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Morphogenesis in Robot Swarms

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Abstract

Morphogenesis allows millions of cells to self-organize into intricate structures with a wide variety of functional shapes during embryonic development. This process emerges from local interactions of cells under the control of gene circuits which are identical in every cell, and is robust to intrinsic noise and adaptable to changing environments.

Constructing human technology with these properties presents a significant opportunity in swarm robotic applications ranging from construction to exploration. Morphogenesis in nature may use two different approaches: hierarchical, top-down control or spontaneously self-organizing dynamics such as reaction-diffusion Turing patterns. In this paper, we provide a demonstration of purely self-organizing behaviors to create emergent morphologies in large swarms of real robots. The robots achieve this collective organization without any self-localization, and instead rely entirely on local interactions with neighbors. Results show swarms of 300 robots that self-construct organic and adaptable shapes that are robust to damage. This is a step towards the emergence of functional shape formation in robot swarms following principles of self-organized morphogenetic engineering.

Summary

Endowing robot swarm systems with biological morphogenetic behavior, making swarm shape formation – emergent, adaptive and robust.

Introduction

While human technology is typically constructed by an external builder (humans or robots), most spatially-organized biological systems dynamically create their own physical shapes. This process of shape-formation is called morphogenesis and it occurs in a distributed, self-organized and emergent manner. For example, collectives of insects, such as ants, construct bridges to traverse terrains (fig. 1(A)i.). Organisms such as slime mold and bacteria create colonies with regular spatial geometries to optimize nutrient transport and consumption (Figs. 1(A)ii. and iii.). Multicellular organisms provide the most impressive example of morphogenesis, where massive collections of cells combine and actively collaborate during embryo development to build complex tissues and organs (fig. 1(A)iv.). Having a functional shape and organization is important for survival, because it allows organisms to inhabit certain ecological niches and thrive in given environments.

Two broad principles of spatial patterning exist in biological morphogenetic systems (1).

- A. *Top-down control.* In some tissues, cells first access information about their location, and then make cell fate choices according to this positional information (2). The control system is distributed—all cells have the same regulatory circuits, or genetic program—, but the positional information is achieved by means of an effective coordinate system, which may be created by molecular gradients or other mechanisms (3, 4).
- B. *Local self-organisation.* As an alternative to positional information, spatial patterning may be controlled by purely local self-organization – spontaneous

symmetry breaking processes, such as chemical reaction-diffusion (RD) systems (5). The mathematics of such processes (such as Turing patterns (6)), has been extensively studied over the past half century (7). These processes can only produce relatively simple periodic patterns, but they do so without the cells requiring access to any positional information, and due to their reliance on feedback mechanisms are very robust to noise.

Segmentation of the *Drosophila* embryo is a paradigmatic example of the first principle, in which each segment is genetically controlled individually (8), while the patterning of mouse digits is an example of the second principle, where each digit is a repetition of the same local process (9).

The recent new field of *morphogenetic engineering* introduces the principles of natural morphogenesis into human engineered systems (10). More specifically, it uses the distributed control paradigm of developing tissues to program the generation of structures that are both robust and show predictable behavior. Ideally, such systems should display a high degree of autonomy, self-regulation, and some degree of active self-repair or regeneration in the case of damage. In the area of swarm robotics, where the swarm consists of simple identical robots, a key challenge is to design control algorithms for achieving complex behaviors and shapes, based on robots interacting only with their local environment and their neighbors. Swarm morphogenesis might be achieved by the principles (A) or (B) above, or a combination of the two. Top-down approaches (A) could have the advantage of creating any arbitrary shape, while the self-organized approaches (B), although more limited in the patterns they can create, would have the advantage of being emergent, naturally scalable, robust to failure of individual agents, and flexible, i.e., exhibiting the type of swarm intelligence seen in natural swarms (11).

Potential applications of such morphogenetic approaches in swarm engineering are numerous: Self-constructing buildings which naturally adjust their structure to the geometry of their location, reconfigurable robots which adapt their shape for different tasks, self-organized swarms of satellites (12) for mapping, or search and environmental monitoring. Nanomedicine could also benefit from having self-organizing swarms of nanoparticles for more efficient drug targeting and delivery (13). Ultimately, machines functioning in this way could achieve dynamically-changing physical structures—*programmable matter* (14, 15)—, and as such, would open-up a whole new world of machinery.

In the field of robotics, the problem of controlling the configuration of a group of robots has been receiving increasing interest, although mostly in theoretical studies based on simulations rather than real robot swarms. The target behaviors for the swarm have included collective navigation and flocking, trail formation, seizing and enclosing a target, and gap crossing, but rarely focused on controlling the shape of the swarm per se. Control systems have included rule-based schemes (16-18), density-based schemes (19, 20), attraction/repulsion based on simple signals or gradients (21-29), or have employed more complicated interactions between signals such as reaction-diffusion systems (30, 31), gene regulatory networks (GNRs) (32-35) and swarm chemistry (36) (for a more extensive

review, see (37)).

However, most prior work required precise motion or sensing abilities such as measuring angles to neighbors. Furthermore, when adaptability to different scenarios was tested with real robots (16, 17, 18, 22, 28, 30, 32, 33), no more than thirty agents were used. In particular, properties such as self-healing of swarm morphologies have mostly been tested in simulations (20, 24, 31, 32, 33, 36), with some exceptions (16). As validation has been mainly simulation-based, or using few real robots, it is unclear whether self-organized morphogenesis algorithms proposed so far would cross the reality gap and scale up in a large swarm of simple, noisy robots.

A significant breakthrough in the field of swarm robotics was made by Rubenstein *et al.* when they created the kilobot, a minimal, low-cost robot designed to enable swarm experiments in large numbers (38). Two years later, they specifically demonstrated the shape formation capabilities of this robotic platform (39), in which a swarm of 1024 robots successfully arranged itself into pre-defined morphologies, such as a starfish shape, in a decentralized manner. This impressive result was achieved with only local communication between neighboring robots. However, it depended on the hierarchical control principle mentioned above (A)—each robot had an explicit image of the final shape that should be created, and every robot had access to a coordinate system constructed by the kilobots themselves, such that each robot knew its relative position within the swarm. The shapes were thus not fully “emergent” (principle B above) thus placing limitations on their ability to be adaptable, scalable and robust. A more recent study from the same group extended the approach to create swarm shapes by “disassembly” of the swarm using a light attraction/repulsion system (40), but it still relied on the same top-down approach.

Here, we chose a specific biological inspiration to address the problem of shape formation—namely, spontaneous self-organized patterning (principle B) that occurs in some examples of multicellular tissue development. Although the many cells in a tissue do different things (e.g., becoming different cell types, or migrating in different directions), they all contain the same gene regulatory network (GRN)—the same genomic “program” (Figs. 1(B)i. and ii.). Biological cells continually sense their neighborhood and communicate with other cells with the help of signaling molecules, thus creating an interconnected network. The design of the GRN leads to spatially non-uniform patterns of gene activity in which different genes are activated in different cells in a coordinated manner. These molecular patterns are then responsible for directing secondary processes: Coordinated cell movement (migration), tissue proliferation (cell replication) or apoptosis (cell death), which physically shape the tissue. Since our individual robots cannot replicate, our goal here was to implement swarm morphogenesis based only on cell movements (migration), which is indeed known to drive a number of well-studied developmental cases, for example gastrulation.

The key goal was to achieve simple biologically-inspired morphologies by purely emergent self-organized morphogenesis (approach B). This would allow morphogenesis

without the robots needing to determine their locations, and thus showing a higher degree of adaptability and robustness. Drawing directly on inspiration from developmental systems, we chose to use reaction-diffusion (RD) circuits, and in particular Turing systems, as they have recently been shown to underlie a number of developmental models (41-43) (fig. 1(C)i.). RD circuits describe a system of interacting molecular species (such as diffusible proteins encoded by the gene circuit) which can encode a genuinely symmetry-breaking reaction which produces spatial patterns of spots or stripes (fig. 1(C)ii.). Although such patterns are limited to periodic arrangements, in nature they have led to morphologies with a variety of useful functions. Their lack of dependence on positional information removes the potential errors that such self-localization mechanisms would experience. Furthermore, we explored whether feedback could be observed between patterning and tissue movement. In other words, could examples be found in which robot movements would be driven by the “molecular” pattern, but where the consequent alterations in swarm shape would also feedback to alter the pattern. This is a studied phenomenon in development, known as *morphodynamic patterning* (44, 45), and believed to provide intrinsic adaptability and self-repairing behavior. These results were achieved in a real but very simple swarm technology, in which the shape-forming behavior of the collective swarm is reliable, even when the behavior of the individual robots are relatively unreliable, thus requiring the collective whole to be greater than the sum of its parts.

Results

The swarm robotic platform that we used for our work is the kilobot (38). Kilobots are minimal robots designed to enable swarm experiments in large numbers. Three main functionalities were used: movement, robot-to-robot communication and a multi-color LED for experimental monitoring (fig. 2(A)). In kilobots, locomotion is achieved by two motors that generate vibrations for the legs resulting in non-holonomic movement with a large amount of noise. Communication is performed by passing infrared messages and is limited in range (see Methods for more details). Noisy distance measurements to neighbors can directly be extracted through communication, but not angle, i.e., when receiving a message, a robot cannot detect from which direction the message arrived. The lack of directional sensing and the degree of noise in motion and communication were ideal to demonstrate robust self-organized collective behavior (morphogenesis) even with robots that are simple and unreliable—a key goal for robust but economical technologies.

The morphogenetic mechanism explored was the interaction of the two activities described above (fig. 2(B)): Pattern formation driven by GRNs, and migration or “tissue movement”—the collective motion of the individual kilobots responsible for re-shaping the swarm morphology. These two processes should happen simultaneously (not sequentially) thus directly interacting with each other to achieve dynamic morphogenesis.

For the first part, pattern formation, the Turing system was used as the underlying mechanism, comprising a GRN of two virtual molecules, U and V , conceptually represented in fig. 2(C)i. Each robot kept track of its own concentrations of U and V , and the interactions between the two molecules were configured as an activator-inhibitor network, where molecule U acted as an activator and molecule V acts as an inhibitor. The change in concentration of each molecule was given by the reaction-diffusion equations:

$$\frac{\partial u}{\partial t} = Rf(u, v) + D_u \nabla^2 u$$

$$\frac{\partial v}{\partial t} = Rg(u, v) + D_v \nabla^2 v$$

$$f(u, v) = (Au + Bv + C) - \gamma_u u$$

$$g(u, v) = (Eu - F) - \gamma_v v$$

The reaction part of the equation could be solved directly on each kilobot, just by using the current values of U and V . For the diffusion part, the values of both the activator and inhibitor of each neighbor in range was necessary, which can be obtained via message passing (fig. 2(C)ii. —details given in Methods). In fig. 2(C)iii., we also show examples of different Turing patterns produced by varying a parameter of the reaction-diffusion equations. Green activation of the LEDs was programmed to appear where the concentration of the activator U was high (i.e., above a threshold value). By varying parameter C , the type of pattern (spots, stripes or inverted spots) could be controlled. For the purpose of this paper we term the green spots, *Turing spots*.

The second process—migration, or *tissue movement*—allowed robots to reposition themselves from areas with low activator U to areas with high activator (Turing spots), given in fig. 2(D). This mimicked the flow of cells seen in natural morphogenesis, or could alternatively be seen as equivalent to localized tissue growth in the region of the green spots, and localized cell death in between (as seen during digit formation in tetrapods (46)). There were two conditions for a kilobot to start moving: (a) It must detect that it is on the outer side of the swarm (“edge detection”) which is based on the estimate of the relative change of the local swarm density, and (b) it must detect a local concentration of U lower than a certain threshold value. To relocate robots we used an edge-following algorithm where each individual robot moved along the outer edge of a group of static robots, while attempting to maintain constant distance to its current nearest neighbor. Finally, the robots were programmed to stop when in proximity to a Turing spot, i.e., when they detected a neighbor with a high concentration of U , thus creating an accumulation of kilobots around the Turing spots. The details of the movement algorithm are given in Methods. An example of kilobot movement, following the previously described movement algorithm is given in fig. 2(D)ii.

