

Meiotic Inheritance and Gene Dominance in Synthetic Sympatric Speciation

William Booker

Robotics, Evolution, Adaptation, and Learning Laboratory
School of Computer Science
Gallogly College of Engineering
University of Oklahoma
Norman, OK 730191101
Email: william@thebookers.net

Dean Hougen

Robotics, Evolution, Adaptation, and Learning Laboratory
School of Computer Science
Gallogly College of Engineering
University of Oklahoma
Norman, OK 730191101
Email: hougen@ou.edu

Abstract—**Speciation is a critical process in both evolutionary biology and evolutionary computation.** It helps us understand the development of life on Earth and can improve evolutionary algorithms' abilities to find global maxima. In recent years, there have been considerable efforts to understand this process and uncover new techniques to simulate it. While there are many approaches for doing so, few examine gene inheritance and expression mechanisms. This paper seeks to address this shortcoming by demonstrating how simple changes to these mechanisms can radically alter a population's ability to speciate. Specifically, we find that simulated meiotic inheritance with complete genetic dominance significantly improves a population's divergent capability, even absent other speciation mechanisms.

I. INTRODUCTION

Speciation describes the natural tendency for homogeneous populations to split and form discrete groups through the continuous process of evolution [1]. It underpins our understanding of biology and it is fundamental to the development of life on this planet. Additionally, speciation shows promise in the realm of evolutionary computation, as a mechanism by which to find optimal solutions in multi-modal solution spaces.

Evolutionary biologists define distinct types of speciation including *allopatric speciation*, in which isolated populations acquire new traits independently, and *sympatric speciation*, in which a single population diverges over time. We are mostly concerned with sympatric speciation, as it is less well understood in biology and has significant untapped potential for improving evolutionary computation.

While there are many methods for inducing types of branching in evolutionary algorithms, such as such as crowding [2], niching [3]–[5], population topologies [6], island models [7], and clustering [8], [9], these approaches require assumptions about the solution space which must be explicitly tailored to each problem. Ideally we would like to find a more general solution, where the algorithm speciates correctly in a number of different environments.

There have been numerous studies of biological speciation, including studies of living organisms [10]–[13] and simulations [14]–[16]. One of the most commonly hypothesized mechanisms driving speciation is sexual selection, specifically *assortative mating* in which one or both mates (generally the

female) is only willing to mate with individuals exhibiting particular traits [10]–[13], [16], [17]. Assortative mating is hypothesized to induce sympatric speciation because assortative mating has the potential to isolate sub-groups within a population, allowing sub-groups to adapt to distinct niches within the environment, if such niches exist.

II. HYPOTHESES

We hypothesize that speciation into available niches may be facilitated by appropriate gene inheritance and expression mechanisms, without the need for additional mechanisms such as assortative mating. In particular, we hypothesize that meiotic inheritance facilitates speciation by preserving gene integrity and that genetic dominance can bolster this effect by allowing genes with no immediate value to be preserved in the population.

To test these hypotheses, we developed an agent-based simulation, similar to that of Woehrer et al. [16]. Woehrer conducted a 2×2 factorial study using a population of simulated Darwin's finches. To survive, the finches needed to evolve beaks appropriately sized for the seeds available in their environment. The study contrasted assortative mating with random mating (factor one) and used two different distributions of seed sizes (factor two). The seed distributions were bimodal and uniform to provide two niches and no niches, respectively. Speciation was common in simulations that featured both assortative mating and niches but not otherwise.

However, unlike that study, which used a simple gene model consisting of a single real-valued gene to determine beak size for each finch and used blending inheritance for offspring, we developed a more biologically plausible diploid gene model with a polygene determining each finch's beak size. We then compared simulated finches evolved with this gene model using either blending or meiotic (discrete) inheritance and phenotypes determined using either incomplete or complete dominance. Borrowing the two factors of the Woehrer study and adding two additional factors (gene inheritance and phenotypic expression) with two values each, produced the following $2 \times 2 \times 2 \times 2$ factorial study. Our specific hypotheses regarding the outcomes of this study are as follows:

H₁ *Meiotic inheritance will allow for speciation even in the absence of assortative mating.* This is the first key hypothesis behind our research. Note that for speciation to occur, there must still be distinct niches to fill. This means that we expect to see speciation with meiotic inheritance for the bimodal seed distribution, not for the uniform seed distribution. However, for the uniform seed distribution the unstable branching (and merging) observed by Woehrer et al. [16] is likely to be retained in assortative mating populations.

H₂ *Complete dominance will enhance the effect of meiotic inheritance on speciation.* This is the second key hypothesis behind our research. Again, there must still be distinct niches to fill, so we expect to observe speciation for bimodal seeds, not uniform seeds. Unstable branching (and merging) is again likely for assortative mating populations with uniform seeds. Note that while complete dominance is expected to enhance the effect of meiotic inheritance on speciation, it is not expected to make speciation possible in the absence of meiotic inheritance.

