Sympatric Speciation in a Simple Food Web

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Abstract: Observations of the evolution of species groups in nature, such as well recognized Galapagos finches, have motivated much theoretical research aimed at understanding the processes associated with such radiations. The Penna model is one such model and has been widely used to study aging. In this paper we use the basic Penna model to investigate the process of sympatric speciation in a simple food web model. 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 directly manipulate the food source, that is, its size distribution, and monitor the changes in the populations structures. Sympatric speciation is obtained for the consumer species in both webs, and our results confirm 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 imprinting-like mechanisms, in order to discuss adaptation by natural selection.

Introduction

According to classical theories of speciation, mating signals diversify, in part, as an incidental byproduct of adaptation by natural selection to divergent ecologies [1]. Nevertheless empirical evidence in support of this hypothesis is limited [2, 3, 4] and is a matter of controversy [5].

A. Observations and Measurements in Nature

A great living example of evolution in action are Darwin’s Finches, a group of 13 finch species of
the Galapagos Islands. The beaks of each species is 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 analysis of these birds have revealed that the changes in beak morphology can occur very quickly, even within the course of a single season.

The sexual imprinting-like mechanism is apparently ubiquitous in Darwin’s finches and is present in some form species of all orders of birds examined so far. Song is a culturally transmitted trait learned during a short sensitive period early in finch’s life, and later used in courtship and mate choice. Males typically sing a simple, short song, and retain it unaltered throughout life. Females do not sing but do learn songs that are later used in mate choice of hybridizing birds and of the hybrids themselves. It has been shown that as a consequence of beak evolution there have been changes in the structure of finch vocal signals (Podos).

The diversification of beak morphology and body size of the finches has shaped patterns of vocal signal evolution, such birds with large beaks and body sizes have evolved songs with comparatively low rates of syllable repetition and narrow frequency bandwidths. 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 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. Allopatric speciation models assume that the initial population is suddenly divided into two geographically isolated subpopulations, which then diverge genetically until they become reproductively isolated. However many migratory birds do not seem to fit the basic requirement of long periods of geographical isolation needed for allopatric speciation, which led to the proposal of a sympatric speciation mechanism. Sympatric speciation corresponds to the division of a single local population into two or more species. Understanding how sympatric speciation can be driven has thus attracted much theoretical effort.

According to Darwin, sympatric speciation is driven by disruptive, frequency-dependent
natural selection caused by competition for diverse resources. Recently several authors have argued that disruptive sexual selection can also cause sympatric speciation. Here, we use the Penna model to examine this process [14]. The model assumes that competition for resource and sexual selection are the dominant forces acting on the population. We explore sympatric speciation within simple food webs with different sexual imprinting-like mechanisms.

Model description
The Penna model for biological aging is based entirely on Darwinian evolution and mutations. Originally focused on problems of biological aging, applications to several different evolutionary problems substantially increased its scope [15].

A. Penna Model
In the sexual version of the Penna model used here, each individual has two bitstrings inherited from mother and father, respectively. Gametes (single bitstrings) are produced by random crossover between these two bitstrings, followed by one random mutation. Each female of age ten or above tries many times to find randomly a male aged ten or above for mating, and if she succeeds she gets two offspring, having one of the father’s gametes and one of the mother’s gametes as its two bitstrings. The offspring’s sex is fixed randomly. If at a specific bit position, one of the two bitstrings 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. Ten out of the 32 possible positions are randomly selected as dominant, the remaining 22 as recessive. There is a competition for space and food given by the logistic Verhulst factor. The complete Fortran program is listed in [16].

B. Speciation Model
In the first simulations using the Penna model with phenotype to get sympatric speciation [17, 18] it has been considered that competition for resources changes according to the ecology. In our model the competition does not change, and fitness and mate choice depend on the same trait. A new pair of non-age structured bitstrings is added to the original one, to represent the individual’s phenotype. The phenotypic characteristic is measured by counting the number of recessive bit positions (choosen 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. The mutation probability per locus of this phenotype is set to 0.5 in all simulations.