A conceptual example of the execution of the morphogenesis algorithm is given in fig. 2(E). Swarms started from an initial shape, with arbitrary low morphogen concentrations.

As soon as the pattern was formed and the Turing spots were established, individual bots (in blue) started moving and settling on locations adjacent to the Turing spots. In parallel with the movement, the Turing pattern adjusted to the new shape by changing the morphogen concentrations in both the newly positioned bots and the bots that had already become a part of the Turing spots (denoted in light green). This process of tissue movement and pattern adaptation continued, resulting in the emergence of a shape.

Computer simulations were used to explore how the combination of Turing patterns with movement can spontaneously and reliably give rise to morphogenesis (fig. 3(A)). To conveniently monitor the states of the kilobots and the local concentrations of the virtual molecules, we used the color of the LEDs. As shown in fig. 3(A), the LED color depends on the level of the activator U , ranging from green (as highest level) through teal, blue and purple at decreasingly lower levels, until the LED is turned off for very low values. We explored the parameter space of the Turing pattern around the values provided in Miyazawa *et al.* (47). As shown in fig. S1, replication of the type of patterns obtained by varying parameters A and C was successful, hence confirming results shown in that work. We also explored what types of patterns would result in better morphogenesis based on our approach, i.e., spots, stripes or inverted spots. Neither stripes nor inverted spots were useful, as these patterns resulted in many of the edge robots experiencing high concentrations of U , and thus being restricted from moving. By contrast, normal spots worked well, as they tended to appear on the edge of the swarm but they left significant numbers of edge robots with low concentrations of U . They provided a good compromise between number of robots that could move (in areas of low concentration) and areas of “growth” where moving robots would accumulate (the spots themselves). Parameter values that maximized the number of the spots on the edge without becoming stripes were considered as a good starting point for a complex morphology to develop (values given in Methods).

The morphogenesis approach was then validated on a real swarm of 300 kilobots. The objective was to transform an initially disc-shaped swarm into a more interesting morphology displaying an array of “tentacles” or protrusions. An interesting question was whether regular morphologies could be generated (e.g., with a 4-fold symmetry of protrusions), and/or more dynamic organic shapes reminiscent of simple organisms. Ideally, the shape-formation process should be emergent, adaptive and robust. The program that had been tested previously in simulation (emulating the Turing GRN) was run in the robots, and starting from the initial disc shape (fig. 3(B)), the swarms were able to re-organize themselves into new coherent shapes. In the case shown in fig. 3(B), five Turing spots emerged—four on the surface of the swarm, roughly equidistant to each other and one in the center. Subsequently, when the edge robots started to move, they reliably relocated from regions with low concentrations of the Turing molecules (no LED illumination) to the vicinity of the Turing spots (green LED). Over a short time, robots built-up around the four spots to create four protrusions—showing a 4-fold symmetry. Occasionally individual kilobots were “lost” from the swarm, but this was a relatively rare event, and the vast majority remained in the evolving morphology. Fig. 3(C) shows the results from three more experiments, in which the same basic shape, with 4-fold symmetry was created. A close-up of the stages in the growth of a single protrusion can be seen in

more detail in fig. 3(D). Reliability of this emergent morphogenesis was high. The successful parameter values were able to create robust organic shapes every time (nine runs performed in total with an initial circular morphology), and five of these produced the 4-fold symmetry highlighted by the white dashed boxes in Figs. 3(B) and (C). From the nine runs, six of them were replicates with the same Turing parameters, motion rules and experimental conditions. The approximate running time of each experiment was around three hours. The regular shape shown in Figs. 3(B) and (C) was highly reproducible, but it must be noted that it was transient—further evolution of the swarm led to a more dynamic morphologies, which were studied next. The complete summary of all these experiments is given in the supplementary materials, fig. S2.

An important question was whether morphogenesis really emerged from patterning or simply from robots moving around the swarm. To test that, three experiments were performed in which robots had initial random concentrations and patterning was switched off (meaning that they would keep the same concentration throughout the experiment and no reaction-diffusion was taking place). Motion rules, number of robots and initial circular shape were kept the same as in the previous experiments. We then compared both set of experiments and demonstrated that Turing patterning is essential for the emergent morphogenesis process, and that shapes cannot grow from random patterning (fig. S3(A)i.). Shape index was used as the metric to compare experiments (details in Methods).

The process of swarm morphogenesis, besides producing shapes in an emergent manner, also proved to be a dynamic and adaptive process. If we changed the initial configuration of the swarm to a rectangle, the patterning process adapted to this and the shape again evolved Turing-driven protrusions (at each corner) as shown in fig. 4(A). To quantitatively test that, we compared the set of replication experiments with initial circular shape with a set of five experiments starting from a rectangle and having the same code as the circular experiments. Results showed that shapes grow indistinguishably even though they started from different initial configurations and therefore had a different initial shape index (fig. S3(A)ii.). In addition, we ran the same program on a smaller swarm (110 kilobots) to explore the impact of swarm size. These tests produced a similar pattern, but with three protrusions instead of four—resembling the letter T (fig. 4(B)). This is consistent with Turing patterning systems, where for a given parameter settings the frequency of the spots remains the same irrespectively of the surface size, i.e., smaller surfaces do not have smaller Turing spots, but fewer.

Another important question, related to swarm adaptability, was whether *morphodynamic* processes occur. This describes the scenario in which a large-scale feedback loop is observed—pattern drives morphology, but the change in swarm shape also feeds back to alter the molecular pattern (44, 45). Fig. 4(C) shows two examples of the molecular pattern shifting through the swarm, while the shape changes. In this first case (fig. 4(C)i.) this is a necessary part of the growth of a protrusion. The spot always maintained its position at the distal tip of the protrusion, even though the tip did not consist of the same robots over time (growth occurred by new robots arriving and adding to the existing protrusion). This is an important mechanism for tip-extension. If the spot were static

(remaining in the same group of robots throughout) then it would gradually become enclosed and “hidden” by non-green robots. Any subsequently arriving robots would continue to edge-follow their way right past the spot, to a different part of the swarm, and growth of the protrusion would be frozen. In the second case (fig. 4(C)ii.), a Turing spot could be seen to shift through the tissue. This type of pattern adjustment endows the swarm with a powerful form of adaptability. If the evolving shape is not compatible with an optimal periodic arrangement (either due to random noise, or constraints in the environment) the pattern can adjust and thus self-correct its own morphogenesis. The adjustment of this molecular pattern could occur either as a gradual shift or as a more abrupt reorganization—in both cases settling to a new, more stable configuration. Driven by this morphodynamic processes, our swarm produced a variety of other morphologies, whose main feature was that they are very organic, or organism-like shapes. Fig. 4(D) shows a variety of swarm shapes, with tentacle-like protrusions growing out of them. Individual quantification of morphologies is shown in fig. S3(B)i. as supplementary material.

The swarm also showed robustness to direct swarm damage. We explored a couple of damage scenarios – cutting off the protrusions, and cutting the whole swarm in half. In the first case, either the original protrusion re-grew (fig. 5(A)), or the loss of one protrusion promoted the growth of others (on the other side of the swarm in the case of fig. 5(B)). Again, this demonstrated the value of the self-organizing behavior. From any given state of the pattern and morphology, the Turing mechanism always pushed the pattern towards an even-spaced periodic one—whether from the initial un-patterned configuration, or from a perturbed pattern due to damage. For supplementary quantitative analysis on this first case, see fig. S3(B)ii. In the second case, when the swarm was cut into two roughly-equal parts, the two halves re-fused to create a single swarm relatively fast (fig. 5(C)). The self-organizing dynamic of the Turing spots actually facilitated the merging of the two swarms, contributing to the robustness of the system.

Finally, we quantified the varying and dynamic morphologies created by our robot swarms (fig. 6). We considered the outer contour of the swarm shapes as the main feature to analyze (as this represents the pure morphology of the system) and chose two shape analysis metrics to quantify it: the shape index and the minimum number of characterizing points (48, 49) (details in Methods). The first measure gave an indication of how much the shape was different from a circle, and the second measured the roughness of the contour. We tracked the dynamical change of the shapes over time from nine experiments, starting from the initial, roughly-circular shape, finishing with the final evolved shape. By plotting the values of the two measurements for each experiment over time we produced a trajectory of the swarm through morphospace (50) (fig. 6(A)). Three clear features of these trajectories can be seen – the starting position, a transient region of a regular morphologies, and a dynamic region of variable shapes – which will be discussed in the next section (fig. 6(B)).

Discussion

In summary, we have successfully endowed a large swarm of 300 robots with a self-organized morphogenetic behavior (described as approach B in the introduction). It is directly based on the principles of developmental biology, and results in emergent, adaptive, and robust shapes. Rather than using pre-defined patterns and explicit information about where each robot is, we used a GRN which implemented a self-organizing Turing process as the basis for the pattern formation. This was translated into physical shape change using the concept of robot migration (in analogy with natural developmental biology). Analysis of swarm shape over time revealed the over-arching control process involved. Starting from the initial circular conditions, all swarms moved in a consistent direction through morphospace (fig. 6(B)). This movement represented the emergent but reliable process of protrusions forming on the outer edge of each swarm (blue region). The second feature was the region of transient regular 4-fold morphologies (green region), which are highlighted in dashed white boxes in fig. 3. The third feature was a region of morphospace in which the swarms accumulated. They drifted around this region in a dynamic, adaptable way, but reliably staying within this particular shape space (red region). Thus, both the dynamic adaptability and the shape predictability could be understood within this plot of the morphospace.

A key question was whether the phenomenon of *morphodynamic patterning* could be found within our robot swarms—a dynamical process documented in the biological literature (44, 45). We indeed demonstrated the existence of this large-scale feedback loop between the patterning process and the changes of the shape morphology (fig. 4(C)). On the one hand, the “molecular” patterning process drives the physical shape change (of the swarm), but on the other hand, changes to the shape (which act as boundary conditions for the Turing system) feedback to cause the molecular pattern to change. As in biology, this feature makes the swarm more dynamic and adaptable. In particular, the same types of morphology were created when starting from different initial shapes, and also upon damage to the swarm from external perturbations (when the researcher “cuts” protrusions off the swarm, or cuts the swarm in half).

Another important feature of this system is scalability. In human technology, the reliability of the whole machine often depends on the reliability of the components (“the strength of the chain is in the weakest link”). The decentralized and collective nature of our system avoids this problem. Even though a few robots are lost during morphogenesis, this does not impede the remaining swarm to fulfill its function (and indeed it is reminiscent of real embryo development, in which not all cells survive). Loss of robots can occur for a variety of reasons—loss of digital IR messages, inaccuracy in distance estimation and unreliable movements of robots—, all of which relate to the general lack of reliability of these relatively simple, cheap kilobots. Despite this, the swarm as a whole continues to control its global shape, even when reduced to less than one third of its original size, or when physically “damaged”.

This work is an important step in the direction of human-designed hardware showing the dynamic and organic adaptability of living organisms. Although the shapes were not

formed with a particular task in mind, this proof-of-concept should be extended to create functional shapes. The conditions that lead to adaptability and regeneration are understood at a general level (the self-organizing of Turing systems, and the feedback of morphodynamics). However, a more detailed theoretical understanding will help to engineer these systems for specific tasks, improving our control of the shapes that emerge. An important idea is to explore greater interactions with the outside world, such as getting the whole swarm to collectively navigate towards an external light source, surrounding and herding foreign objects, searching an environment for areas of interest, or building environment-driven structures (e.g., dynamic bridges to “flow” over a river). In these cases, external cues would influence the GRN state (e.g., gene production), thus directing the growth of the swarm and possibly resulting in whole swarm movement. Overall, we believe these results provide a glimpse into the future of “programmable matter” in which the limits to the design and flexibility of useful machines may be restricted only by our imagination.

