Four Classes of Morphogenetic Collective Systems

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Abstract

We studied the roles of morphogenetic principles—heterogeneity of components, dynamic differentiation/re-differentiation of components, and local information sharing among components—in the self-organization of morphogenetic collective systems. By incrementally introducing these principles to collectives, we defined four distinct classes of morphogenetic collective systems. Monte Carlo simulations were conducted using an extended version of the Swarm Chemistry model that was equipped with dynamic differentiation/re-differentiation and local information sharing capabilities. Self-organization of swarms was characterized by several kinetic and topological measurements, the latter of which were facilitated by a newly developed network-based method. Results of simulations revealed that, while heterogeneity of components had a strong impact on the structure and behavior of the swarms, dynamic differentiation/re-differentiation of components and local information sharing helped the swarms maintain spatially adjacent, coherent organization.

Introduction

Self-organizing behaviors of biological collectives have been subject to many scientific inquiries (Reynolds, 1987; Ben-Jacob, Cohen & Gutnick, 1998; Parrish & Edelstein-Keshet, 1999; Camazine et al., 2001; Sole & Goodman, 2000; Vicsek & Zafiris, 2012). They have also been enthusiastically applied to engineering problem solving as a new paradigm and methodology for decentralized, distributed problem solving by collaborative artificial agents (Kennedy & Eberhart, 1995; Bonabeau, Dorigo, & Theraulaz, 1999; Leonard & Fiorelli, 2001; Dong and et al., 2001-2005; Pfeifer, Iida, & Bongard, 2005; Engelbrecht, 2005; Baldassarre, Parisi, & Nolfi, 2006; Braha, Minai, & Bar-Yami, 2006; Doursat, 2008; 2011). Typical assumptions made in the existing literature are that the system components interact with each other mostly locally and make decisions at individual levels, which eventually leads to the emergence of non-trivial (and potentially useful) macroscopic behaviors. Those models have been successful in reproducing various self-organizing patterns and adaptive functionalities. However, theoretical models used in earlier studies were predominantly focused on homogeneous physical collectives and animal populations. While their simplicity is by itself a virtue in some regard (Vicsek & Zafiris, 2012), they are often too simple to capture more complex phenomena seen in real-world biological collectives, such as multi-cellular organisms’ morphogenesis and physiology, termite colony building and maintenance, and growth and self-organization of human social systems. These systems operate with highly sophisticated within-system regulation mechanisms, or “programs” (Doursat, 2008; 2011).

What are common among those real-world complex biological collectives are heterogeneity of components, dynamic differentiation/re-differentiation of components (i.e., dynamic switching of component types/roles), and local information sharing among components that influence their differentiation. These morphogenetic principles are often absent in earlier models of biological collective behaviors, and they have not been fully utilized in engineering applications either. Here we define a morphogenetic collective system as a system made of a large number of components that self-organize to form nontrivial structures and behaviors using these morphogenetic principles.

There is growing literature of analytical and numerical studies on self-organizing behavior of biological collectives (Vicsek & Zafiris, 2012; Vicsek et al., 1995; Mogilner & Edelstein-Keshet, 1999; Kunz & Hemelrijk, 2003; Hemelrijk & Kunz, 2005; D’Orsogna et al., 2006; Szabo et al., 2006; Chuang et al., 2007; Newman & Sayama, 2008; Paley et al., 2008; Chate et al., 2008; Romanczuk, Coulzin, & Schimansky-Geier, 2009; Tian et al., 2009; Bernoff & Topaz, 2011). It is repeatedly reported that there are a small number of universal classes of collective behaviors, such as disordered, highly ordered, rotational, critical, and jamming patterns, as well as various forms of phase transitions between those classes (Vicsek & Zafiris, 2012). Most of these results are based on the assumption that collectives are homogeneous in terms of their components’ kinetic and behavioral properties. Within-population variations are rarely considered in those theoretical models.
There are some studies that considered the effects of heterogeneity within biological collectives. Graves et al. studied mixed-species bird flocks in Amazonia and created a computational model of them (Graves & Götting, 1993). More recently, Couzin et al. studied self-sorting of a fish school caused by physical variations among individuals (Couzin et al., 2002). His group also studied collective decisions of a swarm influenced by a small number of informed individuals, or leaders (Couzin et al., 2005). We also proposed the Swarm Chemistry model (Sayama, 2009, 2010, 2012a,b) to explore self-organization of swarms made of kinetically distinct types of particles. However, these studies still assumed that within-population variations are variations of fixed individual properties. None of them considered a more sophisticated form of dynamic, adaptive changes of behavioral rules of individuals within a population, potentially through local communication and information sharing.