The death probability by intraspecific competition, for extremal phenotypes, is given by:

$$V_{<(<)(>)}(t) = \frac{pop_{<(<)(>)} + pop_m}{(Capacity * SourceD(k))}$$  \hspace{1cm} (1)

where $pop_{<(<)(>)}(t)$ accounts for the population with phenotype $k < 16$ and $k > 16$, respectively.

The Verhulst factor for intermediate ($m$) phenotypes is:

$$V_m(t) = \frac{pop_m + (pop_{<} + pop_{>}) * 0.5}{(Capacity * SourceD(k))}$$  \hspace{1cm} (2)

$Capacity * SourceD(k)$ is the carrying capacity of the environment as seen by each individual, since it depends on the number $k$. 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, $SourceD(k)$ is the first species of a chain food. It may, for instance, represent plants with a given size distribution. Individuals with extremal phenotypes ($pop_{<}$, $pop_{>}$) 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 phenotypes ($pop_m$) compete among themselves and also with half of each population presenting an extremal phenotype (eq. 2).

Finally we refer to mating selectiveness, where 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 (assortative mating) if this locus is set to 1. At the beginning of the simulations all females are non-selective. The mutation probability for this locus is set to 0.001. Females that are selective choose mating partners according to one of the following mating strategies.

*Mating strategy 1*

If a female has phenotype $k < 16(\geq 16)$ it prefers a male with phenotype $k < 16(\geq 16)$. This sexual imprinting-like mechanism is ubiquitous in female.

*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 \( (k_F - k_M)/32 \), where \( k_F \) is the female phenotype and \( k_M \) is the male phenotype.

Results and Discussion

A. Two species food web
Here the consumer (a herbivore) has genetical properties and evolves for 250 generations with a constant food distribution, which is the first species. 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 individuals with extremal phenotypes:

\[
SourceD(k) = \begin{cases} 
1.0 - \frac{|16 - k|}{20.0} & \text{Before} \\
0.1 + \frac{|16 - k|}{20.0} & \text{After} 
\end{cases}
\]  

(3)

For the mating strategies 1 and 2 the second species phenotypic distributions are the same, left part of fig[1]. This is an interesting result since in strategy 1 the female knows the drift direction of the ecology and it is easy to understand why the 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 ecology is driving their preferences in the same way as with choice 1.

For the mating strategy 3 (right part of fig[1]) 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.

A. Three species food web
The consumer (a predator) feeds solely on the herbivore and has genetical properties. The herbivore also has genetical properties, but no mating preference, and evolves for 250 generations with a given food distribution - the first species (which consists of the same plants of the previous case). Now, when the first species distribution suddenly changes, the phenotypic
FIG. 1: Phenotypic distributions of the second species, in a food chain of two species, for mating strategy 1 or 2 (left part) and for mating strategy 3 (right part), before and after the sudden change of the first species distribution.

FIG. 2: Phenotypic distribution of the second species in a food chain of three species; there is no sexual selection for this species.

distribution of the second species, as a consequence, also changes - fig 2. In this figure the red distribution is stable but the blue one is not and sometimes there are more individuals with one of the extremal phenotypes than the other.

The effects of the different mating strategies for this food chain are the same as those of the previous one - fig 3.

The most important difference between the two food chains is the speciation velocity, mea-
FIG. 3: Third species phenotypic distributions for mating strategies 1 or 2 (left part) and mating strategy 3 (right part).

Sured through the time evolution of the fraction of selective individuals in the populations. Fig. 4 shows that intermediate phenotypes disappear faster in the two species food chain than in the three species one.

FIG. 4: Comparison between fractions of selective individuals using mating strategy 1, for the two different food chains.

Another difference is in the variance of the distributions per phenotype of the two chains (left parts of figs. 1 and 3). The red and blue distributions for the two species chain present a larger variance than the equivalent ones for the three species chain. Also the mean phenotypes after speciation (blue distributions) in the two species chain are at 4 and 28, while in the three
species case, at 6 and 26. It means that the mean difference between extremal phenotypes for the two species chain is smaller than for three species one.

These results are limited to be compared with those from real finches observations, not only because we are using a toy model but mainly because natural evolution is a too complicated process!!.

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