

Toward computational evolution: Incorporating ecological interactions and conditional dispersal into biologically-inspired algorithms

Joshua L. Payne

Computational Genetics Laboratory, Dartmouth Medical School,
Lebanon, NH 03756, USA
Joshua.L.Payne@Dartmouth.edu

Abstract. The transition from evolutionary computation to computational evolution will require an increase in the biological realism of today’s nature-inspired algorithms. Ecological competition and conditional dispersal are two ubiquitous forces of natural systems that offer the potential to contribute to this transition. However, in order to effectively incorporate these two features into evolutionary algorithms, their interplay must first be understood in a theoretical context. Here, I extend an established model of ecological competition to include conditional dispersal and analyze the evolutionary dynamics of phenotypic diversification. I then discuss how these results can be used to guide the design of evolutionary algorithms that incorporate ecological competition and conditional dispersal, as a step toward computational evolution.

1 Introduction

In their recent perspective article, Banzhaf *et al.* [1] call for a “more sophisticated dialogue between computational and natural scientists about evolution” in order to address “previously unimaginable or intractable computational and biological problems.” Their article points out that the state of the art in evolutionary algorithms lags far behind our current understanding of natural evolving systems, and argues that the inclusion of more biological and ecological realism could greatly improve the search performance and applicability of nature-inspired optimization algorithms. Moreover, it discusses the potential utility of incorporating spatially-explicit ecological interactions, environmental sensing, and repertoire exploitation into population-based optimization methods. These additions offer the potential to increase system evolvability, by facilitating the emergence of novel genetic combinations and better maintaining genetic diversity. This new class of algorithms is referred to as *computational evolution*, a novel paradigm of computational science that could greatly improve the breadth of problem domains to which nature-inspired optimization algorithms are applied and provide natural scientists with better tools for performing evolutionary and ecological experiments *in silico*.

Spatial interactions are often included in evolutionary algorithms by mapping individuals onto the vertices of a network and restricting inter-individual interactions to occur between individuals that share an edge in the network. Such cellular evolutionary algorithms (cEA) typically employ some form of local selection, where parents are selected based on their fitness from within some spatially localized neighborhood. However, to the best of my knowledge, ecological interactions between individuals, such as phenotype-dependent competition, have not yet been considered in the context of cEAs. In natural systems, ecological interactions abound, affecting population diversity and the emergence of novel species [2,3]. Further, cEA's typically assume that individuals are completely sessile, and cannot disperse from their spatial location during their life cycle. In natural populations, dispersal is ubiquitous and a force of paramount importance, influencing species abundances and distributions, population dynamics, and population-level responses to environmental perturbations [4,5,6]. Recent results have demonstrated that dispersal rates are often contingent on local environmental cues. This is referred to as conditional dispersal, a strategy that has been observed in numerous species. For example, dispersal rates in the collared flycatcher *Ficedula albicollis* increase when local offspring quality or quantity decreases [7]; in the butterfly *Melitaea cinxia*, dispersal rates increase when local conspecific density increases [8]; and in the nematode *Caenorhabditis elegans*, dispersal rates increase in the face of strong environmental fluctuations [9]. As conditional dispersal employs environmental sensing, it also allows for repertoire exploitation, where individuals can effectively 'remember' old environmental conditions, so they can respond appropriately when they are encountered again. In addition to ecological interactions and conditional dispersal, these are two generic features of computational evolution [1] that offer the potential to improve the performance of cEAs.

While ecological interactions and conditional dispersal may bring evolutionary algorithms closer to computational evolution, the interplay of these two features in natural systems is still not fully understood. Indeed, the majority of theoretical models of dispersal ignore phenotypic competition altogether, and assume that individuals disperse unconditionally, without regard to local environmental conditions. In order to effectively incorporate ecological interactions and conditional dispersal into evolutionary algorithms, their coupling must first be understood in the context of natural systems.

To this end, I extend an established spatially-explicit model of ecological competition [2,3] to include conditional dispersal. Beginning with a monomorphic ancestral population, I determine the parameter regions in which phenotypic diversification occurs and monitor the evolutionary dynamics of the dispersal characters.¹ I conclude with a discussion on how these results may guide the inclusion of ecological interactions and conditional dispersal into evolutionary algorithms, as a step toward computational evolution.

¹ The methods and results presented herein are deliberately terse and obfuscated, so as to avoid any copyright conflicts that may occur when the extended version of this article is submitted for publication.