When one looks at real-world biological collectives, there are a number of examples where more complex forms of heterogeneous collectives produce highly intricate patterns and behaviors that look almost self-evidently “designed” by someone or something (Doursat, 2008, 2011; Turner, 2007). Such instances can be found at every scale in biology. For example, Ben-Jacob et al. reported very complex, heterogeneous, even intelligent, information processing and motion control taking place in bacteria societies (Ben-Jacob, Cohen & Gutnick, 1998; Ingham & Ben-Jacob, 2008; Ben-Jacob, 2009). Social insects are another well-studied example, where dynamic switching of different roles driven by local information sharing realizes highly efficient division of labor (Camazine et al., 2000; Bonabeau, Dorigo, & Theraulaz, 1999; Bonabeau et al., 1999; Campos et al., 2000; Beshers & Fewell, 2001). Among the most interesting and complex examples are the incredibly sophisticated, large-scale mounds built and maintained by termites (Turner, 2000, 2007, 2011). A termite mound operates as if it were a carefully designed and fully integrated physiological system, inside which individual termites “differentiate” to play various different roles. The complexity of such real-world biological collectives were not fully captured in the earlier literature of collective behaviors mentioned above.

**Four Classes of Morphogenetic Collective Systems**

As briefly reviewed above, the dynamics and capabilities of different types of morphogenetic collective systems are yet to be fully understood. Recent increase of studies that incorporate at least part of the morphogenetic principles indicates the promising nature of this direction of research. In order to systematically study the effects of each of the morphogenetic principles, here we propose the following four distinct classes of morphogenetic collective systems, which are obtained by incrementally introducing morphogenetic principles to agents’ behavioral and communication capabilities (Fig. 1):

A. *Homogeneous collectives,* where agents’ behaviors are determined by a globally defined, uniformly applicable function of observations.

B. *Heterogeneous collectives,* where an agent’s behavior is determined by a function of observations specified by the agent’s static state or type.

C. *Heterogeneous collectives with dynamic differentiation/re-differentiation,* where the heterogeneity of agent behaviors is created and dynamically maintained by transitions of agents’ internal states. Agents’ state transitions are also determined by a function of observations and states.

D. *Heterogeneous collectives with dynamic differentiation/re-differentiation and local information sharing,* where agents can share information (internal states and their observations) with local neighbors, in addition to all the above capabilities.  

Our rationale in defining these four classes is that each morphogenetic principle requires the precedent one. Namely, differentiation/re-differentiation requires multiple states or types of components (heterogeneity), and information sharing would make sense only if agents could change their behaviors according to it (differentiation/re-differentiation). We thus argue that these four classes should represent a natural, straightforward hierarchy of morphogenetic collective systems, arranged in the ascending order of their organizational complexity.

In this classification, Class A includes traditional collective behavior models, including Boids (Reynolds, 1987) and its variants that use homogeneous swarms. More recent models that use heterogeneous swarms (Couzin et al., 2002, 2005; Sayama, 2009, 2012a) belong to Class B. Examples that may be close to those of Class C are the variants of Swarm Chemistry (Sayama, 2010, 2011; Sayama & Wong, 2011) that implemented stochastic differentiation/re-differentiation of agents, though it was not driven by any state-transition function and thus not dynamical or adaptive. Finally, real biological/social morphogenetic systems—such as embryogenesis of multicellular organisms, colonies of eusocial insects and cities in human civilizations—are most likely in Class D. Several models proposed in Morphogenetic Engineering (Doursat, Sayama, & Michel, 2012) also belong here. However, we are not aware of any well-established model of swarm-based collective behaviors that belong to this class.