H₃ *Using the diploid polygene model with blending inheritance will match the outcomes found using a single-gene blending model.* Note that the diploid polygene model is necessary for considering the gene inheritance and phenotypic expression factors in our study. Testing this hypothesis will allow us to verify that differences observed are due to the factors considered in our study, not due to the diploid polygene structure itself. Because this hypothesis is a prerequisite for ensuring that our key hypotheses are appropriately tested, we present results for it first, even though it is a supporting hypothesis rather than a key hypothesis.

III. EXPERIMENTAL DESIGN

Three aspects of the simulation model are based on that of Woehrer, et al. [16]: The island, seeds, and mating. For the reasoning behind that model, consult Woehrer [18]. The remaining three aspects of the simulation model are new: Genetic structure, inheritance, and expression.

A. The Island

The simulation consists of an island 100×100 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. 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.

B. Factor One: Seeds

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 10×10 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 seed (BS) distribution consists of two Gaussian distributions of 2500 seeds each; these distributions are centered at three and eight units, each with a standard deviation of 0.5 units. The uniform seed (US) 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).

C. Factor Two: Mating

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. Each male is only allowed to mate five times per breeding season. The simulation accounts for two types of mating: random mating (RM), where a female will choose any male from the population, and assortative mating (AM), where a female will only pick a male within one unit of its own beak size. When presented with multiple possible mates, the female will choose between them at random. Mating produces a single offspring.

D. Genetic Structure

We conducted experiments using two gene structures. The first structure is the degenerate case of a single gene (SG) consisting of a single floating-point value which for the initial population was sampled from a Gaussian distribution with a mean 5.5 and a standard deviation of 0.5, as used by Woehrer et al. [16].¹ This version was used to test the simulation model, to ensure that any substantially different outcomes observed in our study were due to the considered factors rather than other possible differences in the simulations.

To test the impact of meiotic inheritance and gene dominance on population dynamics, we introduced a diploid polygene (DP) structure. In the new genetic structure, each finch is equipped with two chromosomes, one from each parent. Each chromosome contains an array of one-hundred genes, each represented by a floating-point value. The genes in the initial population are randomly chosen from a uniform distribution with a mean of 0.055 and a range of 0.245.² When mating, the offspring receives one chromosome selected at random from each of its parents. Each inherited gene has a 10% chance to mutate during the process. When a gene is selected

¹ Woehrer et al. specifies a variance of 0.5, but the data suggest a standard deviation of 0.5.

² These values were chosen to mimic the initial populations of the single-gene model. The mean of 0.055 and the range of 0.245 were determined mathematically. The final beak size is equal to the average of two sums of 100 genes, or $\frac{1}{2} \sum_{i=1}^{200} x_i$. The distribution of the beak sizes is normal by the central limit theorem. The mean is $\frac{1}{2}(200 * 0.055) = 5.5$ and the standard deviation is $\frac{1}{2} \sqrt{\sum_{i=1}^{200} \text{Var}(x_i)} = 0.5$ where $\text{Var}(x_i) = \frac{0.245^2}{12}$.

TABLE I

RESULTS. BOLD IS STATISTICALLY SIGNIFICANT AT 1%. ITALICS ARE STATISTICALLY SIGNIFICANT AT 5%. SINGLE GENE COMPARED TO WOEHRER ET AL. [16]. DIPLOID POLYGENE COMPARED TO SINGLE GENE.

Genetic Structure: Inheritance Method: Phenotypic Expression (Dominance):			Single Gene Blending Direct	Blending Incomplete	Diploid Polygene	Meiotic Incomplete	Meiotic Complete
Seed Distribution	Mating Strategy	Populations	Count	Count	Count	Count	Count
Bimodal	Assortative	2	30	25	23	31	20
		1	15	23	21	15	27
		0	3	0	4	2	1
	Random	2	0	0	0	1	33
		1	38	35	35	30	14
		0	10	13	13	17	1
Uniform	Assortative	2+	37	41	41	37	41
		1	0	0	0	0	0
		0	11	7	7	11	7
	Random	2	0	0	0	0	0
		1	<i>23</i>	24	34	44	40
		0	<i>25</i>	24	14	4	8

for mutation, we add a random value taken from a uniform distribution with a range of 0.310 and a mean of 0.³

E. Factor Three: Inheritance

For the single-gene model, the offspring's gene is an average of the beak sizes of the parents plus a small Gaussian random mutation (mean 0, standard deviation 0.2), following Woehrer et al. [16].

For the diploid gene model, we consider both blending and discrete inheritance. For blending inheritance (BI), the genes are averaged between the two inherited chromosomes. For discrete meiotic inheritance (MI), the individual genes remain intact, as they do in biological meiosis.

F. Factor Four: Expression

For the single-gene model, the value of the gene is directly interpreted as the bird's phenotypic beak size.

