Sensitivity of Self-Organized Speciation to Long-Distance Dispersal

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Abstract - **Previous work has shown that speciation can result from the self-organized accumulation of multiple mildly underdominant (nearly neutral) loci in a continuous population, when mating is spatially localized. In contrast, when mating is panmictic, underdominance is quickly eliminated and the population always converges on a single genotype, as predicted by mean-field approximations. The focus of this work is to examine the sensitivity of self-organizing speciation to the assumption of purely localized interactions. We alter the interaction topology from nearest neighbor interactions to panmictic interactions in two ways: (*i*) by increasing the size of the contiguous mating neighborhoods and (*ii*) by allowing for long-distance dispersal of individuals with increasing probability. Our results show self-organized speciation to be robust to mating neighborhood sizes significantly larger than nearest neighbor interactions and to probabilities of long-distance dispersal that fall well into the range of so called "small-world" interaction topologies.**

I. INTRODUCTION

The manner in which underdominance (heterozygote disadvantage) can be introduced and maintained in a population has been a topic of interest in the field of evolutionary biology for quite some time [1]. In a randomly mating population, it is difficult to imagine an evolutionarily reasonable mechanism by which such a polymorphism could possibly be maintained for any significant period of time, or even become established in the first place. However, natural populations certainly do exhibit a great deal of genetic variation, including underdominance (e.g., see [2]). Recently, we have demonstrated a simple mechanism by which within-locus underdominance can be introduced into a continuous, spatially extended population [3]. Assuming that underdominance can be introduced into an interbreeding population, it has been previously shown to persist for extended duration so long as mating is spatially localized [3][4][5][6][7][8]. We have shown that the accumulation of multiple mildly underdominant loci can lead to the self-organization of a continuous, locally mating population into reproductively isolated subgroups, resulting in speciation [3][8].

We define speciation according to Mayr's biological species concept [9] as a group of actually or potentially interbreeding individuals that are reproductively isolated from other such groups. Therefore, two groups are considered separate species if their hybrid offspring are completely inviable. For a review of this concept and other population genetics topics considered in this work, the reader is referred to [10][11].

As the interaction topology of this system changes from purely localized interactions to random interactions, the expected outcome changes from (*i*) speciation into two reproductively isolated groups to (*ii*) fixation upon a single genotype. Localized mating strategies have been observed in many plant [12][13][14][15][16] and animal [17][18][19] populations, so spatially localized interactions may indeed be a better representation of the mating strategies of some biotic communities than are random interactions. However, natural populations are not organized on a grid with strict nearest neighbor interactions. Furthermore, dispersal has been shown to be leptokurtic in many populations [20][21], where the majority of interactions are local, but long-distance interactions also occur with low frequency.

Previous work on "small-world" networks [22] has shown that even when most interactions are spatially localized, only a relatively small number of long-distance interactions are required to reduce the characteristic path length (λ; the shortest path between two individuals, averaged over all pairs of individuals) to be almost as low as that of a random interaction topology. Thus, in some ways, small-world interaction topologies behave like random interaction topologies. In a recent work on spatially-extended predator-prey systems [23], critical thresholds of long-distance interactions were empirically determined that led a population with primarily localized interactions to behave as if the population were well-mixed.

The focus of this manuscript is to study the sensitivity of self-organizing underdominant barriers to gene flow to the relaxation of the assumption of purely localized interactions. In particular, we incrementally transition the interaction topology from purely localized to random interactions in two ways: (*i*) by increasing the diameter of the contiguous mating neighborhoods and (*ii*) by allowing for long-distance dispersal of individuals with increasing probability. In so doing, we hope to elucidate the nature of the phase shift from speciation to fixation.

II. METHODS

A. Population Model

Populations of diploid individuals were modeled using stochastic cellular automata with non-periodic boundary conditions. Each individual in the population could occupy at most one cell in a square lattice at any discrete time step and the lattice was updated synchronously. The size of the lattice was 100×100 cells, unless otherwise noted. In every iteration, each cell i was repopulated by the offspring of two parents selected from the mating neighborhood of cell i with probability P_i^{sel}, as follows;

$$P_i^{sel} = \frac{f_i}{\sum_{j \in N} f_j} \qquad (1)$$

where f_i is the fitness of the individual located in cell i and N denotes the set of individuals in the mating neighborhood of cell i. Selfing was not permitted (i.e., individuals were not allowed to mate with themselves). The size and shape of the mating neighborhoods investigated in this study are detailed in the subsequent section.