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1Here we consider information sharing as explicit signal transmission among agents to share externally unobservable information about their internal states and observations with local neighbors. This should not be confused with kinetically transferred information theoretic waves propagating in swarms that were studied in recent literature (Wang et al., 2012).
Figure 1: Four classes of morphogenetic collective systems proposed in this paper. Variables $s_i$, $o_i$, and $a_i$ represent the internal state of agent $i$, the observation it receives from the environment, and the corresponding action it takes (e.g., acceleration), respectively. A: Homogeneous collectives. Agents’ behaviors are determined by a function of observations, $F(o)$. B: Heterogeneous collectives. Each agent has its own static state ($s_i$), and $F$ takes $s_i$ as an additional argument as well as $o_i$. C: Heterogeneous collectives with dynamic differentiation/re-differentiation. Agents’ states can dynamically change according to another function, $G(s)$. D: Heterogeneous collectives with dynamic differentiation/re-differentiation and local information sharing. Arguments of the functions are sets of $s_i$ and $o_i$ within the agent’s neighborhood, which represents the local information sharing.

**Model: Morphogenetic Swarm Chemistry**

To study qualitative and quantitative differences in possible morphologies and behaviors between the four classes, we have developed a mathematical model of morphogenetic collective systems by implementing new rule-based state transition and local information sharing capabilities in the Swarm Chemistry model (Sayama, 2010, 2012b). Swarm Chemistry is naturally suitable for this research task because it already can represent both homogeneous and heterogeneous collective systems in its model framework.

In the extended model, the design of a swarm is specified in three parts: a recipe $R$, a preference weight matrix $U$, and a local information sharing coefficient $w$. Definitions of these parts are as follows:

**Recipe $R$:** A list of different kinetic parameter settings for multiple swarm states. Each entry in a recipe is composed of a relative frequency of a particular state within the swarm and its kinetic parameter settings (e.g., local perception range, normal speed, strengths of kinetic forces, etc.). This part of the specification is the same as in our earlier studies (Sayama, 2009, 2010).

**Preference weight matrix $U$:** A $n \times (n + 5)$ rectangular real-valued random matrix where $n$ is the length of the recipe, i.e., the number of possible states of agents in a swarm. Its contents represent how each observation component (defined later) affects the agent’s preference for a particular state choice.

**Local information sharing coefficient $w$:** A real number in $[0,1]$, which determines how much information about the neighbors’ states and observations are to be shared and incorporated into the agent’s own state transition.

Each agent in a swarm in this extended model has its own state $s_i$, in addition to position $x_i$ and velocity $v_i$. The movement and state transition of agents is simulated as follows:
**Step 1.** An agent computes its action (acceleration) based on its neighbors’ relative positions and velocities using the standard Swarm Chemistry simulation algorithm [Sayama 2009].

**Step 2.** Before making any actual movement, the agent also computes an \((n + 5)\)-dimensional observation vector \(o_i\) that summarizes the situation the agent is in. More details of this vector will be discussed later.

**Step 3.** Once all the agents computed their actions and observation vectors, each agent updates its velocity according to the computed acceleration, and then moves using the updated velocity.

**Step 4.** The agent computes a state preference vector \(u_i = (1 - w)Uo_i + wU\langle o\rangle_i\), where \(\langle o\rangle_i\) is the average of observation vectors of other agents in the local neighborhood. If there are no other agents found in the neighborhood, \(u_i = Uo_i\) regardless of \(w\).

**Step 5.** The agent checks if the \(s_i\)-th component of \(u_i\), \(u_{i}(s_{i})\), is negative. If this is the case, it means that its current state is not preferable in the current situation, and therefore the agent attempts, with probability \(1 - \exp(u_{i}(s_{i}))\), to choose a new state. A new state will be chosen as the next value of \(s_i\), via a roulette selection where \(\exp(u(s))\) is used as the selection weight for state \(s\).

The observation vector \(o_i\) plays an important role in this model. While there are many choices for how to construct an observation vector, we used the following definition as an initial step of our investigation. The first \(n\) components of \(o_i\) are all 0’s except for the \(s_i\)-th component that is set to 1. This part embeds the information about the agent’s current state into the vector so that it can be superposed and averaged with other agents’ states. The remaining five components of \(o_i\) are as follows:

- \(|(x)_i - x|^2 / R_i^2\): Square of the relative distance from the average position of other agents in the neighborhood \(\langle x\rangle_i\). \(R_i\) is the perception range in the parameter set the agent is currently using. If there are no other agents nearby, this is set to 0.

- \(|v_i|^2 / v_{in}^2\): Square of the ratio of the agent’s current velocity and the normal velocity \(v_{in}\) in the parameter set the agent is currently using.