For the diploid gene model, the value of each chromosome is determined by considering its genes to be a polygene and summing them. Here we consider both a complete dominance (CD) and an incomplete dominance (ID) model. In the complete dominance model, the larger of the two polygene values is chosen for the finch's beak size. In the incomplete dominance model, the values of the two polygenes are averaged to determine the phenotypic beak size, resulting in the special case of no dominance. For the purposes of inheritance, this choice is arbitrary as neither model affects the actual genetic material that is passed on to the offspring, although the phenotypic value may, of course, affect survival.

IV. RESULTS

Qualitative results are shown in Figure 1, which plots phenotype versus generation for several typical runs. The first row

³The mutation range of 0.310 was determined empirically. We iteratively tested mutation ranges until the standard deviation of the change in beak size consistently averaged at 0.2 to match the mutation seen in the single-gene case.

(subfigures a–d) are results from the single-gene model; rows two through five (subfigures e–t) are results using the diploid polygene model with one row for each combination of the inheritance and expression factors. The second row (subfigures e–h) shows blending inheritance and incomplete dominance, the third row (subfigures i–l) shows blending inheritance and complete dominance, the fourth row (subfigures m–p) shows meiotic inheritance and incomplete dominance, and the fifth row (subfigures q–t) shows meiotic inheritance and complete dominance.

There is one column in Figure 1 for each combination of the seed distribution and mating strategy factors. The first column (subfigures a, e, i, m, and q) shows bimodal seeds and assortative mating, the second column (subfigures b, f, j, n, and r) shows bimodal seeds and random mating, the third column (subfigures c, g, k, o, and s) shows uniform seeds and assortative mating, and the fourth column (subfigures d, h, l, p, and t) shows uniform seeds and random mating.

Numerical results are shown in Table I, which gives the count of the number of populations present at the end of each run for the various conditions. A population count of 2 shows speciation while 0 shows extinction. A count of 1 may show directional selection (the population moved to fill one niche in the bimodal seeds case) or simply that the population never diverged (in the case of uniform seeds). A count of 2+ shows that the population diverged into multiple unstable populations.

Starting with the results for the single-gene model, Subfigure 1a shows speciation in the case of bimodal seeds and assortative mating, Subfigure 1b shows directional selection in the case of bimodal seeds and random mating, Subfigure 1c shows a complex and unstable pattern of branching, merging, and branch extinction for the case of uniform seeds and assortative mating, and Subfigure 1d shows a single population not anchored to a particular seed size for the case of uniform seeds and random mating. Looking at the results column for

