Impact of Inheritance Methods on Synthetic Sympatric Speciation

Abstract

Speciation, the process at the heart of evolutionary biology, has been a topic of intense scientific study for centuries. Understanding its finer points is critical to understanding the evolution of life on this planet and predicting how it may continue to change and develop over time. The introduction of genetic algorithms in artificial intelligence applications has raised further interest in the field, as a better understanding of speciation may enable us to create more robust programs for confronting difficult problems.

Thankfully, we now have computer simulations that can model large populations which enables us to better understand the finer details of speciation. However, no simulation is perfect; any real-world phenomenon must be simplified before it can be modeled, and these simplifications have the potential to reduce the accuracy of the simulation. This paper seeks to identify and address one such oversimplification in the paper Sexual Selection, Resource Distribution, and Population Size in Synthetic Sympatric Speciation by Mark Woehrer and demonstrate how the use of non-destructive inheritance is critical to maintaining genetic diversity in an evolving population.

Background

In evolutionary biology, there are two distinct types of speciation: allopatric speciation, where isolated populations acquire new traits independently, and sympatric speciation, where a single population diverges over time. Of the two types, allopatric speciation is better understood. Intuitively, it makes sense that isolated groups would evolve different traits over time. Sympatric speciation, on the other hand, has proven to be a more challenging issue to tackle. In sympatric speciation, a single population splits into multiple species despite potential resource competition and interbreeding. We have no way of telling when a population may undergo sympatric speciation, largely because the mechanisms behind the process are not well understood.

In the *Speciation* paper, the researchers hypothesized that sexual selection may be key to inducing sympatric speciation in a population. They hypothesized that sexual selection may reproductively isolate sub-groups within the population, which could then evolve different traits in a similar manner to allotropic speciation. To test this hypothesis, the researchers set up a 2x2 factorial study using a simulated population of finches. In the study, the researches created two different distributions of seeds, bimodal and uniform, and observed the differences in population dynamics between finches that utilized sexual selection and those that did not.

The most startling conclusion to come from this experiment was that given a bimodal seed distribution, a population that utilized sexual selection would diverge to cover all available niches while a population that mated randomly would converge to cover only one. This result goes against conventional wisdom, as any species is highly incentivized to take advantage of all available niches in its environment. The convergence exhibited in the bimodal seed random mating scenario is known as bottlenecking, and typically only occurs in small, declining populations. To see bottlenecking occurring in a large, healthy population

suggests that there may be a lurking oversimplification in the simulation.

Hypothesis

The cause for the population convergence in the bimodal seed random mating simulation was due to the oversimplification of genetic inheritance. Averaging the beak sizes of the parents inhibits a population's ability to maintain genetic diversity, which leads to population collapse in multiniche environments.

Overview

This research consisted of three steps: the replication of the initial experiment, the introduction of a genetic structure, and the introduction of meiotic inheritance.

First, we recreated the simulation from the *Speciation* paper to the best of our ability. To check that this attempt was successful, we attempted to replicate the experimental results from the *Speciation* paper.

Second, we introduced an inheritance model that better represents genetics in the natural world. The rules of genetic inheritance were amended so that the offspring's beak size was still an average of the parents' beak size. This step serves as a control study, allowing us to conclude that the changes in the third stage's results were due to the introduction of meiotic inheritance, rather than the introduction of the new genetic structure.

Third, we replaced the averaging method of inheritance with biologically accurate meiotic inheritance and observed the change in population dynamics from the first two experiments.

Methods - Experimental Replication

The initial simulation is designed to replicate the simulation from the *Speciation* paper. The details of this simulation are summarized in the following paragraphs. For a more in-depth analysis on the reasoning behind the choices made, please consult the original paper.

The simulation consists of an island 100x100 units in size, filled with seeds and inhabited by a population of finches. Each finch has a known beak size, age, gender, energy-level, and location. Each seed has a known size, energy-level and location.

The simulation begins by generating 400 finches with a roughly equal number of males and females. This initial population has a mean beak size of 5.5 and a variance of 0.5 (gaussian distribution). These finches have their energy level set to zero and are randomly spread around the island. The island then undergoes an annual cycle consisting of a dry season and a mating season. This cycle repeats 1000 times during the simulation.

The dry season lasts 100 days, and begins by spreading 5000 seeds randomly around the island. Each day, each bird has a chance to forage for food. The foraging is performed in a random order. Each bird searches a 10x10 plot of the island and consumes the first seed it finds that falls within one unit of its beak size. This search costs the finch 0.1 units of energy. Any finch that has less than zero units of energy at the end of the day is declared dead and removed from the population.