Materials and Methods

Study design

The objective of our study is to demonstrate that the morphogenesis algorithm produces emergent morphologies in large swarms of real robots. One hundred and twenty-two computer simulations of 1000 agents were performed to find the most suitable parameters for the reaction-diffusion equations. Experiments with swarms of real robots were conducted to validate our algorithm. Concretely, one experiment with a swarm of 110 robots, one experiment with a swarm of 250 robots and thirteen experiments with a swarm of cca. 300 robots were conducted. From the thirteen experiments, eleven corresponded to experimental replicates with the same code and experimental conditions, divided in two sets with different initial configuration. Six of them were initialized with a circular shape, whereas the other five were initialized with a rectangular shape. Three additional experiments were conducted on a swarm of 300 robots to test the rehabilitation properties of the morphogenesis algorithm. Finally, another three extra experiments with a random morphogenesis algorithm on a swarm of 300 robots with the same code and experimental conditions were conducted as control. Therefore, twenty-one experiments with large swarms of real robots were conducted.

Morphogenesis algorithm

The morphogenesis algorithm gets executed in a loop on each individual robot. It consists of the same sequence of updates, which run in parallel and asynchronously on all kilobots of the swarm. The algorithm can be summarized in four basic steps as:

1. Communication
2. Patterning
3. Motion

In the first step, all the inputs, i.e., messages received from neighboring robots are processed. Next, the values of the two morphogens (U and V) of the gene regulatory network (GRN) are calculated, which underlies the swarm patterning process. Depending on these values and some additional conditions (like edge detection), a robot updates its movement state and halts or activates its motors accordingly in the last step. The robot also sets the values of the message variables that it broadcasts and the color of the LED light, which depends on the value of the activator U . We summarize the algorithm in fig. 7(A) and give the details of the implementation of each of these steps in the following text.

1. Communication

The primary kilobot inputs are the received messages from other surrounding kilobots (fig. 7(B)). For passing a message, an infrared broadcast is used and the message itself has a payload of 9 bytes. It can be received by any kilobot within communication range (~ 10

cm) and the frequency of the message broadcast is “hardwired” in the kilobots and happens at regular intervals. At any point in the program, the content of the message values can be updated, and they will be transmitted at the next broadcast interval. On the receiving side, when a kilobot detects an incoming message, a program interrupt is generated, and a user-defined handler function processes the received message. In our program, we used a function that stores each incoming message in a circular buffer. The messages from this buffer are emptied and processed at the beginning of each of the main loop executions.

We used 8 out of 9 bytes for our message payload and we transmitted the values of 5 variables. First is the (locally) unique ID value of a kilobot that took up 2 bytes of the message. The second is the number of neighbors that a robot has, and used 1 byte. The robots can be in one of several states which is also transmitted in a 1 byte. The remaining 4 bytes are used for the Turing patterning process, namely to transmit the value of the U and V morphogens of a robot, each one taking 2 bytes.

As the morphogen concentrations of U and V are stored as single-precision floating point numbers (4 bytes each) inside the kilobots, they have to be converted to half-precision on the transmitter side and then decoded to single-precision on the receiving robot side (with a small percentage of error incurred during conversion). The reason is that the 9 bytes message that kilobots can send needs to include the other information described above (ID, state and number of neighbors). Out of the 16 bits available in the 2-bytes, half-precision floating point numbers, 10 bits are used for the fraction of the number, the next 5 bits for the exponent of the number and 1 bit for the sign, as described in the IEEE 754 standard.

After a message from the receiving buffer is processed, it is stored in a so-called neighbors’ table. The neighbor’s ID, its number of neighbors and its state are stored as they are. The received bytes of the morphogens U and V are converted to single-precision floating point numbers and stored. Additionally, a time stamp is added to each message, which is the current kilo tick number of the bot. The neighbors’ table keeps the most recent messages received from the neighbors in range for a certain amount of time and older messages are discarded (set at 2 seconds old).

2. Patterning

The state of the gene regulatory network of each robot is responsible for the patterning process of the whole swarm. The equations for the Turing patterning system are given in fig. 7(C)i. These are reaction-diffusion equations that give the rate of change of the morphogens U and V , where R is the reaction parameter and D_U and D_V are the diffusion parameters. The production of U and V is given by functions f and g and it depends on the synthesis and on the degradation of U and V . The two functions (f and g) are linear functions given in fig. 7(C)i. The parameter values of the linear equations used in our experiments are the following: $A = 0.08$, $B = -0.08$, $C = 0.03$, $\gamma_u = 0.03$, $E = 0.1$, $F = 0.12$ and $\gamma_v = 0.06$. The synthesis terms are limited between zero and user defined maximum values, which for our experiments are given as: $\text{syn}U_{\max} = 0.23$ for U and $\text{syn}V_{\max} = 0.5$ for

V. The reaction parameter is $R = 160$ and the diffusion parameters are $D_U = 0.5$ and $D_V = 10$ for U and V correspondingly. In our implementation of these equations we use a discrete version with a time step $dt = 0.00005$.

The morphogen diffusion (fig. 7(C)ii.) is emulated with the help of the message passing of the morphogen concentrations of the robots. At a given moment, each robot has information about its neighbors' morphogen (U and V) concentrations. By subtracting these neighboring morphogen values from its own and then summing up these differences, each robot determines the net morphogen diffusion that takes place. This allows the robot to edit its own morphogen values, either by increasing or decreasing them due to "diffusion". With the help of the kilobot's LEDs, the Turing pattern can be visible in the swarm. We used different LED colors for different ranges of values of the morphogen U , defined as follows: green LED for $U > 4.0$, teal for $U > 3.0$ and $U \leq 4.0$, blue for $U > 2.0$ and $U \leq 3.0$, purple for $U > 1.0$ and $U \leq 2.0$ and the LED was off for $U \leq 1.0$.

3. Motion

The process of edge detection is relevant for updating the robot state and is the main process responsible for determining if a robot moves or not. It is based on estimation of the relative difference of local swarm density, as illustrated in fig. 7(D)ii. Each robot transmits the number of its own neighbors N to the robots in range and in return, it receives the same information N_i from them. If an individual robot's own number of neighbors N is smaller than the average number of its neighbor's neighbors NN , then the robot is on the outer edge of the swarm. The intuition is that if robots are on the inner part of the swarm, they would have an approximately similar number of neighbors. The threshold for detecting an edge robot that was used, $edge_{th}$, had a value of 0.8.

Due to the inherent noise in the kilobot swarm, some messages from robots are not received or dropped. This can potentially impact the edge detection and make it unstable. In order to compensate for this, instead of taking the current number of neighbors, or the current average of neighbor's neighbors, an approximate running average is used, given with:

$$avgNNs = \alpha \times curr.avgNNs + (1 - \alpha) \times old.avgNNs$$

for the average number neighbor's neighbors and:

$$N_s = \alpha \times curr.Ns + (1 - \alpha) \times old.Ns$$

for the average number of neighbors, where $\alpha = 0.0001$.

After a kilobot detects itself on the edge, motion might start (described below). The default movement in our approach is the *edge following* movement. It is based on orbiting movements, where the aim of a moving robot is to maintain a constant distance to a static one (fig. 7(D)i.). The orbiting robot is moving in one of the preferred directions (clockwise or counterclockwise) while estimating the distance to the static robot based on

the messages it receives. If the distance is larger than the predefined one (d_{th}), the robot starts rotating in a direction that brings it closer to the static robot. As soon as this movement brings the robot to a distance less than d_{th} , it switches to the opposite direction of rotation. This constant switching of rotation direction produces a forward motion, thus moving the robot in a circle around the static one. The edge following algorithm is a simple extension of this orbiting algorithm. Namely, there is a swarm of static robots, instead of just one, and a moving robot goes around the edge of this static swarm by always orbiting its nearest neighbor.

The *recover* movement (approaching), moves a robot towards a static one, bringing it to a predefined distance of d_{th} , the threshold distance. It is used when a robot is too far from a swarm and needs to “recover”. The movement starts by the robot rotating in an arbitrary direction and measuring the change of distance from the static robot. If the change is negative, this means that the robot is approaching the static robot and the current direction of rotation is maintained. If this change is positive, i.e., the distance to the static robot is increasing, then the robot switches the direction of movement. It does so by selecting the nearest neighbor from the swarm as a static robot and approaching it until it is at a distance lower than d_{th} .

There are three motion-related states in which a robot can be: WAIT, EDGE FOLLOW and RECOVER, as shown in fig. 7(D)iii. There is one central stationary state, the WAIT state, from which a robot can transit into one of the two moving states—EDGE FOLLOW or RECOVER. The EDGE FOLLOW and RECOVER states are both blocking states, meaning that if a robot is in this state, then all neighbors that are receiving messages from it cannot initialize movement. This constraint is due to the design of the movement algorithms, related to the EDGE FOLLOW and RECOVER state, coming from the kilobots lack of directionality sensing.

The properties of each state are the following:

- The WAIT state is the default kilobot state, in which the robot it is not moving, it is just updating its GRN and checking if the conditions for transitioning into the EDGE FOLLOW or RECOVER state are fulfilled.
- In the EDGE FOLLOW state, the kilobot is performing the *edge following movement*.
- In the RECOVER state, the kilobot’s goal is to *approach the swarm*, in case it drifted too far away from it.

The main rules for transition between the states are summarized in Table 1. Unless this rule allows a state transition to be triggered, the kilobot will by default stay in its current state. There are a few common functions and constants that are used for the state transition rules:

- `edge_detected()`: *TRUE* if robot on the edge of the swarm.
- `check_wait_state()`: *TRUE* if neighboring robot(s) are in the WAIT state.

- `dist()`: returns distance to a specified neighbor robot.
- `dist_to_Turing()`: returns distance to the nearest neighbor with a Turing spot (if applicable).
- `dist_far`: upper distance limit beyond which a robot is considered too far from the swarm.
- `dist_th`: distance threshold used for the edge following movement.
- `ALL`: all neighbors.
- `NN`: nearest neighbors.

A robot that is in the `WAIT` state can transit to `EDGE FOLLOW` if it is on the edge, no other neighbors are moving, and it is not a part of, or in near proximity to a Turing spot. The transition in the opposite direction (from `EDGE FOLLOW` to `WAIT`) occurs only if a robot is no longer on the edge, is close or became part of a Turing spot, if the kilobot that it is currently trying to orbit is also moving and additionally if it goes too far away from the swarm.

If a robot is too far away from the swarm, it instantly switches to the `RECOVER` state via the `WAIT` state. The robot remains in this state until satisfactory distance to the swarm is achieved, after which it switches back to the `WAIT` state.

