Parameters: $T=10$, $b=2$, $M_F=0.5$, and $R=10$.

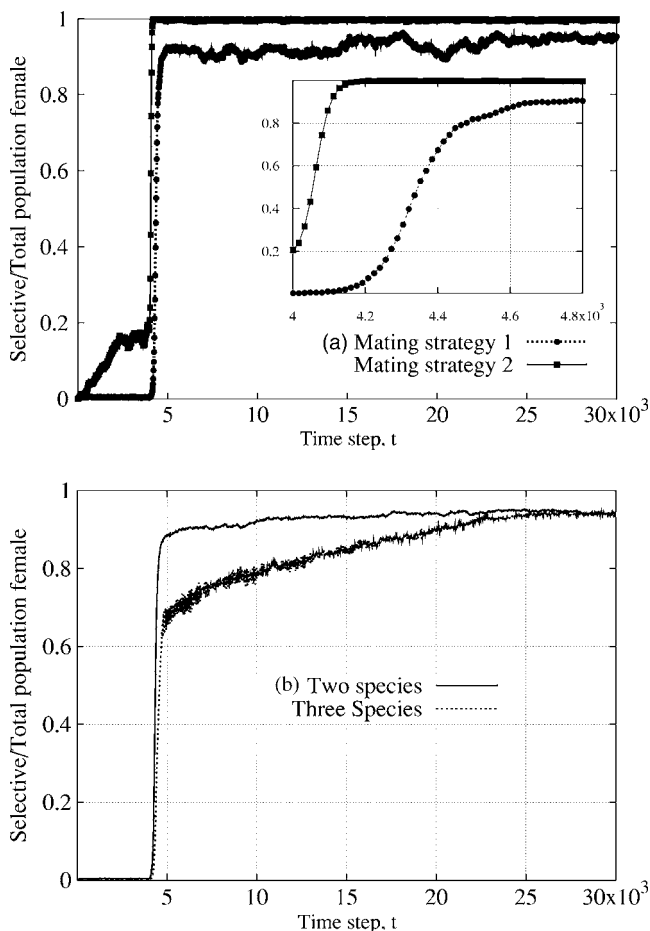


FIG. 5. Comparison between the fractions of selective females. (a) First food web scenario using different sexual imprints. (b) Comparison between speciation velocities for the two different food chains, using mating strategy 1. The fraction of selective females increases faster for the first than for the second scenario.

When speciation occurs, the populations of the new sympatric species, the predators with $k < 16$ and $k > 16$, oscillate with the same frequency as the herbivores, see Fig. 3(b), open circles. However, the amplitude of these oscillations is small if compared to the herbivores, which makes the phenotype distribution of the predators, shown in Fig. 4(a), filled square, to remain stationary. In this case the phase difference of 3 steps between the herbivores and predators oscillations does not change, even for different values of the parameters of the model.

The most important difference between the two food chains is the speciation velocity, measured through the time evolution of the fraction of selective individuals in the populations. Figure 5 shows that intermediate phenotypes disappear faster in the two species food chain than in the three species. We may conclude that higher level consumers take longer to speciate when the distribution of the basal resource is altered.

IV. CONCLUSIONS

We present an individual-based model to investigate the sympatric speciation process in food webs of two and three

species. The genomes of the individuals are represented by two pairs of bit-string, one of them related to genetic diseases and age-structured, and the other related to a phenotypic characteristic, as for instance, the beak morphology. Competition among individuals depends on their phenotypes, as well as their mating preferences.

We obtain a disruptive selection, followed by reproductive isolation driven by sexual selection in both food webs. Comparing the results for two and three species food webs we conclude that higher level consumers take longer to speciate when the distribution of the basal resource changes abruptly. A process of speciation that possibly fits into our model and respective results is the one that has occurred with one of the three lineages of the Darwin's finches, named the tree finches. There are six species in this group; all of them,

except the vegetarian finch, *P. crassirostris*, are insect eaters. Inside this lineage, according to analysis made in mitochondrial DNA sequences [9], the vegetarian finch diverged from the ancestral stock before the divergence of the rest of the tree finch group.

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