B. Interaction Topologies

Several forms of mating neighborhoods were investigated. At one extreme, the mating neighborhood of the cell in question comprised the entire population. In this case, mating was random with respect to the spatial location of an individual. This is commonly referred to as global mating or panmixia. At the other extreme, mating could only occur within purely localized neighborhoods comprising only the cell itself and its eight nearest neighbors. We refer to this mating strategy as 3×3 localized mating.

In order to analyze the robustness of the speciation process presented in [3][8] to the assumption of 3×3 localized mating, we altered the mating neighborhood in two ways. First, we incrementally increased the diameter (d) of square $d{\times}d$ mating neighborhoods from $d = 3$ (3×3 localized mating) to $d = 100$ (global mating). Second, we considered 3×3 local mating neighborhoods interspersed with limited long-distance dispersal. Specifically, between generations,

we randomly selected individuals for dispersal with probability p and subsequently randomly permuted the spatial location of these dispersing individuals. A schematic diagram of these interaction neighborhoods is provided in Figure 1.

C. Evaluating Fitness

As in [3][8], individuals comprised $L \in \{2,4,6,8,10\}$ bi-allelic loci, depending upon the experiment in question. Alleles are denoted by lower case and capital letters (e.g. *AaBBcc*), where case does not imply dominance, but affects the epistatic interaction of alleles, as detailed below. The fitness f of an individual i was assessed according to the following fitness function:

$$f_i = \frac{1 - U_i + E_i}{1 + E_{max}} \qquad (2)$$

where a perfect fitness of unity is reduced by an underdominance penalty (U) and increased by an epistatic bonus (E) and then subsequently renormalized such that maximal fitness is again unity. Underdominance occurs when the heterozygote is less fit than either homozygote, at a given locus. The underdominance penalty is computed as the proportion of heterozygous loci in an individual's genotype. For example, consider a two-locus system ($L = 2$) and an individual that is heterozygous at a single locus. This individual will receive a fitness penalty of $U = 1/2$. Similarly, in a ten locus system ($L = 10$) an individual heterozygous at a single locus will receive a milder fitness penalty of $U = 1/10$. Thus, the degree of underdominance in our model is inversely proportional to L. Only those individuals heterozygous at all loci were considered inviable (*e.g. AaBbCc*). Epistasis is defined as the nonlinear interaction of genotypes at different loci in their overall
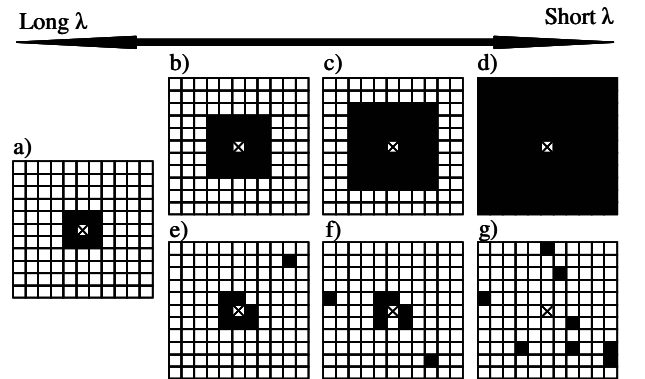

Fig. 1. Schematic diagram of representative types of mating neighborhoods for a given cell (x). Mating neighborhoods comprised the cell itself as well as those shown in black. a) 3×3 local neighborhoods, b-d) local neighborhoods with increasing relative neighborhood size (δ), and e-g) 3×3 local neighborhoods with increasing probability of long-distance interactions (*p*). Characteristic path length (λ) decreases from left to right.

contributions to fitness. The epistatic bonus (E) is computed as the product of an epistatic coefficient (ε) and the maximum of the number of homozygous loci with the same case, such that only individuals homozygous at all loci receive maximal fitness. This simple fitness function was chosen since both the degree of underdominance and the degree of epistasis being modeled are directly tunable. For example, the degree of underdominance can be decreased by simply increasing the number of loci (L) and the degree of epistasis can be increased by increasing the epistatic coefficient (ε). For the experiments reported here, the epistasis coefficient was held constant ($\varepsilon = 0.1$). A sample instantiation of this fitness function for a two-locus system is provided in Figure 2 ($\varepsilon = 0.1$).