Summary of the morphogenesis algorithm

Below is a serial outline of the program that the kilobots execute (patterning and motion). It is worth noticing that the kilobots run several processes such as sending and receiving messages following a timer-interrupt approach. Only the main functions and variables are presented here. A link to the source code can be found at the end of this article.

program main:

```

u, v, id, state ← initialize_variables() // Random initial concentrations for molecules U and V, random
                                     // initial id, robot in WAIT state, message with random
                                     // concentrations starts to be sent

A ← 0.08, B ← -0.08, C ← 0.03,  $\gamma_u$  ← 0.03, E ← 0.1, F ← 0.12,  $\gamma_v$  ← 0.06, Du ← 0.5, Dv ← 10,
R ← 160,  $\Delta t$  ← 0.00005, synUmax ← 0.23, synVmax ← 0.5

MAX_DIST_NEIGH ← 85 // Maximum distance in millimeters to neighbors for the diffusion term

```

neigh_table ← create_empty_list() // Initializes neighbors table to store their messages

while TRUE:

// Messages from neighbors are processed and neighbors table is updated. It also

// calculates running averages for number of neighbors and number of neighbors' neighbors

n_neighbors, *neigh_table* ← process_inputs(*neigh_table*)

if *state* = WAIT **then**

$u, v \leftarrow \text{update_GRN}(u, v, A, B, C, \gamma_u, E, F, \gamma_v, D_u, D_v, R, \Delta t, \text{syn}U_{\max}, \text{syn}V_{\max},$
 $\text{MAX_DIST_NEIGH}, \text{neigh_table})$

end if

if *kilo_ticks* ≥ 20000 **then** // Movement starts after about 10 minutes, when pattern is stable

state ← update_movement(*state*, *neigh_table*)

end if

show_concentration(*u*) // The color of the LED depends on concentration of molecule *u*

id ← local_unique_id(*id*) // If a neighbor has the same ID, another will be chosen at random

update_message(*id*, *n_neighbors*, *state*, *u*, *v*) // It updates the message that will be sent

end while

end program

algorithm update_GNR:

input: internal concentrations *u* and *v* of molecules U and V,
parameters *A*, *B*, *C*, γ_u , *E*, *F*, γ_v , *D_u*, *D_v*, *R* of the linear model,
incremental step Δt for the discretization,
maximum production rates *synU_{max}*, *synV_{max}* for molecules U and V

maximum distance MAX_DIST_NEIGH in millimeters to neighbors for the diffusion term
neighbors table $neigh_table$ with all the information from neighbors

output: new concentrations u and v of molecules U and V

$laplace_u \leftarrow 0, laplace_v \leftarrow 0$

// The Laplace operator is calculated

for $i \leftarrow 1$ **to** $length(neigh_table)$ **do**

$neighbor \leftarrow neigh_table[i]$

if $distance(neighbor) \leq MAX_DIST_NEIGH$ **then**

$laplace_u \leftarrow laplace_u + concentration_u(neighbor) - u$

$laplace_v \leftarrow laplace_v + concentration_v(neighbor) - v$

end if

end for

$creation_u \leftarrow A*u + B*v + C$

$creation_v \leftarrow E*u - F$

if $creation_u < 0$ **then**

$creation_u \leftarrow 0$

else if $creation_u > synU_{max}$ **then**

$creation_u \leftarrow synU_{max}$

end if

if $creation_v < 0$ **then**

$creation_v \leftarrow 0$

else if $creation_v > synV_{max}$ **then**

$creation_v \leftarrow synV_{max}$

end if

$creation_u \leftarrow creation_u - \gamma_u*u$

$creation_v \leftarrow creation_v - \gamma_v*v$

$u \leftarrow u + \Delta t^*(R^*creation_u + D_u^*laplace_u)$

$v \leftarrow v + \Delta t^*(R^*creation_v + D_v^*laplace_v)$

return u, v

end algorithm

algorithm update_movement:

input: state $state$ of the robot,
neighbors table $neigh_table$ with all the information from neighbors

output: new state $state$ of the robot

if $state = \text{EDGE_FOLLOW}$ **then**

if edge_follow_to_wait() **then**

$state \leftarrow \text{WAIT}$

 stop_motors()

else // Stays in EDGE_FOLLOW state

$nearest_neigh \leftarrow \text{find_nearest_neighbor}(neigh_table)$

 // By moving around the nearest robot, an edge-following movement is achieved

 move_around($nearest_neigh$)

end if

else if $state = \text{WAIT}$ **then**

if wait_to_edge_follow() **then**

$state \leftarrow \text{EDGE_FOLLOW}$

 start_motor_right()

```

else if wait_to_recover() then

    state ← RECOVER
    start_motor_right()

else // Stays in WAIT state

    do_nothing()

end if

else if state = RECOVER then

    if recover_to_wait() then

        state ← WAIT
        stop_motors()

    else // Stays in RECOVER state

        nearest_neigh ← find_nearest_neighbor(neigh_table)

        // By moving towards the nearest neighbor, the bot tries to get back to the swarm
        move_towards(nearest_neigh)

    end if

end if

return state

end algorithm

```

Quantifying swarm morphologies

Shape characterizing points

In the field of landscape ecology, it is of great interest to quantify the heterogeneity of landscapes by identifying and analyzing spatial homogeneous patches (48) in order to counteract the effects of human-induced biodiversity, as Moser *et al.* point out in (49). In their work, they analyze the relation between shape complexity of the patches and richness

of plant species. In particular, they propose a metric of geometric complexity based on the contour of the patches which can be useful here. This metric is called *number of shape characterizing points* (NSCP), and it is defined as the minimum number of points required to define the shape. The idea is that the greater the NSCP, the more complex the shape is. As a result, this metric can potentially describe the morphology of the protrusions by means of the spikiness of shapes. In their work, they propose to calculate the polygon defining the patch and take only the vertices forming an angle of less than 160 degrees.

In our work, all the points in the contour of each shape were obtained using the *findContours* function included in OpenCV 3.2.0 using *CHAIN_APPROX_NONE*. To calculate the number of characterizing points of the shape, the length of the array resulting from applying the following algorithm to the array of all contour points with a threshold of 160 degrees was obtained:

algorithm shape_characterizing_points:

input: array P containing all points of the shape contour,
angles threshold t between 0 and 180 degrees

output: array Q containing points in the same order from P with angles $< t$ for all three consecutive points

$Q \leftarrow P$

if Q contains at least 3 points **then**

$base \leftarrow 1$

for $k \leftarrow 2$ **to** length(Q) **do**

$angle \leftarrow$ compute internal angle from points Q_{base} , Q_k and Q_{k+1}

// Q is circular. When $k = \text{length}(Q)$, then $Q_{k+1} = Q_1$

if $angle \geq t$ **then**

$Q \leftarrow$ remove point Q_k from Q

else

$base \leftarrow k$

end if

end for

end if

return Q

end algorithm

Perimeter-area ratios

The simplest metrics to measure shape complexity are those using the perimeter and area of the shapes in question. In our scenario, the area of the swarm is practically constant, as the number of robots remains the same throughout the experiment—with the exception of the few ones which get lost and the gaps between robots. The perimeter then describes how the contour of the swarm grows/shrinks over time. The longer the protrusions, the bigger the perimeter. Therefore, a metric involving perimeter can be a good estimate of the development of the shape.

Among all perimeter-area ratios, we decided to use a dimensionless one to allow for comparison across experiments, even with different swarm sizes. Moreover, we were interested in comparing the shapes during the morphogenesis process with the initial circular configuration of the swarm. The metric with all these features was *shape index*, which is a measure of the circularity of a shape. Its formula is:

$$shape\ index = \frac{perimeter}{2\sqrt{\pi area}}$$

As can be seen, the shape index of a circle is 1. This metric can be useful to quantify how the swarm develops morphological features and how different it becomes from a circle (shape index greater than 1).

To calculate the shape index of the shapes in our work, we used the built-in functions *contourArea* and *arcLength* of OpenCV 3.2.0 to calculate the area and perimeter of the shape, respectively. The contour used for this metric was the result of applying the algorithm *shape_characterizing_points* to the contour with all the points with a threshold of 160 degrees, as described in the subsection above.

Supplementary Materials

Figure S1. Parameters exploration in simulation.

Figure S2. Summary of fifteen different runs of the morphogenesis algorithm.

Figure S3. Quantitative analysis of emergence, adaptability and robustness.

Movie S1. Morphogenesis in Robot Swarms.

References

1. J. B. A. Green, J. Sharpe, Positional information and reaction-diffusion: two big ideas in developmental biology combine. *Development* **142**, 1203-1211 (2015).
2. L. Wolpert, Positional information and the spatial pattern of cellular differentiation. *Journal of Theoretical Biology* **25**, 1-47 (1969).
3. J. B. Gurdon, P.-Y. Bourillot, Morphogen gradient interpretation. *Nature* **413**, 797-803 (2001).
4. D. Summerbell, J. H. Lewis, L. Wolpert, Positional information in chick limb morphogenesis. *Nature* **244**, 492-496 (1973).
5. A. Gierer, H. Meinhardt, A theory of biological pattern formation. *Kybernetik* **12**, 30-39 (1972).
6. A. M. Turing, The chemical basis of morphogenesis. *Phil. Trans. R. Soc. Lond. B* **237**, 37-72 (1952).
7. J. D. Murray, *Mathematical Biology, II Spatial models and biomedical applications* (Springer-Verlag, New York, 2001).
8. J. Jaeger, Manu, J. Reinitz, Drosophila blastoderm patterning. *Current opinion in genetics & development* **22**, 533-541 (2012).
9. J. Raspopovic, L. Marcon, L. Russo, J. Sharpe, Digit patterning is controlled by a Bmp-Sox9-Wnt Turing network modulated by morphogen gradients. *Science* **345**, 566-570 (2014).
10. R. Doursat, H. Sayama, O. Michel, Morphogenetic engineering: reconciling self-organization and architecture, in *Morphogenetic Engineering: Toward Programmable Complex Systems*, R. Doursat, H. Sayama, O. Michel, Eds. (Springer, Berlin, Heidelberg, 2012), chap. 1.
11. M. Brambilla, E. Ferrante, M. Birattari, M. Dorigo, Swarm robotics: a review from the swarm engineering perspective. *Swarm Intelligence* **7**, 1-41 (2013).
12. C. J. M. Verhoeven, M. J. Bentum, G. L. E. Monna, J. Rotteveel, J. Guo, On the origin of satellite swarms. *Acta Astronautica* **68**, 1392-1395 (2011).
13. S. Hauert, S. N. Bhatia, Mechanisms of cooperation in cancer nanomedicine: towards systems nanotechnology. *Trends in Biotechnology* **32**, 448-455 (2014).
14. E. Hawkes, B. An, N. M. Benbernou, H. Tanaka, S. Kim, E. D. Demaine, D. Rus, R. J. Wood, Programmable matter by folding, in *Proceedings of the National Academy of Sciences* **107**, 12441-12445 (2010).
15. S. C. Goldstein, J. D. Campbell, T. C. Mowry, Programmable matter. *Computer* **38**, 99-101 (2005).
16. N. Mathews, A. L. Christensen, R. O'Grady, F. Mondada, M. Dorigo, Mergeable nervous

systems for robots. *Nature Communications* **8**, 439 (2017).

17. R. O'Grady, A. L. Christensen, M. Dorigo, Swarmorph: Morphogenesis with self-assembling robots, in *Morphogenetic Engineering: Toward Programmable Complex Systems*, R. Doursat, H. Sayama, O. Michel, Eds. (Springer, Berlin, Heidelberg, 2012), chap. 2.
18. K. Gilpin, D. Rus, Modular Robot Systems. *IEEE Robotics & Automation Magazine* **17**, 38-55 (2010).
19. J. Nembrini, A. F. T. Winfield, Emergent swarm morphology control of wireless networked mobile robots, in *Morphogenetic Engineering: Toward Programmable Complex Systems*, R. Doursat, H. Sayama, O. Michel, Eds. (Springer, Berlin, Heidelberg, 2012), chap. 10.
20. J. Cheng, W. Cheng, R. Nagpal, Robust and self-repairing formation control for swarms of mobile agents, in *Proceedings of the 20th national conference on Artificial intelligence (AAAI'05)*, pp. 59-64.
21. Y. Liu, C. Gao, Z. Zhang, Y. Wu, M. Liang, L. Tao, Y. Lu, A new multi-agent system to simulate the foraging behaviors of Physarum. *Natural Computing* **16**, 15-29 (2017).
22. H. Oh, A. R. Shiraz, Y. Jin, Morphogen diffusion algorithms for tracking and herding using a swarm of kilobots. *Soft Computing* **22**, 1833-1844 (2016).
23. J. Jones, Influences on the formation and evolution of Physarum polycephalum inspired emergent transport networks. *Natural Computing* **10**, 1345-1369 (2011).
24. R. Thenius, M. Dauschan, T. Schmickl, K. Crailsheim, Regenerative abilities in modular robots using virtual embryogenesis, in *Adaptive and Intelligent Systems*, A. Bouchachia, Ed. (Springer, Berlin, Heidelberg, 2011), pp. 227-237.
25. L. Bai, M. Eyiurekli, D. E. Breen, An emergent system for self-aligning and self-organizing shape primitives. *Second IEEE International Conference on Self-Adaptive and Self-Organizing Systems*, 445-454 (2008).
26. T. Schmickl, K. Crailsheim, A navigation algorithm for swarm robotics inspired by slime mold aggregation, in *Swarm Robotics*, E. Şahin, W. M. Spears, A. F. T. Winfield, Eds. (Springer, Berlin, Heidelberg, 2007), pp. 1-13.
27. T. Schmickl, K. Crailsheim, Trophallaxis among swarm-robots: A biologically inspired strategy for swarm robotics. *The First IEEE/RAS-EMBS International Conference on Biomedical Robotics and Biomechatronics*, 377-382 (2006).
28. R. Groß, M. Bonani, F. Mondada, M. Dorigo, Autonomous self-assembly in a swarm-bot, in *Proceedings of the 3rd International Symposium on Autonomous Minirobots for Research and Edutainment*, K. Murase, K. Sekiyama, T. Naniwa, N. Kubota, J. Sitte, Eds. (Springer, Berlin, Heidelberg, 2006), pp. 314-322.