2 Methods

I consider a spatially-explicit, individual-based birth-death process in continuous time. Individuals are described by their spatial location (x, y) in the unit square, ecological character u , and conditional dispersal character (v^x, v^y) . The ecological character u is used to denote a morphological, behavioral, or physiological trait. The two-dimensional character (v^x, v^y) is used to parametrize the individual's conditional dispersal function, which I assume takes the form of a step function. All characters are kept in the range $[0, 1]$, except for the dispersal character v^x , whose upper limit is left unbounded.

The fitness, birth rates, and death rates of individuals, as well as the schedule of birth and death events, are as described in [2,3]. In short, the birth and death events occur asynchronously and in proportion to the population-level birth and death rates. The intensity of both spatial and phenotypic competition follow a Gaussian, such that the strength of competition between any two individuals increases as either spatial or phenotypic distance decreases. Thus competition is more intense between either phenotypically similar and/or spatially proximal individuals. There exists an optimal ecological character that yields maximal carrying capacity, and carrying capacity decays according to a Gaussian as the ecological character deviates from this optimum [2].

We consider asexual reproduction. In a reproduction event, the phenotype (u, v^x, v^y) is inherited faithfully from parent to offspring, but is subjected to Gaussian mutation. The inherited dispersal characters (v^x, v^y) are used to displace the offspring from the parent's spatial position. The distance an offspring disperses is conditioned on local environmental quality, defined as the individual's death rate d . Conditional dispersal is assumed to take the form of a step function. The threshold of the step function is encoded in v^x and its height in v^y . The response of an individual conditional dispersal function to its environmental cue d is

$$\sigma_d(v^x, v^y, d) = \begin{cases} 0, & \text{if } d < v^x \\ v^y, & \text{otherwise} \end{cases} \quad (1)$$

This response is used as the standard deviation of a Gaussian distribution with mean zero, from which a dispersal step $(\Delta x, \Delta y)$ is drawn. The disperser is then given the spatial coordinates $(x_i + \Delta x, y_i + \Delta y)$.

3 Experimental Design

The model is parameterized by the widths of three Gaussian kernels: the carrying capacity, spatial competition, and phenotypic competition functions. In this study, we hold the width of the carrying capacity function fixed at $\sigma_K = 0.3$, the width of the spatial competition function fixed at $\sigma_s = 0.2$, and systematically vary the width of the competition function within the range $0.1 \leq \sigma_c \leq 0.6$.

The ecological character is initialized at the value that maximizes carrying capacity $u = 0.5$, and the dispersal characters are initialized at $v^x = 0.7$ and

$v^y = 0.1$. For each value of σ_c , we run 10 independent simulations. In each simulation, we allow the population to evolve for 80,000 generations and measure the evolutionary dynamics of the phenotypic traits.

4 Results

In line with the non-spatial case [2], phenotypic diversification was observed whenever the width of the competition kernel was less than the width of the carrying capacity kernel ($\sigma_c < \sigma_K$). In Figure 1, I depict the evolutionary dynamics of the phenotypic character u for three Gaussian competition kernels. Note that phenotypic diversification only occurs when $\sigma_c < 0.3$.

For all values of σ_c considered, the dispersal threshold v^x evolved toward the population-level average death rate, $d = 1$ (Figure 2). This implies that evolution favored conditional dispersal strategies with sessile behavior in low-competition environments and dispersive behavior in high-competition environments.

5 Discussion

I have investigated a spatially-explicit, individual-based model of phenotypic evolution that includes ecological competition and conditional dispersal. This model has revealed that conditional dispersal does not interfere with phenotypic diversification when reproduction is asexual and that selection favors dispersal strategies in which individuals emigrate from high-competition environments.

This study provides a theoretical basis for the inclusion of ecological interactions and conditional dispersal in evolutionary algorithms, as a step toward computational evolution. The two main insights are: (i) for a Gaussian phenotypic competition function to promote diversification, it must possess a narrow kernel width and (ii) it is possible to include conditional dispersal without impeding the diversification process, so long as reproduction is asexual, as in evolutionary strategies.