Offspring were created from selected parents *via* independent assortment (uniform recombination). If the offspring produced was inviable ($f_i = 0$), then that cell was treated as empty in the subsequent generation. For simplicity, mutational events were not considered. For all runs, the population was initialized in multi-locus Hardy-Weinberg equilibrium (i.e., all allele values are randomly initialized in equal proportions) in order to avoid any initial bias in average allelic effects or spatial organization. All experiments were performed in Matlab (The Mathworks, Natick, MA). Further details of each individual experiment are provided in the next section.

III. EXPERIMENTS

A. *Self-Organizing Barriers to Gene Flow*

We first briefly review our previous results [3][8] regarding self-organization in systems with underdominant loci. When mating is restricted to 3×3 local neighborhoods, self-organizing barriers to gene flow repeatedly emerge, and when mild disruptive epistasis is present (e.g., fitness as in Figure 2), this results in speciation. A graphical depiction of a representative two-locus population is provided in Figure 3a. Initialized in multi-locus Hardy-Weinberg equilibrium, the population self-organized into groups of genetically compatible individuals separated by hybrid zones, most of which were permeable, allowing underdominance to persist for extended duration. Over time, underdominance was slowly eliminated as the population structure coarsened and hybrid zones coalesced to form impermeable barriers to

	BB	Bb	bb
AA	1	.5	.92
Aa	.5	0	.5
aa	.92	.5	1

Fig. 2. Sample instantiation of the fitness function described in equation 2 for two loci with $\varepsilon = 0.1$.
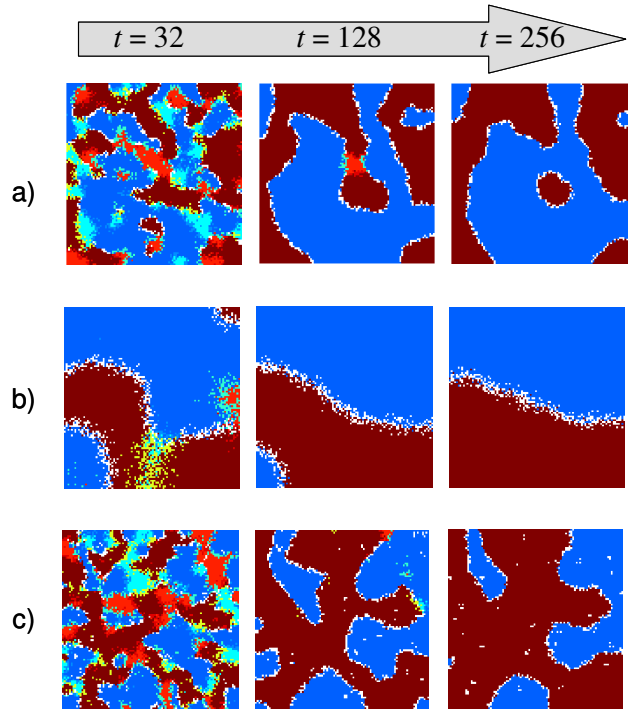

Fig. 3. The evolutionary dynamics of a representative two-locus 100×100 cell population initialized in Hardy-Weinberg equilibrium under mild disruptive epistasis (fitness table as in Figure 2) with (a) 3×3 local mating neighborhoods (relative mating neighborhood size $\delta = 0.03$), (b) 9×9 local mating neighborhoods ($\delta = 0.09$) and (c) 3×3 local neighborhoods following occasional long-range migration events ($p = 0.01$). Note that speciation occurs when all hybrids between viable genotypes are inviable (white).

gene flow. The time to speciation increased exponentially as the number of interacting loci (L) increased ($R^2 = 0.76$, Table 1). In contrast, when mating was panmictic, underdominance was quickly eliminated and the population converged on a single genotype in all trials, as predicted by mean-field approximations [7]. Thus, at one extreme (3×3 local mating) speciation occurs, while at the other extreme (panmixia) fixation on a single genotype occurs.