29. K. Støy, Controlling self-reconfiguration using cellular automata and gradients, in *Proceedings of the 8th international conference on intelligent autonomous systems*, 693-702 (2004).
30. Y. Ikemoto, Y. Hasegawa, T. Fukuda, K. Matsuda, Gradual spatial pattern formation of homogeneous robot group. *Information Sciences* **171**, 431-445 (2005).
31. W-M. Shen, P. Will, A. Galstyan, C-M. Chuong, Hormone-inspired self-organization and distributed control of robotic swarms. *Autonomous Robots* **17**, 93-105 (2004).
32. Y. Meng, H. Guo, Y. Jin, A morphogenetic approach to flexible and robust shape formation for swarm robotic systems. *Robotics and Autonomous Systems* **61**, 25-38 (2013).
33. Y. Jin, H. Guo, Y. Meng, A hierarchical gene regulatory network for adaptive multirobot pattern formation. *IEEE Transactions on Systems, Man, and Cybernetics, Part B (Cybernetics)* **42**, 805-816 (2012).
34. R. Doursat, Organically grown architectures: Creating decentralized, autonomous systems by embryomorphing engineering, in *Organic Computing*, R. P. Würtz, Ed. (Springer, Berlin, Heidelberg, 2008), pp. 167-199.
35. T. Taylor, P. Ottery, J. Hallam, Pattern formation for multi-robot applications: Robust, self-repairing systems inspired by genetic regulatory networks and cellular self-organisation. *Technical Report EDI-INFRR-0971, School of Informatics, University of Edinburgh* (2007).
36. H. Sayama, Robust morphogenesis of robotic swarms [Application Notes]. *IEEE Computational Intelligence Magazine* **5**, 43-49 (2010).
37. H. Oh, A. R. Shirazi, C. Sun, Y. Jin, Bio-inspired self-organising multi-robot pattern formation: A review. *Robotics and Autonomous Systems* **91**, 83-100 (2017).
38. M. Rubenstein, C. Ahler, R. Nagpal, Kilobot: A low cost scalable robot system for collective behaviors, in *Proceedings of 2012 IEEE International Conference on Robotics and Automation*, 3293-3298 (2012).
39. M. Rubenstein, A. Cornejo, R. Nagpal, Programmable self-assembly in a thousand-robot swarm. *Science* **15**, 795-799 (2014).
40. M. Gauci, R. Nagpal, M. Rubenstein, Programmable self-disassembly for shape formation in large-scale robot collectives, in *Distributed Autonomous Robotic Systems*, R. Groß *et al.*, Eds. (Springer, Cham, 2018), pp. 573-586.
41. L. Marcon, J. Sharpe, Turing patterns in development: what about the horse part? *Current Opinion in Genetics & Development* **22**, 578-584 (2012).
42. A. D. Economou *et al.*, Periodic stripe formation by a Turing mechanism operating at growth zones in the mammalian palate. *Nature Genetics* **44**, 348-351 (2012).
43. J. D. Murray, *Mathematical Biology* (Springer-Verlag, New York, 1989).

44. I. Salazar-Ciudad, J. Jernvall, S. A. Newman, Mechanisms of pattern formation in development and evolution. *Development* **130**, 2027-2037 (2003).
45. I. Salazar-Ciudad, J. Jernvall, How different types of pattern formation mechanisms affect the evolution of form and development. *Evolution and Development* **6**, 6-16 (2004).
46. L. Wolpert, C. Tickle, A. M. Arias, *Principles of Development* (Oxford University Press, USA, ed. 5, 2015).
47. S. Miyazawa, M. Okamoto, S. Kondo, Blending of animal colour patterns by hybridization. *Nature Communications* **1**, 1-6 (2010).
48. E. J. Gustafson, Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* **1**, 143-156 (1998).
49. D. Moser, H. G. Zechmeister, C. Plutzer, N. Sauberer, T. Wrška, G. Grabherr, Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. *Landscape Ecology* **17**, 657-669 (2002).
50. P. Mitteroecker, S. M. Huttegger, The concept of morphospaces in evolutionary and developmental biology: Mathematics and metaphors. *Biological Theory* **4**, 54-67 (2009).

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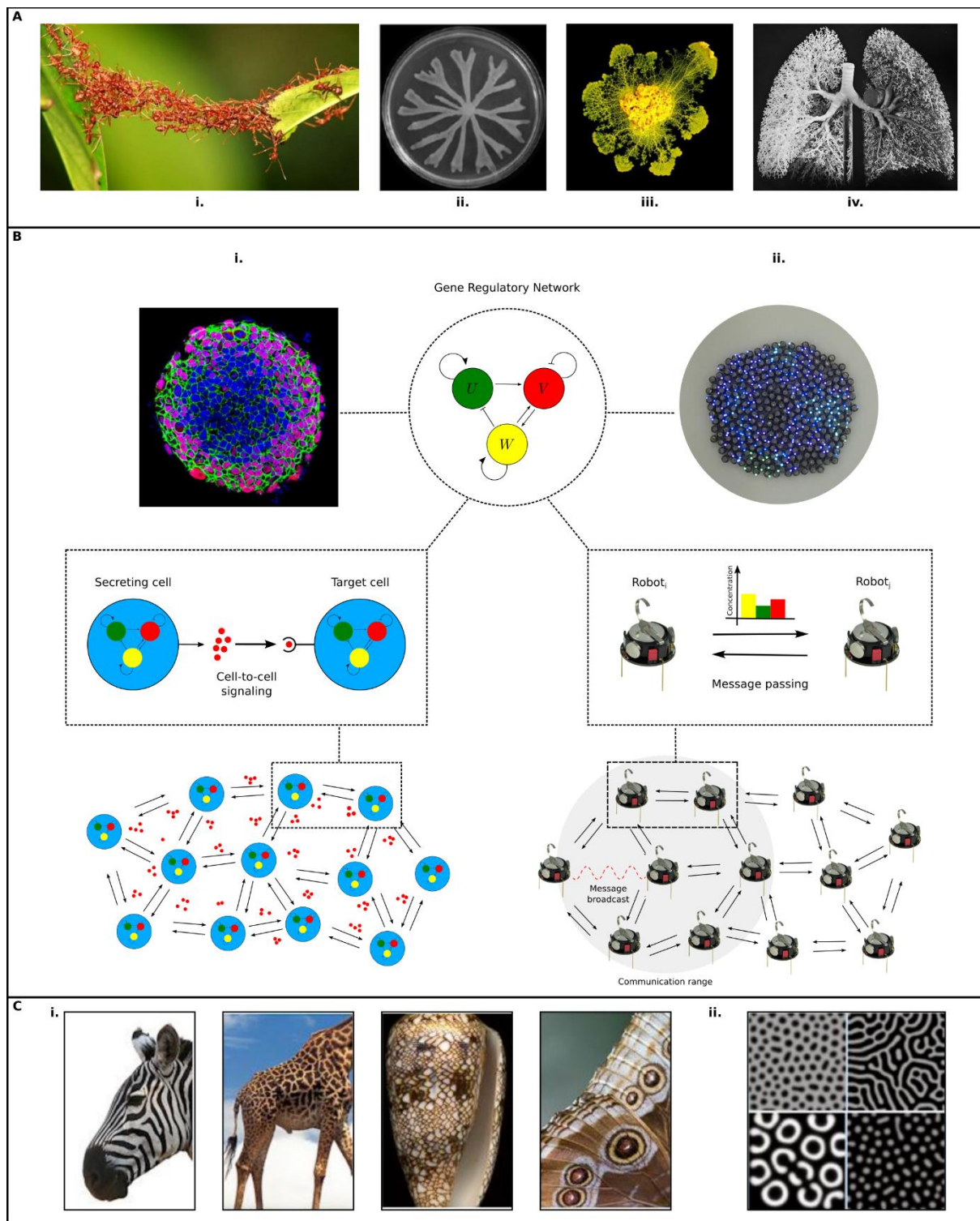


Figure 1. Morphogenesis in natural systems. (A) (i.) Fire ants constructing bridges. (ii.) Bacterial colonies structures formed by swarming. (iii.) Slime mold network for optimal nutrient transport. (iv.) Lungs consisting of a large network of alveoli for respiration. (B) Gene regulatory network (GRN) as the underlying mechanism behind patterning and morphogenesis processes in real tissues (e.g. heart valve) or robot swarms. (i.) Each individual cell has an identical GRN and cells communicate by secreting morphogens or direct cell-to-cell communication. A multicellular tissue consists of many cells that are interconnected and communicate to each other, thus allowing for coordinated tissue behavior. (ii.) Robots emulate this behavior by running the same GRN and communicate to each other by sending messages about their GRN state. (C) Turing patterns in different biological organisms (i.) zebra, giraffe, seashell, butterfly and different types of Turing patterns (ii.) on fish skin.