- \(|v|/ v_{in}\): Square of the ratio of the neighbors’ average velocity \(\langle v\rangle\) and the normal velocity in the parameter set the agent is currently using. If there are no other agents nearby, this is set to 0.

- \(|(v_i - v)|^2 / v_{in}^2\): Square of the relative difference in velocity between the agent and its neighbors. If there are no other agents nearby, this is set to 0.

- \(1\): A constant term.

Although it is a highly constrained, mathematically stylized formulation, this extended Swarm Chemistry model can still describe a wide variety of morphogenetic collective systems, including the four classes proposed in this paper. Specifically, including only one parameter set in \(R\) and letting \(U = 0\) and \(w = 0\) will make a Class A swarm. Including multiple parameter sets in \(R\) with \(U = 0\) and \(w = 0\) will make a Class B swarm. A Class C swarm will be obtained by additionally adopting a non-zero matrix for \(U\) while \(w = 0\). Finally, a Class D swarm will be obtained by adopting non-zero \(U\) and \(w\).

**Experiments**

We conducted systematic Monte Carlo simulations to see if there were any significant differences in the dynamics of morphogenetic collective systems among the four classes. Specifications of swarm designs were configured as follows:

- The number of agents was fixed to 300 for all cases.

- The number of possible agent states \(n\) was set to 1 for Class A swarms, or otherwise \(\xi + 2\) where \(\xi\) is a random integer sampled from a Poisson distribution with mean 1.

- Recipe \(R\) was created by sampling each kinetic parameter’s value from a uniform distribution between 0 and the parameter’s maximum value defined in [Sayama 2009]. The relative frequencies of different parameter settings were determined by randomly dividing 300 into \(n\) portions.

- Preference weight matrix \(U\) was set to all 0’s for Class A and B swarms. For Class C and D swarms, each component of \(U\) was set to 0 for Class A, B and C swarms, while it was sampled from a uniform distribution between 0 and 1 for Class D swarms.

Five hundred independent simulation runs were conducted for each class. Each run was initialized with 300 agents whose positions were randomly distributed in a two-dimensional \(300 \times 300\) (in arbitrary unit) square area and whose velocities were set to 0, and then simulated for 400 time steps. In each time step during the second half of the simulation \((t = 201 - 400)\), the following properties were measured from the agents’ positions and velocities:

- Average speed of the swarm as a whole \(\langle|v|\rangle\), where \(\langle\ldots\rangle\) denotes an average over all the agents hereafter unless noted otherwise.

- Average of absolute speed of agents \(\langle|v|\rangle\).
Figure 2: Construction of networks from swarms. Top: Illustration of the algorithm. A: Spatially distributed agents. B: Ranges of neighbor recognition drawn around the agents. The radius of each range is αd_i (see text). C: Resulting network where pairs of agents that mutually recognize each other as neighbors are connected. Bottom: An example of network construction from a simulated swarm. D: Original swarm snapshot. E: Network constructed from agent positions in D.

- Average angular velocity of the swarm as a whole (⟨(x − ⟨x⟩) × v/|x − ⟨x⟩|^2⟩).
- Average distance of agents from center of mass (⟨|x − ⟨x⟩|⟩).
- Average pairwise distance (⟨|x_1 − x_2|⟩), where x_1 and x_2 are positions of two randomly sampled agents; the average in this case was over 10,000 sampled pairs).

In addition, topological properties of the swarm morphology were also measured. For this task, we constructed a network for each swarm at each time step during the measurement period by connecting agents that were spatially close to each other. More specifically, we first measured a characteristic “neighbor” distance d_i for each agent by calculating the mean of its distances to its k nearest neighbors. The agent then recognized all other agents within distance αd_i as its “neighbors”. Once this was done for all agents, the pairs of agents that mutually recognized each other as “neighbors” were actually connected. We used k = 2 and α = 1.7, which were empirically chosen to approximate cluster structures recognized visually by human experimenters. Figure 2 shows examples of this network construction process.

For each swarm converted to a network, we measured the following topological properties:

- Number of connected components.
- Average size of connected components.
- Homogeneity of sizes of connected components. This was measured by the normalized entropy in the distribution of sizes of connected components. If there was only one connected component, this was set to 1.
- Size of the largest connected component.
- Average size of connected components smaller than the largest one. If there was only one connected component, this was set to 0.
- Average clustering coefficient.
- Link density.