B. *Absolute vs. Relative Mating Neighborhood Size*

In order to determine whether the absolute (d) or the relative (δ) mating neighborhood size is the relevant governing parameter, the following experiment was performed using simulated populations with two underdominant loci ($L = 2$). We varied both the diameter of the overall domain (D) and the diameter of the square contiguous mating neighborhoods (d). Specifically, D was varied in increments of 10 from $D = 10$ to $D = 100$. For each value of D, the diameter of the mating neighborhood was increased starting from nearest neighbor interactions ($d = 3$) in increments of two. For each value of d, 25 independent simulations were performed. In this experiment, long-distance dispersal was prohibited ($p = 0$)

Table 1. Mean and standard deviation of the time to speciation in a 3×3 localized interaction topology with $\varepsilon = 0.1$ as a function of the number of interacting loci (L). Data summarizes 25 independent simulations for each value of L.

L	Mean Generations	σ
2	235.1	63.9
4	319.8	97.8
6	366.6	80.7
8	464.5	96.4
10	819.8	192.8

and all mating interactions occurred within local $d \times d$ neighborhoods. The population was allowed to evolve until one of two events took place: (*i*) the population separated into reproductively isolated subgroups (speciation) or (*ii*) the population converged on a single genotype (fixation). The critical diameter ($d_c(D)$) is defined as the smallest mating neighborhood size such that a speciation event occurred less than 50% of the time for a given value of D.

The size of the critical diameter of the mating neighborhood ($d_c(D)$) increased linearly in D ($R^2 = 0.92$, Figure 4); i.e. the critical value of the relative mating neighborhood size ($\delta_c = d_c(D)/D$) remained approximately constant. This suggests that the evolutionary dynamics of the population are governed by relative, as opposed to absolute, mating neighborhood size in this system. Thus, as long as the ratio of the mating neighborhood size to overall domain size is held constant, qualitatively similar evolutionary dynamics can be expected on different domain sizes. Note that the two-locus system considered in this experiment is quite robust to large relative mating neighborhood sizes. For example, when $D = 100$, the size of the critical diameter was $d_c = 29$, which includes approximately 8% of the
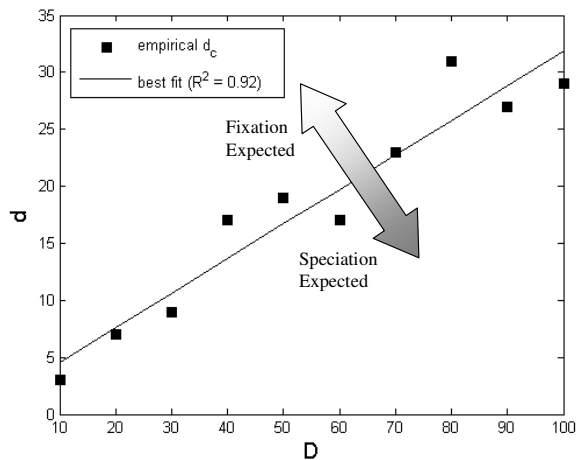

Fig. 4. Critical absolute mating neighborhood size (d_c) as a function of the overall domain diameter (D). The critical absolute mating neighborhood size grows linearly in D ($R^2 = 0.92$).

individuals in the population. While this result may seem surprising, it occurs due to the rapid rate at which the population speciates in the two-locus case (Table 1). Increasing the number of interacting loci (L) increases the time to speciation exponentially (Table 1) and therefore can be expected to affect the size of the critical relative mating neighborhood.

C. Varying the Relative Neighborhood Size: Extension to Multiple Loci

In order to understand the interaction between relative mating neighborhood size and the number of interacting loci, the following experiment was performed. Individuals comprised $L \in \{2,4,6,8,10\}$ interacting loci and each population was initialized in multi-locus Hardy-Weinberg equilibrium on a square lattice with diameter $D = 100$. For each value of L, the following relative mating neighborhood sizes (δ) were tested: $\delta \in \{0.03$ (nearest neighbors), 0.05, 0.09, 0.17, 0.33, 0.65, 1 (panmixia)$\}$. For each value of δ, 25 independent simulations were performed in which the population was allowed to evolve until either a speciation event or fixation event occurred and the number of trials that resulted in speciation and fixation were recorded. These data were used for interpolation to determine the critical relative mating neighborhood size (δ_c), defined as the smallest relative mating neighborhood size such that speciation is expected with probability 0.5 as a function of L. Figure 1 (a,b,c,d) provides a schematic diagram of the way in which the mating neighborhood changes as δ is increased.