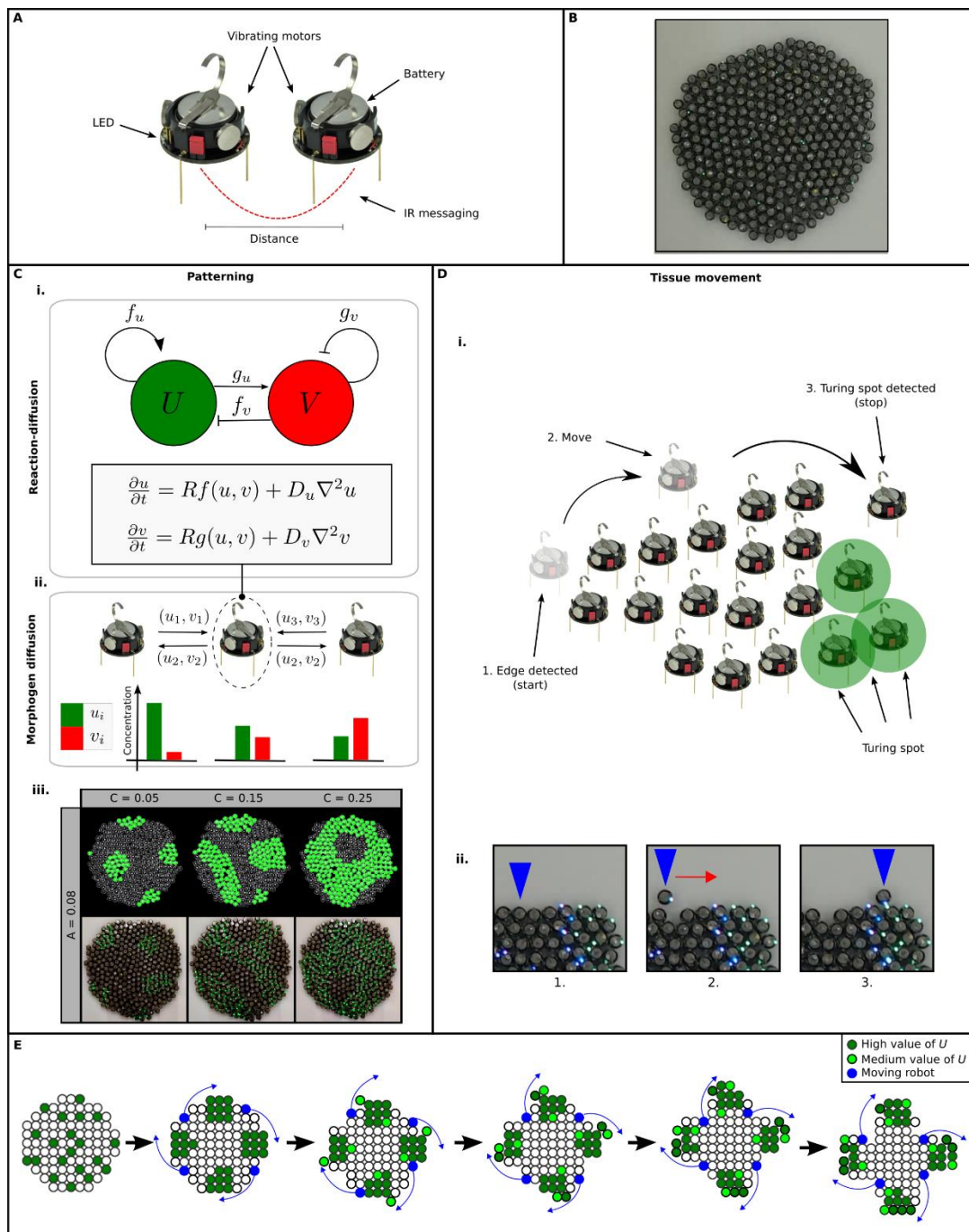


Figure 2. Swarm morphogenesis approach description. (A) Kilobots are small robots, each containing a microprocessor, infrared (IR) receiver/transmitter, a battery, a multi-colored LED and two vibration motors. (B) Top view of a kilobot swarm consisting of cca. 300 robots. (C) A Turing patterning system consisting of two diffusing molecules U (green) and V (red) that act as an activator and an inhibitor, respectively. Each individual robot calculates the values of U and V by using reaction-diffusion equations (i.), and transmits them to neighboring robots (ii.). (iii.) Turing patterns in simulated and real robot swarms for varying values of parameter C . (D) Kilobots move along the surface of the swarm and aggregate around Turing spots (i.). A robot detects that it is on the edge of the swarm (1.), and starts moving along the outer surface of the swarm (2.). It stops (3.) when it gets to the proximity of the Turing spot. (ii.) An example of kilobot movement in a real robot swarm. (E) Conceptual execution of the swarm morphogenesis algorithm. The Turing pattern should be formed (dark green) and several robots on the edge of the swarm (in blue) move and stop in the proximity of the Turing spots. Ideally, the Turing pattern should adjust to the new morphology (light green) by changing its configuration, while other bots continue moving and surround the Turing spots to build up the protrusions of the swarm.

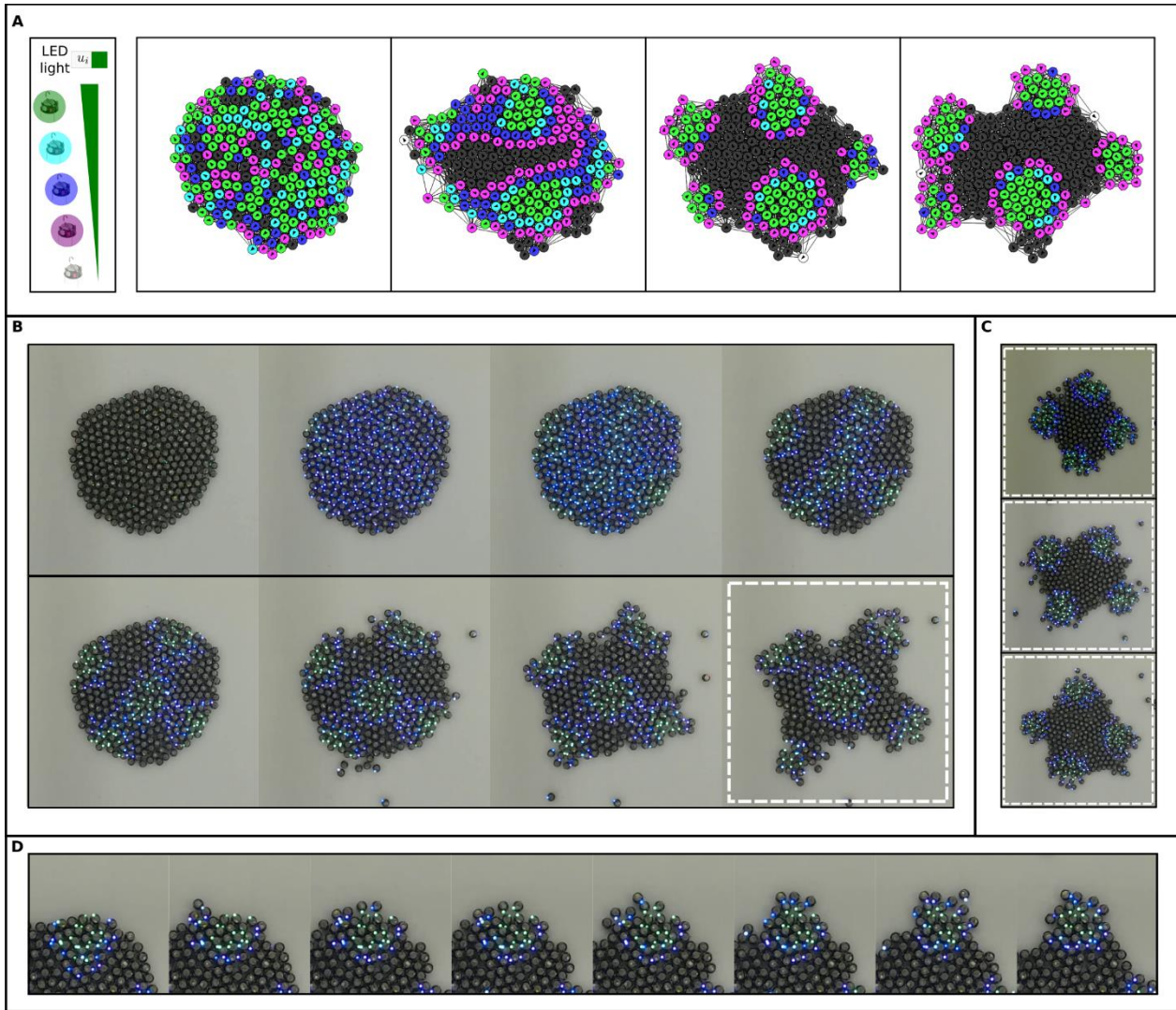


Figure 3. Emergence of swarm morphologies. (A) Morphogenesis in a simulated swarm. Different LED colors indicate different concentrations of the activator U . Initially, a swarm of kilobots is visible with arbitrary concentrations of U . Next, five Turing spots emerged, around which, noticeable protrusions appear (last panel). (B) A temporal sequence of morphogenesis of a kilobot robot swarm (cca. 300 robots). The initial swarm configuration was roughly circular with five distinct Turing spots, including four spots on the edge of the swarm and one spot in the center of the swarm (top four panels). The robots rearranged around the Turing spots (bottom four panels), forming initial protrusions. Finally, a distinct cross-like shape was formed, which consisted of four tentacles with Turing spots on their tips. (C) Three replicates of morphogenesis with cca. 300 robots, which show similar cross-like, four tentacles morphologies. (D) Close-up of a growing tentacle during the swarm morphogenesis process. Starting from a Turing spot in the initial panel, there is a progressive build-up of kilobots around it, resulting in a clear tentacle growth in the final panel.

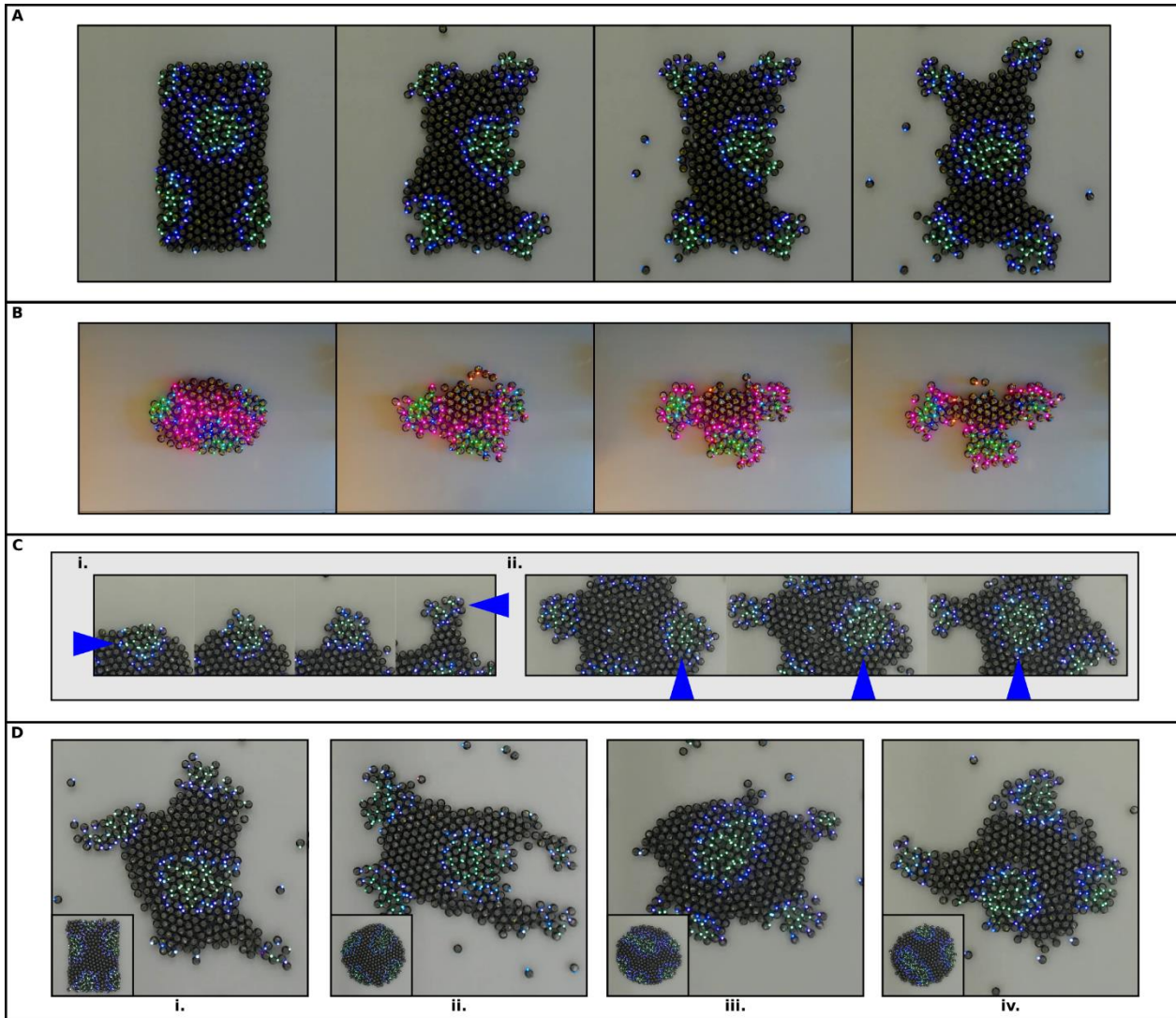


Figure 4. Adaptability of swarm morphologies. (A) Shape formation of a large swarm (cca. 300 robots) starting from a rectangular shape. Four spots emerged on the edges where four tentacles grew, while the central spot moved, adapting to the changing morphology. (B) A temporal sequence of morphogenesis in a smaller kilobot swarm (cca. 110 robots), with the same settings for the Turing parameters as in (A). Three Turing spots drove the formation of a T-like tentacled morphology. (C) Two examples of Turing pattern (spot) adaptation in response to the swarm changing morphology. In (i.) we show adaptation during tentacle growth, where the Turing spot visibly changed shape, size and location during the growth of a single tentacle, always tending to stay on the tip of the outgrowth. In (ii.) starting from the initial spot location on the edge of the swarm, the spot is slightly shifted towards the center of the swarm and after a while it is completely moved to the center, while another spot appears close to its initial location. (D) Four variable swarm morphologies with irregular, organic shapes, obtained from different runs. Inset images show the initial configuration of the swarm. (i.) starts from an initial square morphology, while the swarms in (ii.-iv.) start from circular ones.