Overall, we obtained time series of 5 + 7 = 12 measurements from each simulation run. These time series were further summarized by calculating their respective mean and standard deviation over time. As a result, the structure and behavior of each swarm was characterized by 2 × 12 = 24 outcome variables. Finally, a visual image of the swarm at the end of the simulation (t = 400) was also recorded for visual inspection of the swarm’s topology.

The simulator was implemented in Python using NetworkX (Hagberg, Schult, & Swart, 2008) and PyCX (Sayama, 2013). The code is available upon request.

**Results**

Simulation results are summarized in Table 1 where medians of 24 outcome variables were shown for each class together with p-values obtained using the Kruskal-Wallis median test between the four classes. Statistically significant differences were detected for most of the outcome variables, especially for topological outcome variables, which demonstrates the effectiveness of our network-based topology characterization method. Most of the variables with statistical significance showed clear differences between Class A (homogeneous) and other (heterogeneous) swarms. The temporal mean of the average clustering coefficient was the only outcome variable that did not show statistically significant differences between the classes. This metric may be primarily determined by constraints built in our simulation or network construction algorithms.

We found several notable patterns in Table 1. First, the medians of Class A swarms consistently took the lowest values among the four classes with regard to the temporal standard deviations of measurements (lower half of Table 1). This indicates that the interactions between different types of agents helped produce dynamic behaviors, causing temporal fluctuations of their macroscopic properties. Second, there were clear differences between Class B (with no state

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2Visual snapshots of the swarms’ final configurations for each of the four classes are also available online at http://bingweb.binghamton.edu/~sayama/SwarmChemistry/
Table 1: Comparison of medians of 24 outcome variables between four classes of morphogenetic collective systems. The $p$-values of the Kruskal-Wallis median test were shown in the rightmost column (*: $p < 0.01$, **: $p < 0.001$, ***: $p < 0.0001$). Variables with statistically significant differences were highlighted in color (yellow: high, cyan: low). The intensity of color is adjusted according to the $p$-value of the variable and the distance from overall average. The top half shows temporal means of the 12 measurements while the bottom half shows temporal standard deviations of the 12 measurements.

| Kinetic outcomes | Class A median | Class B median | Class C median | Class D median | K-W test $p$-value |
|------------------|----------------|----------------|----------------|----------------|--------------------|
| average speed of swarm | 2.46921 | 3.63557 | 3.71434 | 4.0491 | 0.00000*** |
| average absolute speed of agents | 7.93488 | 9.14903 | 9.15137 | 9.86948 | 0.00024** |
| average angular velocity of swarm | 0.000381388 | 0.00135725 | 0.000879347 | 0.000775047 | 0.00000*** |
| average distance from center | 144.646 | 375.673 | 215.245 | 206.946 | 0.00000*** |
| average pairwise distance | 197.277 | 521.194 | 302.728 | 284.57 | 0.00000*** |
| number of connected components | 1.54 | 11.65 | 9.91 | 7.8175 | 0.00000*** |
| average size of connected components | 234.013 | 27.7284 | 32.4974 | 41.5561 | 0.00000*** |
| homogeneity of connected component sizes | 0.957634 | 0.647418 | 0.669637 | 0.670815 | 0.00000*** |
| size of largest connected component | 298.633 | 177.26 | 199.48 | 212.645 | 0.00000*** |
| average size of smaller connected components | 1.00075 | 6.93472 | 5.18955 | 5.0891 | 0.00000*** |
| average clustering coefficient | 0.43364 | 0.434347 | 0.433522 | 0.431574 | 0.18211 |
| link density | 0.0164127 | 0.0131673 | 0.0137475 | 0.0136435 | 0.00000*** |