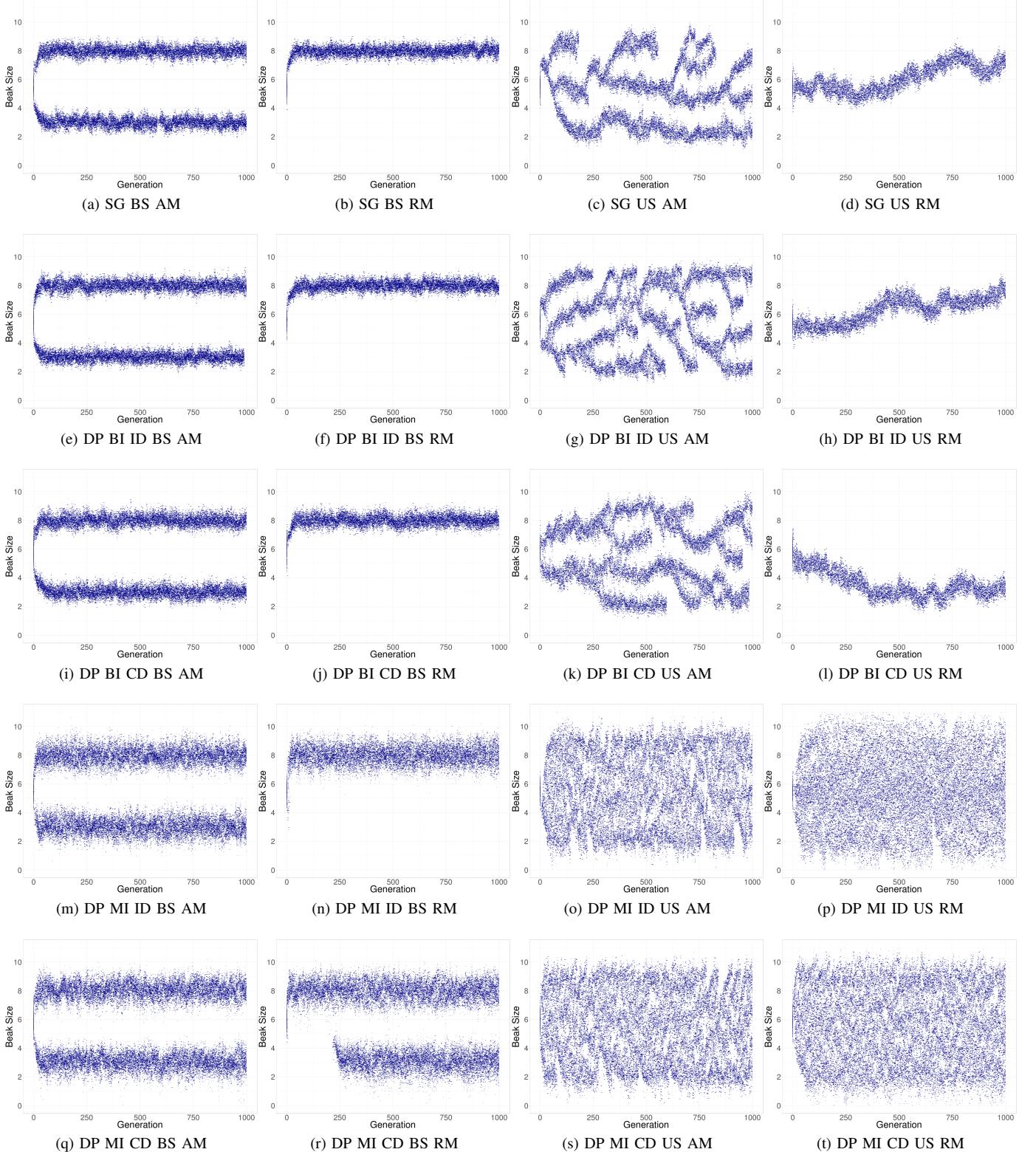


Fig. 1. Typical outcomes. Row one (subfigures a–d): Single gene (SG). Rows two through five (subfigures e–t): Diploid polygene (DP). Rows two and three (subfigures e–l): Blending inheritance (BI). Rows four and five (subfigures m–t): Meiotic inheritance (MI). Rows two and four (subfigures e–h and m–p): Incomplete dominance (ID). Rows three and five (subfigures i–l and q–t): Complete dominance (CD). Columns one and two (subfigures a, b, e, f, i, j, m, n, q, and r): Bimodal seeds (BS). Columns three and four (subfigures c, d, g, h, k, l, o, p, s, and t): Uniform seeds (US). Columns one and three (subfigures a, c, e, g, i, k, m, o, q, and s): Assortative mating (AM). Columns two and four (subfigures b, d, f, h, j, l, n, p, r, and t): Random mating (RM).

the single-gene model in Table I, we can see that these are the most common outcomes for each combination of factors one and two, except the uniform seeds and random mating combination for which the most common result was extinction.

A. Discussion

Results for the single-gene verification experiment conform with what was found by Woehrer et al.: Speciation occurs frequently with bimodal seeds and assortative mating but not for the other three cases. This is fully as expected because bimodal seeds and assortative mating is the only case in which there are both discrete niches and a mechanism that allows for separation of populations. The present simulation does produce substantially more extinctions than the Woehrer simulation for the case of uniform seeds and random mating (25 versus only 13), likely due to minor simulation differences, but our results nonetheless support their hypothesis for this case. Besides this, our current results match those previous results both qualitatively and quantitatively, supporting all of their hypotheses and with no other differences found to be statistically significant (using Barnard's Exact Test and χ^2 -square tests, as appropriate).

Looking at the next two rows of Figure 1 and the next two results columns of Table 1, we see the results for the new diploid polygene structure but retaining blending inheritance from the single-gene model. Both qualitatively and quantitatively, these results differ very little from those of the single-gene model, showing that the more complex gene structure itself has very little effect on the outcome. The largest difference appears to be the fact that speciation is less frequent and, correspondingly, directional selection is more common in the diploid polygene model than in the single-gene model for the bimodal seeds and assortative mating factors. However, these differences are not statistically significant and speciation is still common in the bimodal seeds and assortative mating cases but is not found at all for the other three combinations of resource distribution and mating strategy factors, supporting that general finding of Woehrer et al., as well as all of their individual hypotheses. In addition, there may be some very subtle differences between the incomplete and complete dominance cases, such as a slightly wider dispersion of the phenotypes for complete dominance (compare each subfigure in row three of Figure 1 to the corresponding subfigure in row two) as well as more extinctions for bimodal seeds and assortative mating yet fewer extinctions for uniform seeds and random mating. Again, however, these differences are not statistically significant.

Looking at the final two rows of Figure 1 and the final two results columns of Table 1, we see the results when blending inheritance is replaced with meiotic inheritance. Here the results are strikingly different, both qualitatively and quantitatively. For all combinations of factors one and two, we see a substantially broader spread to the beak sizes. More striking, however, is the fact that speciation is seen for random mating (along with bimodal seeds, of course), whereas for all previous simulations it had only been observed

for assortative mating. This was observed only once for the incomplete dominance case but is by far the most common outcome for the complete dominance case, occurring in 33 out of 48 repetitions. Also quite striking is the coverage of the phenotypic space for the uniform seeds and random mating case for both incomplete and complete dominance.