The simulation accounts for two different distributions of seed sizes: bimodal and uniform. The bimodal distribution consists of two gaussian distributions of 2500 seeds each; these distributions are centered at three and

eight units, each with a variance of 0.5 units. The uniform distribution consists of a single uniform distribution of 5000 seeds ranging from one to ten units in size. In both scenarios, a seed contains between zero and two units of energy (uniform distribution).

After the dry season ends, the remaining finches participate in that year's mating season. During the mating season, each female chooses a single male to mate with. The simulation accounts for two types of mating: random mating, where females will choose any male from the population, and assorted mating, where females will only pick males within one unit of its beak size. Each male is only allowed to mate with five females per year. When presented with multiple possible mates, the female will choose between them at random. Mating produces a single offspring at the location of the mother. The child's beak size is an average of the beak sizes of the parents plus a small gaussian-random mutation (Mean 0, Variance 0.2).

Methods - Introduction of Genetic Structure

The objective of this step is to replace the simplistic inheritance structure with a more robust genetic model while still maintaining the same inheritance process. This step serves as a control study to demonstrate that the changes in the third experiment are a result of the introduction of meiotic inheritance rather than the introduction of the new genetic structure. The mechanics for this genetic structure are as follows.

Each finch is equipped with two sets of genes, one from each parent. Each gene contains an array of one-hundred sub-genes, each represented by a floating point value. The phenotype for the gene is determined by taking the sum of all of the sub-genes. In order to mimic the *Speciation* paper's initial population, the sub-genes in the initial population are randomly chosen from a uniform distribution with a mean of 0.055 and a range of 0.27.

For this experiment, a single gene was used to determine the beak size of the individual. This choice reflects how a single gene, Bmp4, is responsible for most of the variation in beak sizes in real darwinian finches. The finch's beak size is determined by averaging the phenotype of both copies of the simulated Bmp4 gene. This process closely mimics a gene exhibiting incomplete dominance. We also modeled complete dominance by assigning the child the larger of the two phenotypes, and achieved nearly identical results. (Add Appendix)

When mating, the sub-genes of each parent are averaged to determine the sub-genes for the child. Because the beak-size of an individual is determined by averaging the sums of the sub-genes, the child's beak size is always an average of the beak-sizes of its parents. In other words, the phenotype of the gene from each parent is the same as the beak-size of that parent. This approach preserves the original inheritance method in the new genetic structure. To account for the mutation, each sub-gene has a 0.2% chance to randomly change after the averaging process. This value is picked from a uniform distribution with a mean of 0.055 and a range of three.

Methods - Introduction of Meiotic Inheritance

The setup for the third step is nearly identical to that of the second; the only change is the addition of meiotic inheritance. During mating, rather than average the sub-genes of the parent to create a new gene, the child receives a

randomly selected gene from each of its parents. The mutation rate and range remains the same as in the previous step.

Results

The results of this experiment are visualized as a series of population trees. These trees were generated by graphing each individual with respect to its beak-size and generation. The result is a branching structure consisting of a number of population bands, representing how a population is changing as a result of evolutionary pressures.

Control Group

In the first two simulations, we expected that each of our outputs would closely mimic the results of the initial speciation experiment. A graphical comparison of these results is exhibited in figures !!!a-!!!d.

BSAM: Within twenty-five years, the population splits to cover both available niches, centering around beak sizes 3.0 and 8.0. After splitting, both bands are approximately two units in width.

USAM: The population exhibits a seemingly random branching behavior, where each branch is a band about two units in width. Approximately every two-hundred years a branch will split into two separate populations, one tending towards larger beak sizes and one towards smaller beak sizes. Branches go extinct at the same rate as which they spawn.

BSRM: Within twenty-five years, the population converges to cover a single niche of either beak-size 3.0 or beak-size 8.0. The population band is approximately two units in width

USRM: The population is contained within a single band approximately two units in width. This band exhibits up to two units of lateral variation over time.

Experimental Group

In the final simulation, we replaced the previous inheritance system with simulated meiotic inheritance. The results of this experiment are exhibited in figures !!!a-!!!d.

Bimodal Distributions: Both bimodal distributions exhibit nearly identical behavior. Both populations quickly diverge into two large bands approximately four units in size, centered around beak sizes 3.0 and 8.0.

Uniform Distributions: Both uniform distributions exhibit nearly identical behavior. Both populations are contained within a single large band approximately nine units in size, centered around beak-size 5.0.

Analysis

In the first experiment, we were successful in replicating the results from the *Speciation* paper. All four of the population trees from our experiment matched those from the initial paper. Furthermore, in the second experiment we demonstrated that the introduction of the genetic structure had no major impact on population dynamics. This result was as expected, as the inheritance method was designed to replicate the averaging method as closely as possible.