As δ increases (i.e. as mating neighborhoods become less localized), the size of the self-organizing clusters increases more rapidly as the population evolves. Figure 3b depicts the evolutionary dynamics of a representative population evolving on an interaction topology with $\delta = .09$. Increasing the relative neighborhood size increased the width of the hybrid boundaries between groups (compare Figure 3b with Figure 3a) and decreased the time required to eliminate patches of less fit individuals. For example, with $\delta = 0.09$, the mean time to speciation was 122.6 generations (standard deviation = 72.9), while the mean time to speciation in a 3×3 local mating population ($\delta = 0.03$) was 235.1 generations (standard deviation 63.9).

The sensitivity of the evolutionary dynamics of the population to the relative mating neighborhood size (δ) varied as a function of the number of interacting loci (L). Figure 5 shows the probability of a speciation event as a function of the size of the relative mating neighborhood and the number of interacting loci. Speciation became less likely as the size of the relative mating neighborhood and/or
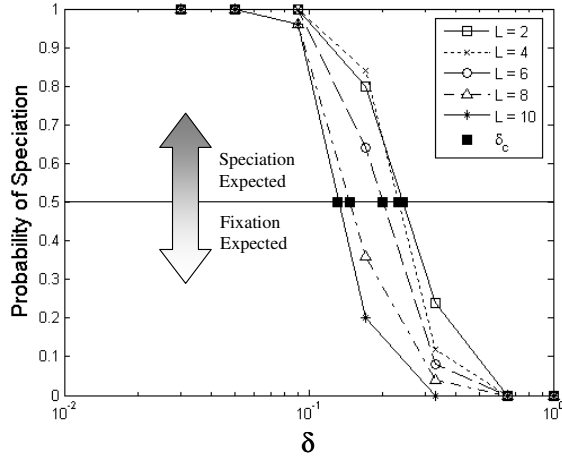
Fig. 5. Probability of speciation as a function of the number of interacting loci (L) and the relative mating neighborhood size ($\delta = d/D$). Each data point denotes the proportion of 25 independent simulations that resulted in a speciation event. The critical points (δ_c) at which the probability of speciation vs. fixation is 0.5 are shown as solid squares.

the number of interacting loci increased. This occurred because the time to speciation increases exponentially in L (Table 1) and therefore populations with more interacting loci are more vulnerable to the disruptive effects of a larger relative mating neighborhood size. The critical size of the relative mating neighborhood (δ_c) decreased linearly in L ($R^2 = 0.95$, Figure 6). Note that the smallest critical value of the relative mating neighborhood size found in these experiments ($\delta_c = 0.13$, $L = 10$) is over four times as large as the relative mating neighborhood size corresponding to 3×3 localized interactions ($\delta = .03$). This finding implies that this speciation process is not restricted to purely 3×3 local mating neighborhoods, but can also occur with larger contiguous mating neighborhoods.

D. Evolutionary Dynamics in Locally Mating Populations with Limited Long-Distance Dispersal

The next series of tests was designed to analyze the sensitivity of the evolutionary dynamics of this system to long-distance dispersal. Once again, individuals comprised $L \in \{2,4,6,8,10\}$ interacting loci and each population was initialized in multi-locus Hardy-Weinberg equilibrium on a square lattice with diameter $D = 100$. The mating neighborhoods of every individual were 3×3 local neighborhoods, but at every generation individuals were randomly selected for dispersal with probability p and the spatial locations of these dispersers were randomly permuted. This process is similar to the random rewiring algorithm used to generate small-world networks [22] with the exception that the arity of each cell in the lattice remains constant in our model. Purely localized mating interactions thus correspond to $p = 0$ and random mating interactions correspond to $p = 1$. In this model, small-world interactions [22] are found in the range $p \in (0.005, 0.1)$ where the
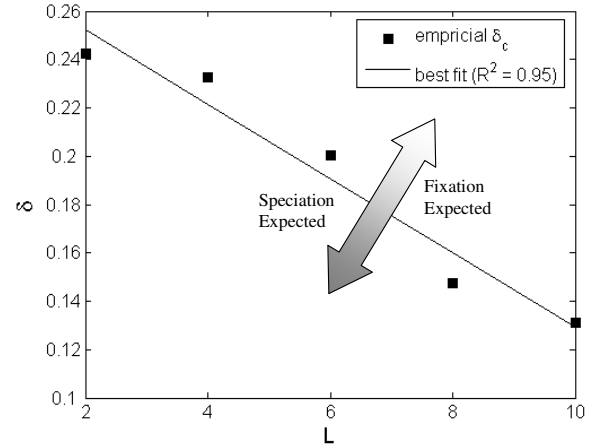