B. Analysis

The introduction of meiotic inheritance radically altered the results of the simulation. Rather than collapsing into narrow bands, each population rapidly expanded to cover the entire range of available seed sizes. While the non-meiotic populations were limited to 2-unit thick population bands, the meiotic populations were stable at an arbitrary range. This trait allowed the meiotic populations to exploit the full range of available resources, particularly notable for the uniform seed distributions.

Furthermore, both meiotic populations exhibited evidence of speciation in the bimodal seeds and random mating scenario. The complete dominance case speciated thirty-three times, while the incomplete dominance case speciated once. This tendency suggests that in meiotic populations, speciation is possible even without sexual selection. The key to this discrepancy lies in the mechanism by which genetic information is passed on to the next generation.

In the single-gene model, we averaged the beak sizes of the parents to determine the beak size of the offspring. This inheritance mechanism destroys important genetic diversity in the population. Barring mutation, any offspring produced using this method will 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 preceded it. Thus, over time, the species begins to coalesce around a single beak size: population convergence. As the inheritance method pushes the population inwards, the high mutation rate pushes the population outwards, eventually reaching equilibrium at two-unit thick population bands. This equilibrium explains why the the population bands are the same width in the single-gene simulation regardless of niche size: the inheritance method is the force pushing the population inwards, not natural selection. This effect also explains why we don't see speciation in the bimodal seeds and random mating scenario for non-meiotic populations. Because the gap between the local maxima at three and eight are more than two units apart, there is no stable population that can contain both, forcing one niche to be abandoned.

Contrast this tendency with non-destructive meiotic inheritance, in which genetic information is passed unaltered from parent to offspring. By keeping the chromosomes the same between generations, meiotic inheritance protects the diversity of the population. There is no guarantee that a offspring's beak size will fall between that of its parents, so future generations can reassert genetic diversity that may not appear in the current distribution of phenotypes. By introducing meiotic inheritance, we removed the pressure towards convergence, allowing the population to diverge to cover the entire range

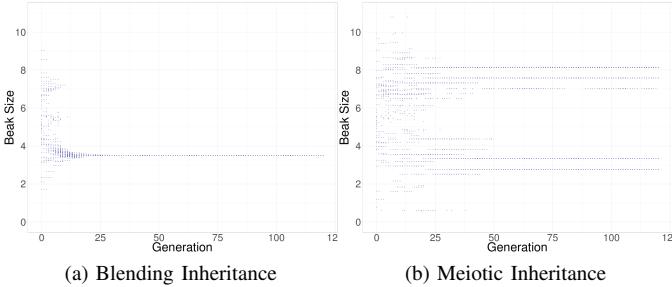


Fig. 2. Typical outcomes for bimodal seeds and random mating scenario with no mutation using diploid polygene and incomplete dominance.

of seed sizes. Because meiotic populations have no tendency for convergence, and are thus stable at an arbitrary range, they can exploit both population niches in the bimodal seeds and random mating scenario.

V. ADDITIONAL EXPERIMENTS

While our initial experiment demonstrates the impact of meiotic inheritance, we developed two additional experiments to help support our analysis and address unexplained results. First, we wanted to confirm our analysis regarding the convergent tendency of non-meiotic inheritance by removing mutation from the simulation and observing the effects. Second, we wanted to explain why incomplete dominance resulted in significantly fewer speciation events than complete dominance in the bimodal seeds and random mating scenario.

For simplicity, in these experiments, we made two changes to the simulation. First, rather than testing all conditions, we only looked at the bimodal seeds and random mating scenario with meiotic inheritance combined with both complete and incomplete dominance and blending inheritance combined only with incomplete dominance. Second, we reduced the initial population size from 400 down to 40 to help smooth out the initial population collapse and subsequent rebound that appeared in our initial experiments.

A. No Mutation

This experiment is designed to illustrate the convergent tendency of non-meiotic inheritance by removing the noise created by mutation. We achieved this effect by reducing the range of the running mutation rate from 0.310 to 0.00. We also quadrupled the initial mutation rate to 0.980 to give the starting population sufficient diversity to reach both niches. Both simulations utilize an incomplete dominance genetic structure.

The results of this experiment are given in Figure 2 and represent the difference between non-meiotic and meiotic inheritance in the absence of mutation. As expected, the non-meiotic population exhibited clear signs of convergence, while the meiotic population retained population diversity throughout the duration of the simulation.