In the third experiment, we used the same genetic structure as the second experiment with the addition of

meiotic inheritance. This addition radically changed the result of the simulation. Rather than collapsing into narrow bands, each population rapidly expanded to cover the entire range of seed sizes. The extremely thick bands observed in this experiment indicates that the population exhibited an extremely high level of genetic variation. Furthermore, in both the bimodal and uniform seed distributions, there is no discernible difference in population dynamics between sexual selection and random mating.

This observation is notable as it seems to directly contradict the results from the initial *Speciation* paper, where the researchers demonstrated that sympatric speciation was a requisite for sympatric speciation. The key to this discrepancy lies in the mechanism by which genes are passed on to the next generation.

In the original experiment, the researchers chose to average the beak-sizes of the parents to determine the beak-size of the child. While seemingly harmless, this approach actually destroys important genetic diversity in the population. Barring mutation, any child produced using this method must have a beak-size between the beak-sizes of its parents. When scaled up, this effect causes each generation to cover a smaller range of beak-sizes than the generation that proceeded it. This process eventually causes the species to coalesce around a single beak-size: population convergence. As the inheritance method pushed the population inwards, the high mutation rate pushed the population outwards, creating a natural-looking population affected by vastly different forces than a biological population.

This difference is responsible for the change in results between the two experiments. The two-unit thick bands represent the equilibrium point between the inheritance method's pressure to converge and the mutation rate's pressure to diverge. By introducing meiotic inheritance in the third experiment, we removed the pressure towards convergence, allowing the population to diverge to cover the entire range of seed sizes. Meiotic populations do not converge because meiotic inheritance is non-destructive. By passing on genes unaltered, meiosis protects the information that encodes for the fringes of the population. There is no guarantee that a child's beak-size will fall between those of its parents, so these unaltered genes can re-exert themselves in future generations.

As may be expected, real-world, biological populations behave far more like the populations in the meiotic inheritance experiment than the populations in the initial experiment. All the divergent pressure in the initial experiment came from mutation, yet mutation is extremely rare in the natural world. In fact, the mutation rate in mammals is as low as 2.2e-9 mutations per base pair per year [1]. Regardless, we still see large amounts of genetic diversity within a single species, and biologically, it is not uncommon for a child to exhibit a more extreme trait than either of its parents.

Conclusion

This experiment demonstrates the paramount importance of inheritance methods in biological simulations and genetic algorithms. A slight change in a population's inheritance mechanism can radically alter the population dynamics, due to the potential introduction of strong evolutionary pressures. For biological simulations, the inheritance process should mimic meiotic inheritance as closely as possible to avoid potential inaccuracy. However,

for artificial intelligence purposes, both inheritance methods may have merit.

The radically different behaviors between the populations with and without meiotic inheritance suggest a potential mechanism to improve the efficiency of certain artificial intelligence programs. One of the initial purposes of the *Speciation* research was to examine how to induce sympatric speciation in order to enable genetic algorithms to find multiple solutions to a problem. Just as the population in the BSRM experiment converged around one of the two maxima, most genetic algorithms are designed to converge around a single possible solution. By changing the algorithm to allow for speciation, these programs could optimize for multiple maxima, enabling them to find several solutions, which would help improve the odds of finding the ideal solution.

Our research suggests two different methods to accomplish this goal: non-destructive inheritance or sexual selection with destructive inheritance. The results of this experiment suggest that the sexual selection method may be best for applications that are looking for a single solution, while the non-destructive inheritance method may be optimal for programs that need to hedge against multiple possible outcomes. Furthermore, the optimal method may be a combination of the two, possibly beginning with population divergence through non-destructive inheritance before honing in on a the optimal solutions through destructive inheritance.

There's also a potential for future research from a biological perspective. The *Speciation* paper demonstrated that populations can maintain genetic diversity through speciation even when the population is strongly pressured to converge. While this convergence was unintentional in the initial experiment, population convergence occurs frequently in the natural world, often in small, declining populations. Biologists hypothesize that during these bottleneck events, speciation can occur very rapidly, and sexual selection might provide insight on the mechanism for this type of speciation.

Finally, it still remains to be seen how sexual selection impacts sympatric speciation in stable populations in the natural world. While we've demonstrated that the *Speciation* paper's results cannot be applied to healthy biological populations, we have not established whether or not sexual selection is a key component of sympatric speciation. In fact, further analysis of our experimental results suggest that there were major differences between the populations with and without sexual selection that aren't evident in the population tree. Specifically, the data suggests that sexual selection does help to create isolated sub-groups within a population, which may be critical to speciation. These avenues of research exceed the scope of this experiment but provide a promising lead into the hidden workings of the natural world.

Works Cited (Working)

[1] - Mutation rates in mammalian genomes. Sudhir Kumar and Sankar Subramanian. http://www.pnas.org/content/99/2/803.full