Fig. 6. Critical value of the relative mating neighborhood size (δ_c) as a function of the number of interacting loci (L). Empirical values correspond to the black squares in Fig. 5.

characteristic path length (λ) is almost as short as that of a random interaction topology, despite a preponderance of local interactions.

For each value of L, the probability of randomly changing the spatial location of an individual was varied from $p = 0.0001$ to $p = 1$ in 20 logarithmically spaced increments. For each value of p, 25 independent simulations were performed in which the population was allowed to evolve until either speciation or fixation occurred and the number of speciation and fixation events was recorded. These data were used for interpolation in order to determine the critical probability of long-distance interactions (p_c) as a function of L. The critical probability of long-distance interactions is defined as the p such that speciation is expected with probability 0.5. Figure 1 (a,e,f,g) provides a schematic diagram showing how the mating neighborhood changes as p is increased.

The effect of including limited long-distance dispersal on evolutionary dynamics is depicted graphically for a representative two-locus population in Figure 3c with $p = 0.01$. Despite the presence of long-distance interactions, the evolutionary dynamics of the population are qualitatively similar to those of a purely 3×3 locally mating population in this case; the population self-organizes into groups of similar individuals with mild boundaries to gene flow between them. As the population structure continues to coarsen over time, these boundaries coalesce and begin to form complete boundaries between subgroups, resulting in speciation. As the speciation process proceeds, long-distance mating interactions between individuals from different groups results in patches of inviable offspring, but this does not significantly alter the overall population structure or disrupt the speciation process.
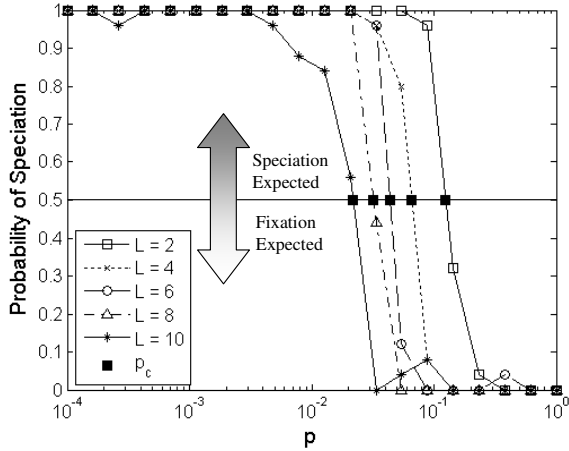
Fig. 7. Probability of speciation as a function of the number of interacting loci (L) and the probability of long-distance interactions (p). Each data point denotes the proportion of 25 independent simulations that resulted in a speciation event. The critical points (p_c) at which the probability of speciation vs. fixation is 0.5 are shown as solid squares.

Fig. 8. Critical value of the probability of long-distance interactions (p_c) as a function of the number of interacting loci (L). The shaded region encapsulated by the dashed horizontal lines denotes the range of p such that the interaction topology possesses a characteristic path length (λ) typically associated with a small-world network (see text). The solid line delineates between the range of p in which speciation is the expected outcome and the range of p in which fixation on a single genotype is the expected outcome. Empirical values correspond to the black squares in Fig. 7.

While the case depicted in Figure 3c shows that the evolutionary dynamics of the population are robust to some long-distance interactions, this result is dependent upon the number of interacting loci (L) and the probability (p) that these long-distance interactions occur. Figure 7 depicts the probability of a speciation event, which is the expected outcome when $p = 0$, as a function of both p and L. As p increases, a phase shift occurs from speciation to fixation on a single genotype as a critical number of long-distance interactions are reached. The critical p at which this phase shift occurs is dependent upon the number of interacting loci. This occurs as increasing L increases the time required for the completion of a speciation event exponentially (Table 1), rendering systems with more interacting loci more susceptible to the disruptive effects of sporadic long-distance mating interactions.