| Topological outcomes | Class A median | Class B median | Class C median | Class D median | K-W test $p$-value |
|----------------------|----------------|----------------|----------------|----------------|--------------------|
| average speed of swarm | 0.109345 | 0.318225 | 0.28713 | 0.262987 | 0.00000*** |
| average absolute speed of agents | 0.0285353 | 0.0849336 | 0.0910742 | 0.0853709 | 0.00000*** |
| average angular velocity of swarm | 0.00185725 | 0.00357737 | 0.00376014 | 0.00401965 | 0.00000*** |
| average distance from center | 0.353114 | 45.9475 | 11.2173 | 4.87346 | 0.00000*** |
| average pairwise distance | 1.11209 | 62.249 | 15.4285 | 6.60913 | 0.00000*** |
| number of connected components | 0.156125 | 2.17945 | 1.86601 | 1.79757 | 0.00000*** |
| average size of connected components | 1.24985 | 4.90952 | 4.20666 | 4.12473 | 0.00000*** |
| homogeneity of connected component sizes | 0.0176554 | 0.0424783 | 0.0458559 | 0.053207 | 0.00000*** |
| size of largest connected component | 0.211601 | 5.37309 | 4.24246 | 4.94907 | 0.00000*** |
| average size of smaller connected components | 0.207179 | 1.54578 | 1.03091 | 1.04183 | 0.00000*** |
| average clustering coefficient | 0.00936916 | 0.0174722 | 0.0165864 | 0.0162297 | 0.00000*** |
| link density | 0.000306748 | 0.000324602 | 0.000351948 | 0.000350871 | 0.00000*** |

transitions) and Classes C & D (with state transitions) regarding temporal standard deviations of the average distance of agents from the center of mass and the average pairwise distance. This is likely due to the fact that, while Class B swarms tend to disperse into smaller clusters easily, agents of Class C & D swarms can stay together and maintain spatially adjacent, coherent organization more often, because adaptive state transitions help initially incompatible agents assimilate into kinetically compatible types.

Finally, we noticed a consistent trend in a number of the outcome variables that the properties of Class C & D swarms sat somewhere in between those in Class A and Class B. This could also be understood in that dynamic state transition, possibly driven by local information sharing, has enabled swarms to adaptively achieve coherence in their structures and behaviors. However, the results also indicate that the swarms in Classes C & D did not simply turn into a more homogeneous state like Class A ones, because nearly all the topological outcome variables showed significant differences between Class A and Classes C & D. Therefore, this apparent trend found in morphogenetic collective systems in Classes C & D must be understood not as simple homogenization but as an emergent shift of higher-level system properties.

Conclusions

In this paper, we proposed a classification of morphogenetic collective systems based on the absence or presence of three morphogenetic principles: heterogeneity of components, dynamic differentiation/re-differentiation of components, and local information sharing among components. Monte Carlo simulations with an extended morphogenetic
Swarm Chemistry model demonstrated that, while heterogeneity of components had a strong impact by itself on the structure and behavior of the swarms, the other two morphogenetic principles, i.e., dynamic differentiation/re-differentiation of components and local information sharing, greatly contributed to the maintenance of spatially adjacent, coherent organization of swarms. Interestingly, many outcome measurements of Class C and D swarms fell somewhere in between those of Class A and Class B. This result indicates that the dynamic, adaptive state transition of components possibly driven by their mutual information sharing is playing an essential role in achieving structural and functional integration of biological and social collectives.

The present study has several fundamental limitations. First, the dynamics of swarms were explored only through a limited number of random parameter sampling and analyzed only using simple median comparisons. It was a reasonable first step of exploration when nothing was known about the model, but this approach would not be able to characterize behavioral diversity and richness of each class of systems or to discover non-trivial behaviors that would be statistically rare but unique and interesting. To fully explore and understand the limit of dynamical diversity of each class, more sophisticated evolutionary or other population-based search methods should be conducted. Now that we have 24 outcome metrics defined, we can try evolving morphogenetic collective systems toward a certain area in this metric space, to examine how closely the swarms of each class can achieve the target properties.

Second, the model we used in this study (morphogenetic Swarm Chemistry) was developed using somewhat arbitrary design decisions. The behavioral rules were exactly the same as those used in previous swarm models, which were limited to agents’ acceleration only. The state transition functions were defined in a rather simple and linear fashion using a product of a preferential weight matrix and an observation vector. Moreover, the variables included in the observation vector were chosen without substantial justification. We will need to consider adopting more open-ended, non-linear forms of representations for observations, state transitions and agent behaviors. We plan to apply genetic programming (Banzhaf et al., 2000) or other symbolic evolutionary search methods (Bongard & Lipson, 2007) to overcome this limitation in the future.

Finally, the scope of the experiments was limited only to “free” self-organization of collectives without any stimuli or constraints. Exposing swarms to such external conditions and measuring their adaptive responses will further clarify the functional differences between different classes of morphogenetic collective systems.

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