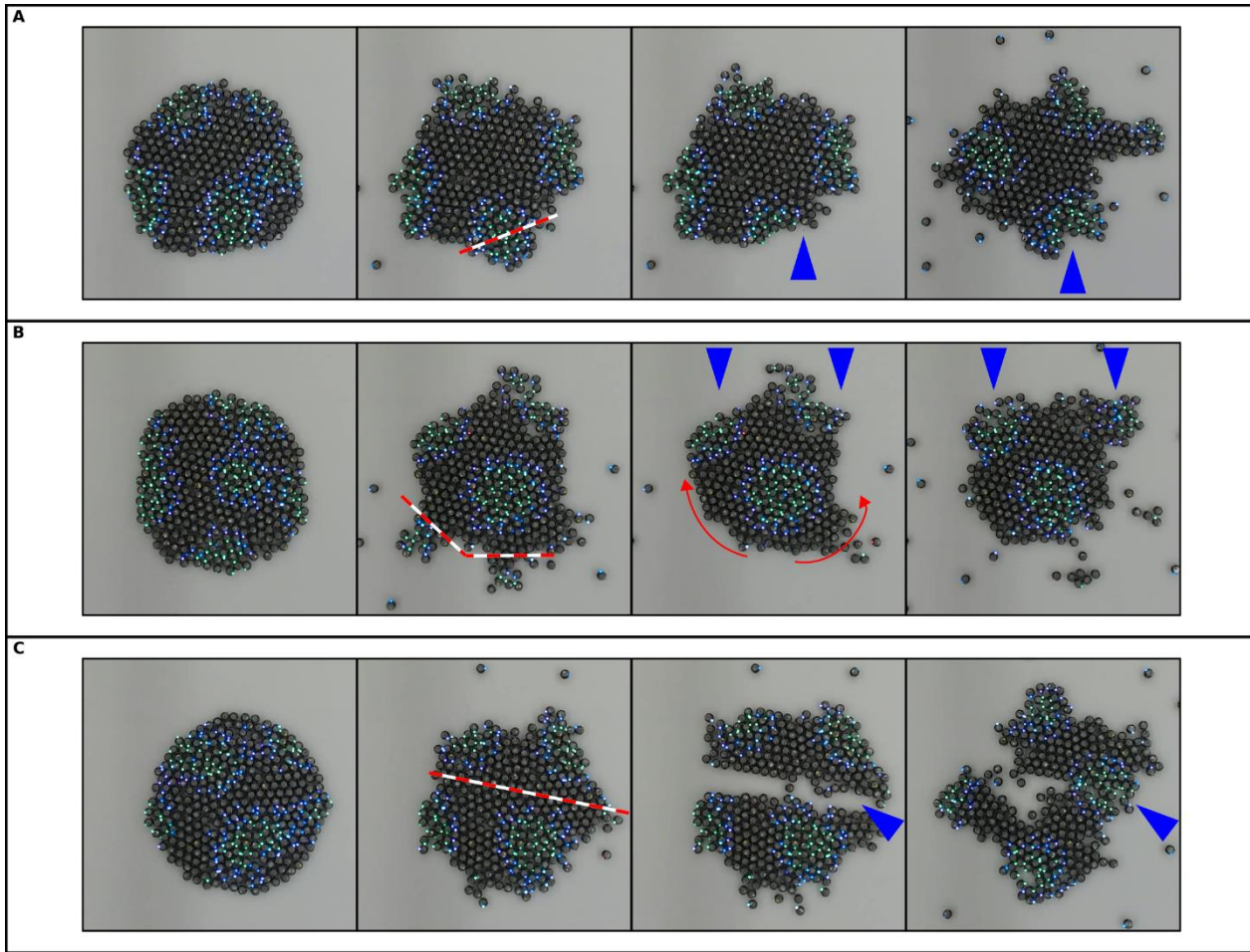


Figure 5. Robustness of swarm morphologies. (A) Regeneration response to minor damage. The starting point was the “standard” four spot pattern, from which four tentacles developed, as visible in the second panel. The robots from one tentacle were removed, as indicated by the red dashed line and left behind a Turing spot with a dent in the middle. After a while the tentacle regenerated with a small dent in the middle. (B) Redirected tentacle growth response. Two tentacles were completely cut off and the whole Turing spots were removed. Unlike the example in (A), where there was some of the original Turing spot remaining, here these tentacles could not grow back. Instead, by cutting them off, we effectively freed up a larger surface of edge robots that could freely move and aided the growth of the remaining two tentacles in the swarm, as visible in the third and fourth panel of the figure. (C) Regeneration response to major damage. The developing swarm was cut in two, approximately equal parts, along the red dashed line. We left the two swarms in close proximity to each other and after a while they managed to merge into one entity again.

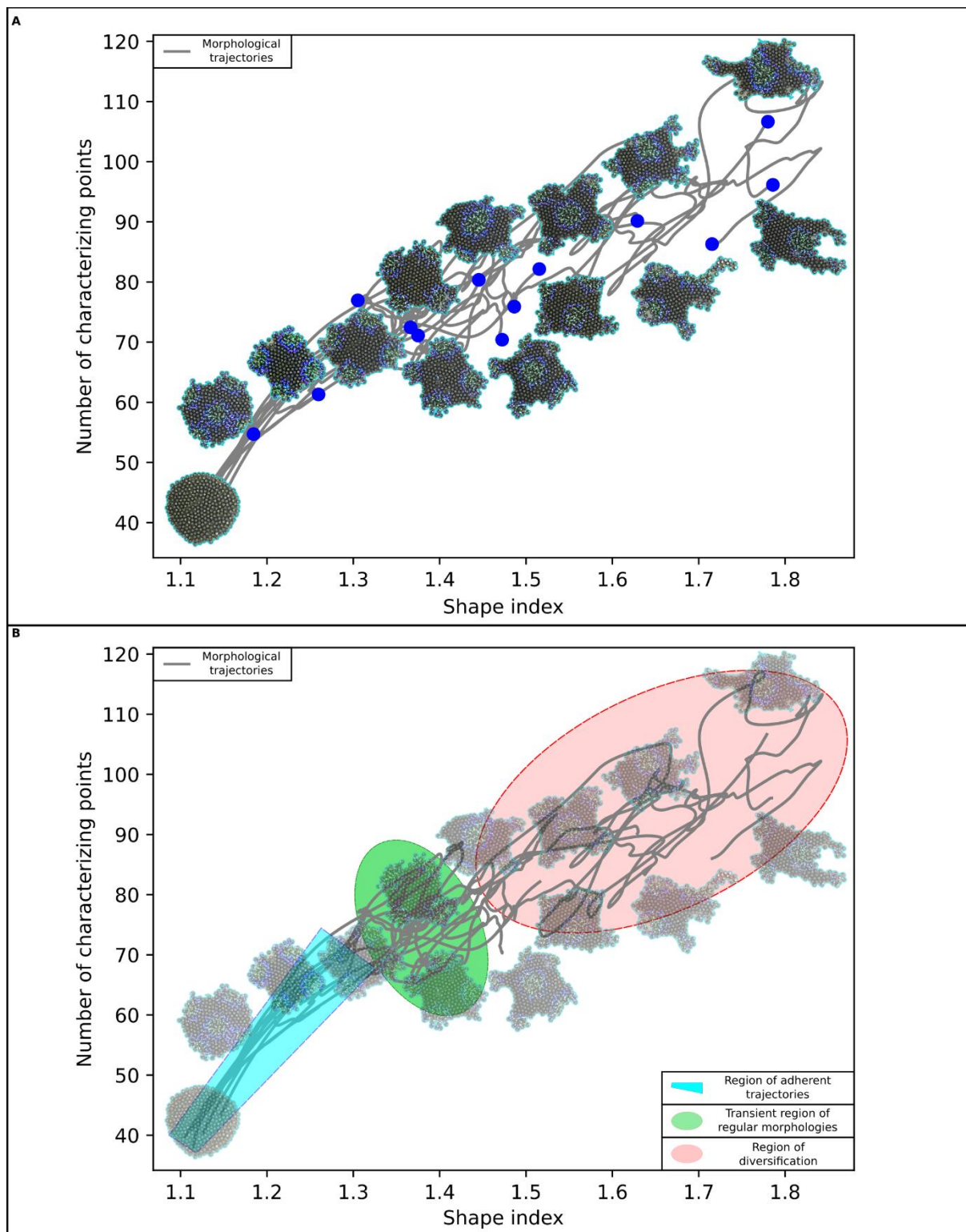


Figure 6. Quantitative analysis of swarm morphologies. (A) Morphospace of nine runs of the morphogenesis algorithm, all starting from an initial circular configuration. Grey lines trace the change of swarm morphologies and the morphospace is populated by both regular (transient) shapes and more organic shapes. The corresponding morphologies are plotted alongside each point. (B) Three distinct regions of morphospace trajectories. The first one is the thin “adherent” region (blue), where all the individual trajectories go through in proximity to each other. Next is the transient region (green) where most of the regular morphologies reside. The third region (red) is where the more organic morphologies reside. Their trajectories in this region are more spread out than in the blue region. However, they still remain in a constrained space.