The critical value of long-distance interactions (p_c) at which the phase shift occurs decreases exponentially in L ($R^2 = 0.89$, Figure 8). As p increases beyond a critical threshold, the population begins to behave as if mating is random; genetic diversity is quickly lost and the population converges on a single genotype. However, the characteristic path length (λ) of the interaction topology resembles that of a small-world network at approximately $p = 0.005$, which is almost an order of magnitude smaller than the lowest critical value obtained ($L = 10$, $p_c = 0.022$). Thus, self-organizing speciation is robust to a large subset of the range in which the interaction topology is considered to be small-world.
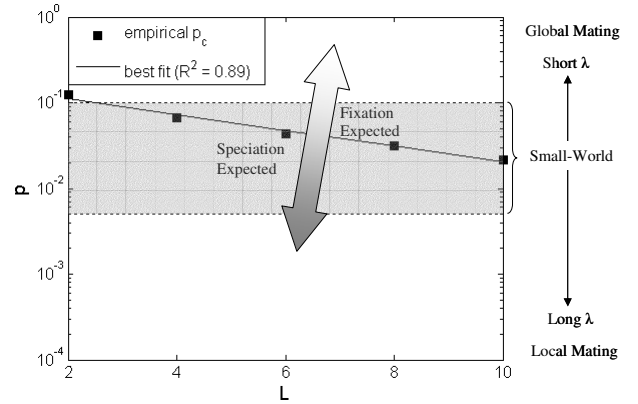
IV. DISCUSSION AND CONCLUSIONS

Even in biotic communities where mating strategies are primarily localized, it is expected that interactions may occasionally occur between previously spatially distant individuals. The focus of this study was on the relaxation of the assumption of purely localized interactions, and how this affects the evolutionary dynamics of self-organized speciation due to multiple underdominant loci [3][8]. We found that the speciation process was robust to contiguous mating neighborhood sizes that could be significantly larger than strict nearest neighbors and that the relative (δ), as opposed to absolute (d), mating neighborhood size was the more relevant governing parameter. This implies that qualitatively similar evolutionary dynamics can be expected on domain sizes larger than those considered herein, so long as δ remains approximately constant. We also found that the speciation process was robust to probabilities of long-distance dispersal (p) that fell well into the range of so-called small-world networks. However, increasing either of these parameters (δ or p) beyond a critical threshold caused a phase transition to behavior similar to that of random mixing, resulting in fixation upon a single genotype. Thus, the structural characteristics of the interaction topology have a pronounced effect upon the evolutionary dynamics of a population.

One metric of particular interest is the characteristic path length (λ) of the potential interaction topology. Spatially localized interaction topologies have a very high characteristic path length, which results in the slow

dissemination of genetic information throughout an evolving population. In contrast, random interaction topologies have a very low characteristic path length and genetic information is able to spread quite rapidly. Analysis of "small-world" networks [22] has shown that it only takes relatively few long distance interactions for the characteristic path length of a primarily localized interaction topology to approach that of a random interaction topology. Preliminary experimentation indicates that the critical values of the relative mating neighborhood size (δ_c) and the probability (p_c) of long-distance interactions found in this study correspond to quantitatively comparable characteristic path lengths. This relation will be studied more rigorously in future work. We also plan to investigate how these governing parameters affect the structural characteristics of the emergent mating topologies [24] of this system, which can differ significantly from the potential interaction topologies studied here. Further, future research will analyze the combined effects of relative mating neighborhood size and probabilities of long-distance dispersal, and focus on other forms of interactions including sex-specific migration.

The results presented herein explore the sensitivity of the evolutionary dynamics of spatially extended populations to the relative size of the interaction neighborhood and to limited long-distance interaction events. These results emphasize the importance of both (*i*) collecting sufficient data to properly determine the true nature of the spatial interactions of the system being studied and (*ii*) building a model that respects the relevant aspects of the interaction topology observed. While such data collection is certainly nontrivial [20][21], the results of this study suggest that these system parameters may play a critical role in governing the dynamics of the population. Interaction topologies commonly employed in models of evolutionary dynamics, such as nearest neighbor interactions, panmictic interactions, or metapopulation structures may be too general and overly simplified to accurately reflect the dynamics of the population one is attempting to model.

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