To incorporate ecological competition into evolutionary algorithms, individual fitness could be discounted in proportion to the individual's phenotypic similarity with spatially adjacent individuals. This form of competition is similar to niching [10], which has been shown to maintain subpopulations on multiple fitness optima, and improve the exploratory power of population-based optimization. While traditional niching methods only consider phenotypic similarity and ignore spatial proximity, it is well known that imposing constraints on the spatial scale of interaction events facilitates the emergence of evolutionary phenomena that would be otherwise impossible in globally interacting systems (*e.g.*, [11][12][13]). Therefore, phenotypic competition should occur at a local spatial scale, and may provide a simple and novel mechanism for the formation and maintenance of population diversity, as a means to increase system evolvability.

The degree of local phenotypic competition could be used as an environmental cue for conditional dispersal. This would endow individuals with environmental sensing, allowing them to escape hostile conditions. Since these condi-

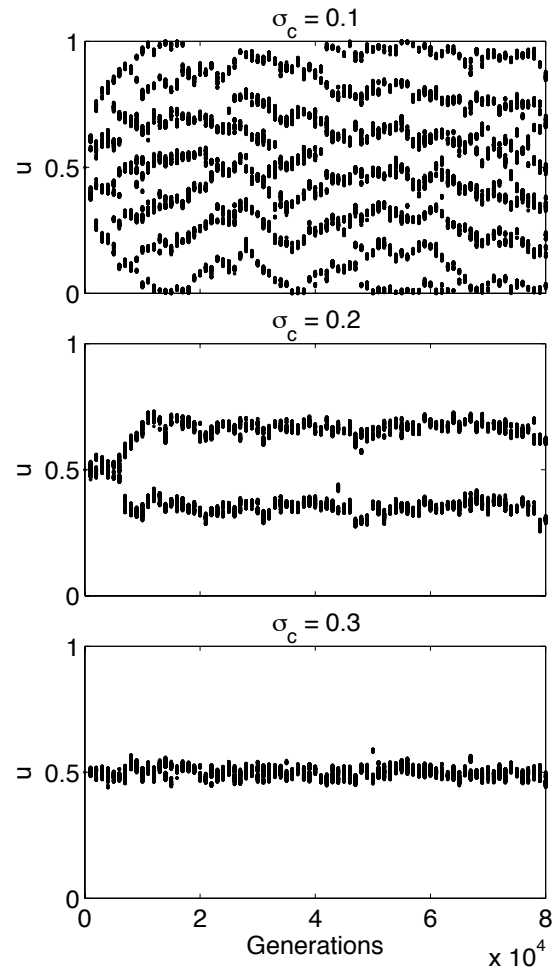


Fig. 1. Evolutionary dynamics of the ecological character u for three Gaussian competition kernels: (top) $\sigma_c = 0.1$, (middle) $\sigma_c = 0.2$, and (bottom) $\sigma_c = 0.3$.

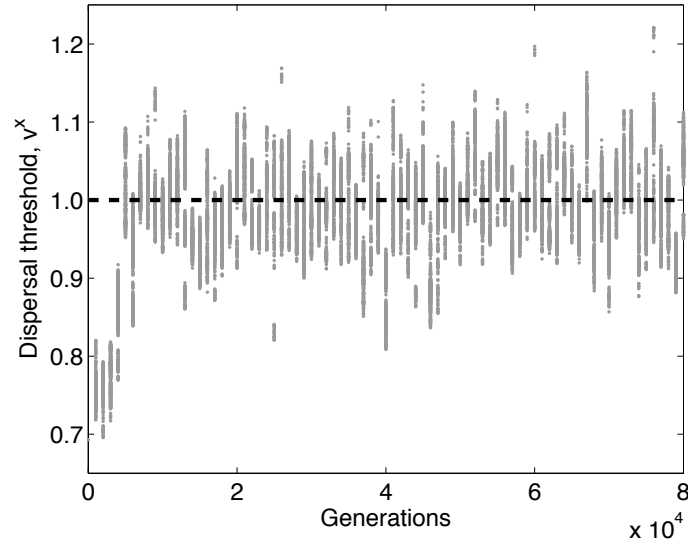


Fig. 2. Evolutionary dynamics of the dispersal threshold v^x for $\sigma_c = 0.6$. The horizontal line represents the population-level average death rate, $d = 1$.

tional dispersal functions may be encoded in the genome, they will be under selective pressure, and individuals will consequently be endowed with repertoire exploitation, allowing them to respond effectively to previously encountered environments and extrapolate their experiences to respond to new environmental conditions. Since dispersal is conditioned on the local environment, which is in turn affected by dispersal events, conditional dispersal provides an opportunity for feedback loops, which are, along with environmental sensing and repertoire exploitation, important features of computational evolution [1].

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