Without the divergent pressure from mutation, the blending inheritance method immediately coalesced around a single beak size. Each generation exhibited less diversity than the

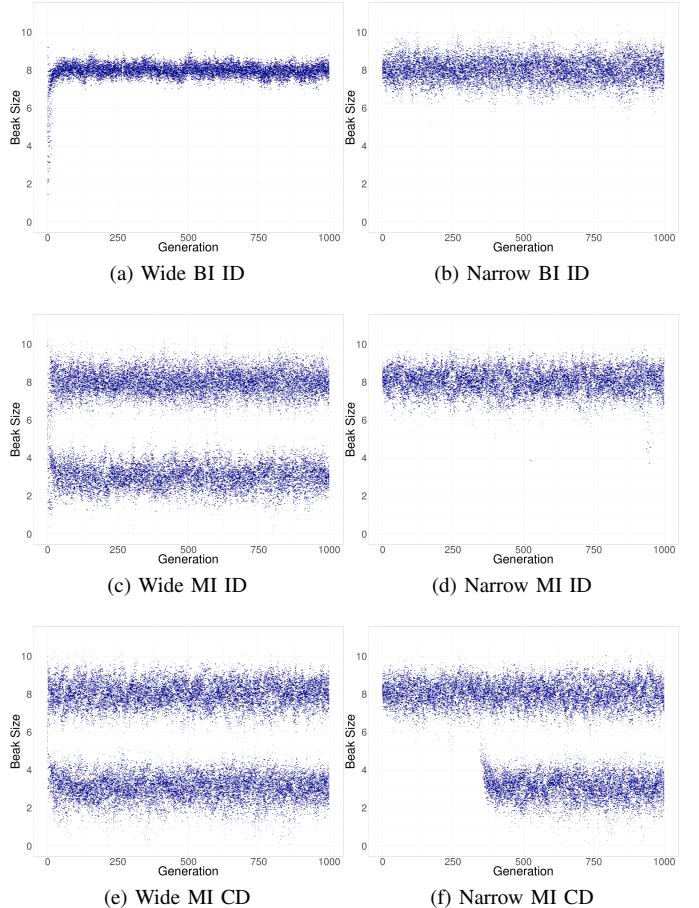


Fig. 3. Typical outcomes for bimodal seeds and random mating scenario with varying initial populations. Row one (subfigures a and b): Blending inheritance (BI). Rows two and three (subfigures c–f): Meiotic inheritance (MI). Rows one and two (subfigures a–d): Incomplete dominance (ID). Row three (subfigures e and f): Complete dominance (CD). Column one (subfigures a, c, and e): Wide initial population distribution. Column two (subfigures b, d, and f): Narrow initial population distribution.

generation that proceeded it, forcing the population to abandon one of the niches within a dozen generations. However, with meiotic inheritance, no such trend appeared. While some chromosomes did die out, the handful that survived were stable for the duration of the simulation. Some phenotypes even temporarily disappeared from the population, only to reemerge in later generations. These observations line up well with what we observe in real-world biological populations, which tend to exhibit a countable number of discrete phenotypes and demonstrate high levels of diversity despite extremely low mutation rates. While the simulated non-meiotic populations may look biologically accurate due to high mutation rates, this experiment demonstrates that they are actually governed by vastly different forces than real-world populations, making them unreliable for predicting biological behavior.

B. Initial Population

Our initial experiment demonstrated that speciation is possible in meiotic populations in the bimodal seeds and random

TABLE II

BIMODAL SEEDS AND RANDOM MATING SCENARIO WITH VARYING INITIAL POPULATIONS. BOLD IS STATISTICALLY SIGNIFICANT AT 1%. MEIOTIC INHERITANCE COMPARED TO BLENDING INHERITANCE.

Inheritance Method: Phenotypic Expression:		Blending ID		Meiotic ID CD	
Initial Distribution	Populations	Count	Count	Count	Count
Wide	2	0	39	43	
	1	45	9	5	
	0	3	0	0	
Narrow	2	0	0	12	
	1	46	48	33	
	0	2	0	3	

mating scenario, but it did not address why complete dominance exhibited far higher rates of speciation than incomplete dominance. We believe that this phenomenon is caused by an unrelated property of gene expression, which enables populations to bridge the evolutionary valley between the two optima via genetic drift. In the case of complete dominance, only one chromosome is actually expressed, thus allowing the non-dominant chromosome to move through the low-fitness valley without reducing the organism's evolutionary fitness. Eventually, these recessive chromosomes can wander into the second niche, and, when matched, they produce an individual capable of exploiting these untapped resources. With incomplete dominance, both chromosomes are expressed, so the population is unable to bridge the gap on its own. By masking the effect of one of the chromosomes, complete dominance acts as a multiplier on the mutation rate, allowing beneficial mutations to develop over the course of several generations rather than within a single individual.

This experiment was designed to test this analysis. Assuming that the change in speciation rates was due to genetic drift through the low-fitness valley, we would expect that increasing the genetic diversity of the initial population would reduce its impact, while reducing the genetic diversity would increase it.

In this experiment, we changed the size of the initial population to see the effects on the extinction rates between incomplete dominance and complete dominance. For the first test, we widened the initial population to cover both niches by quadrupling the initial mutation rate to 0.980. In the second test, we reduced the initial population by halving the initial mutation rate to 0.1225 and moving the mean to 0.80. This change centers the population in the middle of the upper niche.

The results of this experiment are given in Figure 3 and Table II. The first row of Figure 3 represents blending inheritance with incomplete dominance. The second and third rows represent meiotic inheritance with incomplete and complete dominance, respectively.

When the population was widened, both meiotic populations exhibited high rates of speciation; complete dominance exhibited more speciation events than incomplete dominance (43 versus 39), although this difference was not statistically significant. When the population was narrowed, only the

meiotic complete dominance case speciated and the rate of speciation was dramatically reduced (to 12). The non-meiotic population exhibited no speciation events in either scenario. These results suggest that both incomplete dominance and complete dominance are effective in protecting genetic diversity in a population; however, complete dominance enhances speciation rates because it adds a method to bridge potential low-fitness valleys.

VI. CONCLUSIONS AND FUTURE WORK

This research demonstrates the paramount importance of gene inheritance and expression methods in biological simulations and evolutionary algorithms, and illustrates the need for increased scrutiny of an under-appreciated aspect of evolutionary computation. A slight change in a population's inheritance or expression mechanism can radically alter the population dynamics, due to the potential introduction of strong evolutionary pressures. Obviously, for biological simulations, the modeled mechanisms should strive to mimic biological mechanisms as closely as possible. While the applications for machine learning are less clear, we postulate that meiotic inheritance and genetic dominance may have many advantages for inducing speciation in evolutionary algorithms.

Meiotic speciation has an advantage in that it makes very few assumptions about the nature of the solution space. As demonstrated, non-meiotic inheritance has a tendency to collapse into narrow population bands that are only sustained by high mutation rates. If the mutation rate is too low, these narrow population bands run the risk of getting stuck in local maxima before they are able to identify possible solutions. Meiotic inheritance avoids this drawback entirely by inhibiting population collapse during runtime. By keeping the population as wide as the niches will allow, meiotic inheritance is better protected against premature optimization.

In addition, meiotic inheritance has the ability to take advantage of a complete dominance structure, which we discovered is a powerful tool for exploring new niches without increasing the mutation rate. This ability is advantageous, as increasing mutation rates often result in the abandonment of good solutions [19]. Meiotic inheritance is best equipped to utilize this technique, as the amount of genetic drift is not limited by the convergent tendency of the inheritance method.

Finally, and perhaps most importantly, meiotic inheritance may prove useful in situations where the solution space itself is evolving over time. In this case, it's easy to imagine how premature optimization may trap a population in a niche from which it is unable to escape once it becomes unfavorable. Meiotic inheritance is well equipped to deal with such a scenario, given the high level of diversity and the ease with which it exploits new niches. When coupled with the additional search range offered through complete dominance, meiotic inheritance gains a major advantage over blending inheritance in dynamic solution topographies.

Despite these potential advantages, there are limitations to this technique that we would like to address in future work.

The first issue is that our experiments use a dynamic population size, which, while biologically accurate, is uncommon in evolutionary algorithms. To expand the scope of this research, we would like to demonstrate an effective method by which to apply the benefits of meiotic inheritance with a static population size and, going the other way, we would like to explore using variable sized populations in more traditional evolutionary algorithms. Furthermore, many evolutionary algorithms, from traditional binary-coded-decimal genetic algorithms to indirect encoding schemes such as heuristic encoding [20], implicitly utilize a form of meiotic inheritance. In this case it may worth investigating the merits of using a non-meiotic inheritance method to improve population convergence. We hypothesize that for some solution spaces, a combination of meiotic and blending inheritance would provide the optimal search. Methods for integrating both types of inheritance in the same population remains an area of future study. Additionally, the only phenotypic expression possibilities considered in this work were complete dominance and no dominance. However, partial dominance is a known possibility for incomplete dominance and might prove beneficial for balancing exploration with exploitation.

From a biological standpoint, it remains to be seen how sexual selection impacts sympatric speciation in the natural world. While we have demonstrated that sympatric speciation is possible without sexual selection, we have not established whether or not sexual selection is a key component of biological sympatric speciation. Our results should not be haphazardly extended to the biological world because the speciation that we observed in meiotic populations in the bimodal seeds and random mating scenario is likely very different from the speciation exhibited in biological populations. Specifically, for the purposes of this paper, we implicitly defined a species as a visibly distinct population exploiting a niche. However, while useful for evolutionary algorithms, this definition differs from many biological species definitions, which often include the notion that different species are largely reproductively isolated [21]. Thus, it could be argued that the distinct bands that arise in meiotic populations in the bimodal seeds and random mating scenario do not actually comprise distinct species, but rather a single polymorphic species exploiting multiple niches. Further research is required to determine if sexual selection is required for this split population to diverge into separate species, or if there is another potential cause.

In summary, the key findings of this paper are that meiotic inheritance allows for speciation in multi-niche environments without the need for additional mechanisms such as sexual selection, which may have applications in evolutionary computation, and that complete dominance gives populations the opportunity to bridge low-fitness valleys, even when the mutation rate is smaller than the expanses.

REFERENCES

- [1] J. A. Coyne and H. A. Orr, *Speciation*. Sinauer Associates, 2004.
- [2] K. A. De Jong, "An analysis of the behavior of a class of genetic adaptive systems," Ph.D. dissertation, University of Michigan, Ann Arbor, MI, USA, 1975.
- [3] D. E. Goldberg, *Genetic Algorithms in Search, Optimization, and Machine Learning*. Addison-Wesley Professional, 1989.
- [4] J. Horn, N. Nafpliotis, and D. E. Goldberg, "A niched Pareto genetic algorithm for multiobjective optimization," in *Proceedings of the First IEEE Conference on Evolutionary Computation, IEEE World Congress on Computational Intelligence*. IEEE, 1994, pp. 82–87.
- [5] N. Tomko, I. Harvey, A. Philippides, and N. Virgo, "Many hands make light work: Group evolution and the emergent division of labour," in *Proceedings of the European Conference on Artificial Life*. Paris, France: MIT Press, Aug. 2011, pp. 805–812.
- [6] J. Sarma, "An analysis of decentralized and spatially distributed genetic algorithms," Master's thesis, George Mason University, Fairfax, Virginia, 1998.
- [7] D. Whitley, S. Rana, and R. B. Heckendorn, "The island model genetic algorithm: On separability, population size and convergence," *Journal of Computing and Information Technology*, vol. 7, no. 1, pp. 33–47, 1999.
- [8] R. Gras, D. Devaurs, A. Wozniak, and A. Aspinall, "An individual-based evolving predator-prey ecosystem simulation using a fuzzy cognitive map as the behavior model," *Artificial Life*, vol. 15, no. 4, pp. 423–463, 2009.
- [9] A. Aspinall and R. Gras, "K-means clustering as a speciation mechanism within an individual-based evolving predator-prey ecosystem simulation," in *Proceedings of the 6th International Conference on Active Media technology*, ser. Lecture Notes in Computer Science, A. An, P. Lingras, S. Petty, and R. Huang, Eds., vol. 6335. Berlin, Heidelberg: Springer-Verlag, 2010, pp. 318–329. [Online]. Available: <http://dl.acm.org/citation.cfm?id=1886192.1886235>
- [10] O. Seehausen and J. J. M. van Alphen, "Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria?" *Ecology Letters*, vol. 2, no. 4, pp. 262–271, 1999.
- [11] C. R. B. Boake, "Flying apart: Mating behavior and speciation," *BioScience*, vol. 50, no. 6, pp. 501–508, 2000.
- [12] J. W. Boughman, "Divergent sexual selection enhances reproductive isolation in sticklebacks," *Nature*, vol. 411, no. 6840, pp. 944–948, 2001.
- [13] C. Bleay and B. Sinervo, "Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: Implications for the formation and maintenance of coadapted gene complexes," *Behavioral Ecology*, vol. 18, no. 2, p. 304, 2007.
- [14] U. Dieckmann and M. Doebeli, "On the origin of species by sympatric speciation," *Nature*, vol. 400, no. 6742, pp. 354–357, 1999.
- [15] M. Doebeli and U. Dieckmann, "Speciation along environmental gradients," *Nature*, vol. 421, no. 6920, pp. 259–264, 2003.
- [16] M. Woehler, D. Hougen, and I. Schlupp, "Sexual selection, resource distribution, and population size in synthetic sympatric speciation," in *ALife 13. The Thirteenth International Conference on the Synthesis and Simulation of Living Systems*. MIT Press, Jul. 2012, pp. 137–144, **Best Paper Award**. [Online]. Available: <http://mitpress.mit.edu/sites/default/files/titles/content/alive13/978-0-262-31050-5-ch020.pdf>
- [17] T. M. S. Network, "What do we need to know about speciation?" *Trends in Ecology & Evolution*, vol. 27, no. 1, pp. 27–39, 2011. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/S0169534711002618>
- [18] M. K. Woehler, "Sexual selection, resource distribution, and genetic drift in simulated ecological speciation," Ph.D. dissertation, University of Oklahoma, Norman, Oklahoma, 2016.
- [19] W. M. Spears, "Simple subpopulation schemes," in *Proceedings of the Evolutionary Programming Conference*, vol. 3, 1994, pp. 296–307.
- [20] B. P. Carlson, "Phenotype operators for improved performance of heuristic encoding within genetic algorithms." Ph.D. dissertation, University of Oklahoma, Norman, Oklahoma, 2016.
- [21] N. A. Campbell and J. B. Reece, *Biology*, 8th ed. Benjamin Cummings, 2008.