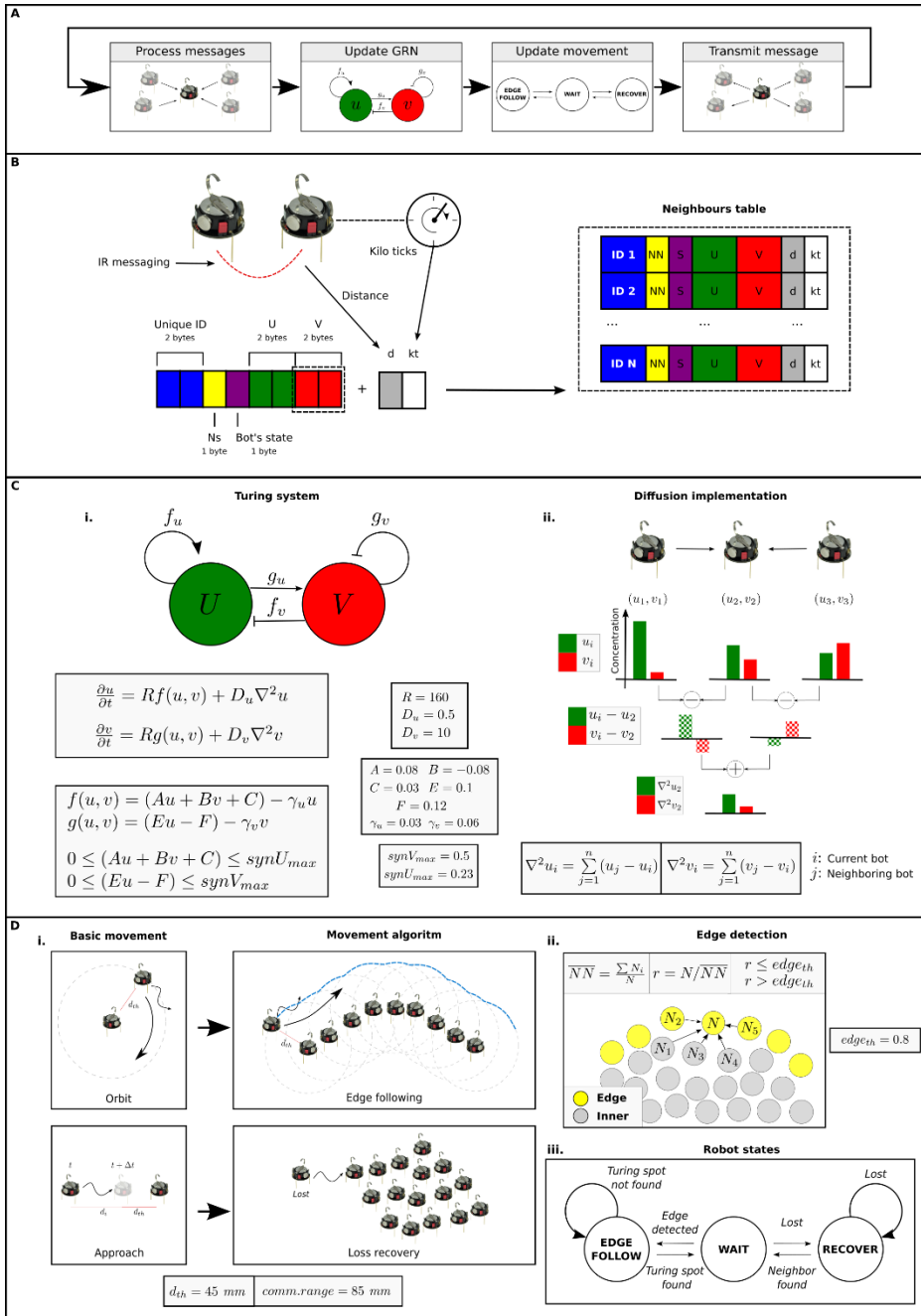


Figure 7. Morphogenesis approach implementation details. (A) Morphogenesis algorithm execution loop. (B) Each kilobot broadcasts an 8-byte message containing its ID, number of neighbors, state and the values of the two morphogens of the Turing system. Received messages are stored in a neighbors' table, together with the distance to the transmitting robot and the kilotick time stamp. (C) A linear Turing system (i.), consisting of two morphogens, whose concentration is determined by solving the reaction-diffusion equation on each robot. Morphogen diffusion (ii.) is calculated by first comparing (subtracting) the morphogen values of each neighbor, to a robot's own morphogen concentrations and then these differences are summed up, yielding the net diffusion of each morphogen. (D) Orbiting and approaching movements are the basis for edge following and loss recovery movement (i.). When an orbiting robot is moving around its current nearest neighbor, the resulting movement is edge following. If the robot is approaching its nearest neighbor from a given swarm, the result is loss recovery movement. (ii.) By calculating the ratio of the average local density of kilobots (NNs) to its own number of neighbors (N), given a threshold r_{th} , a robot determines whether it is an edge bot (yellow) or not (gray). (iii.) Three robot states: WAIT, EDGE FOLLOW and RECOVER. The WAIT state is a static, non-blocking state. In the other two states, a robot performs the corresponding movement algorithms described in (i.).

Table 1. Transition rules for switching between kilobots states.

	WAIT	EDGE FOLLOW	RECOVER
WAIT	<i>default</i>	<ul style="list-style-type: none"> • edge_detected() • check_wait_state(ALL) • dist_to_Turing () > dist_th 	<ul style="list-style-type: none"> • dist(NN) > dist_far
EDGE FOLLOW	<ul style="list-style-type: none"> • dist_to_Turing () < dist_th • !edge_detected() • !check_wait_state(NN) • dist(NN) < dist_far 	<i>default</i>	N/A
RECOVER	<ul style="list-style-type: none"> • !check_wait_state(NN) • dist(NN) < dist_far 	N/A	<i>default</i>

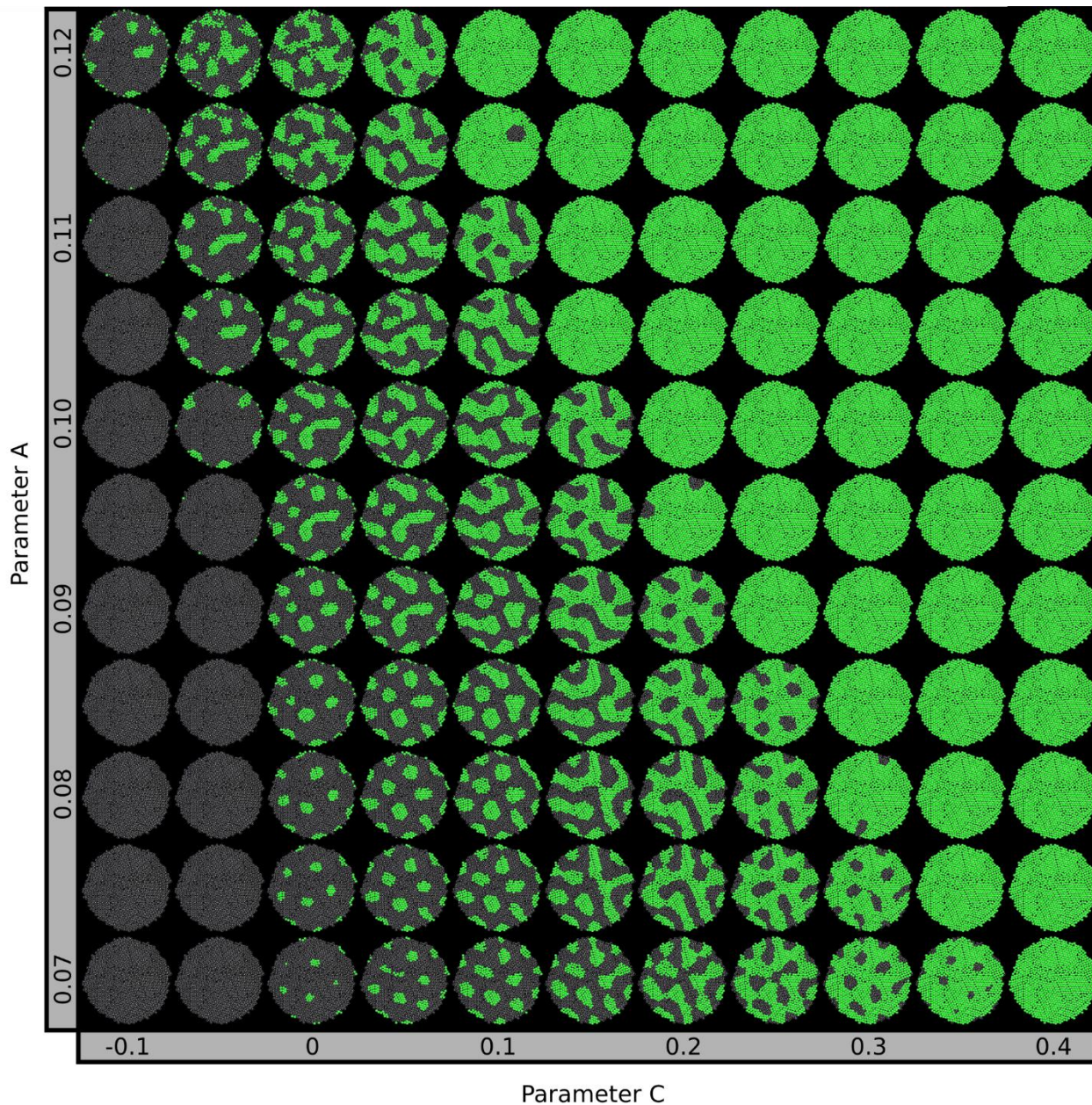


Figure S1. Parameters exploration in simulation. As shown in Miyazawa *et al.* (47), different types of patterns can be obtained by varying parameters A and C (B and E as well) in the linear reaction-diffusion model. We performed a similar exploration of the parameter space defined by parameters A and C for reproducibility purposes in the simulator Kilombo. The other parameters were the same as shown in Fig. 7. Number of agents was set to 1000, and the same seed was used for all runs. Snapshots were taken after the patterns were stable, i.e., no substantial change in concentration was seen. Colors indicate concentration of molecule U , where green is a value greater than 4 units and no color means a value less than or equals to 4 units.

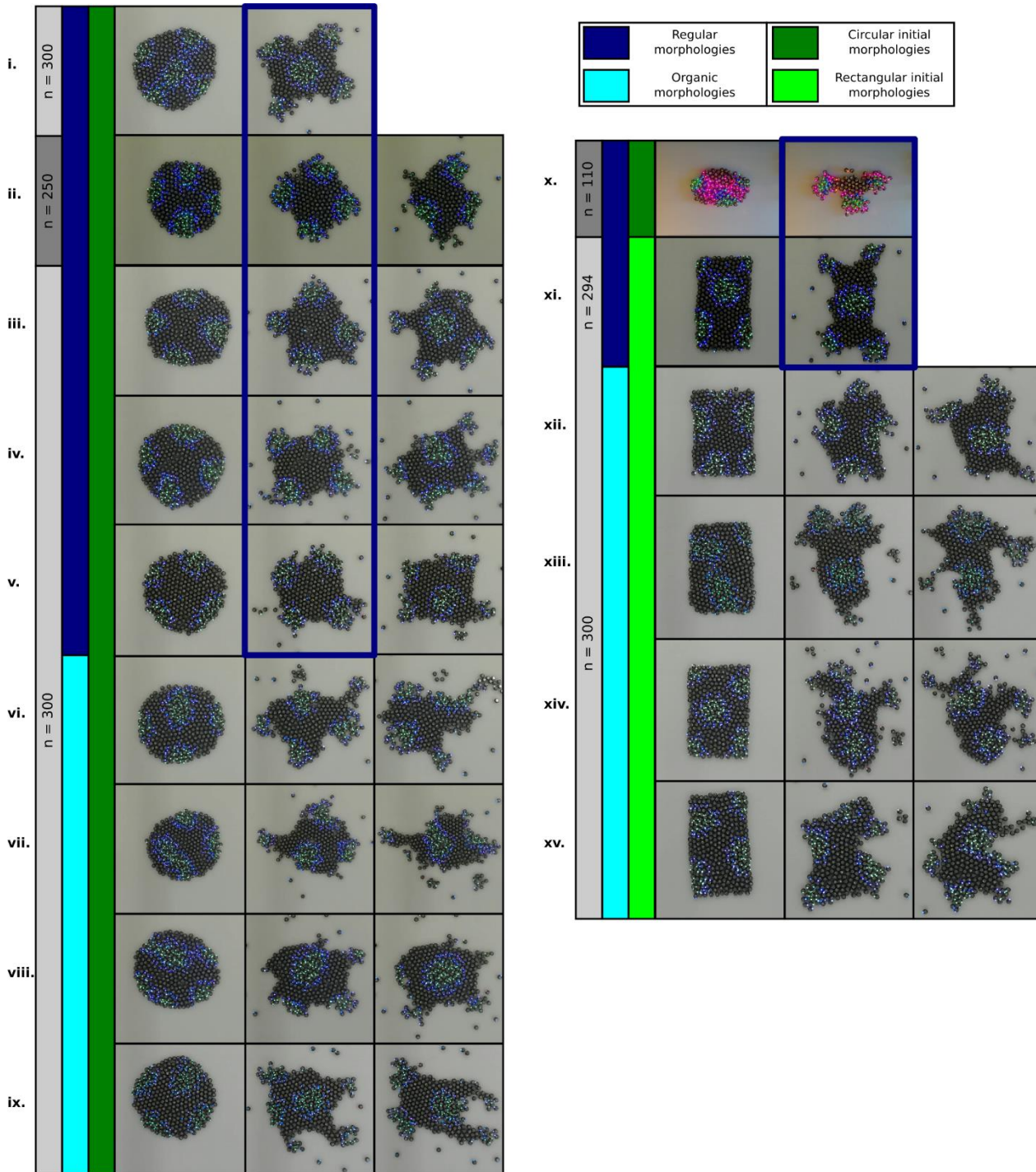


Figure S2. Summary of fifteen different runs of the morphogenesis algorithm. (i.-ix) are morphologies emerging from an initial circular shape, with an approximately similar number of robots (number given as n). (i.-v.) form “regular” (4-fold) morphologies, while the rest (vi.-ix.) make more organic shapes. In (x.) the swarm has an initial ellipse shape and it is significantly smaller (110 robots) than the other runs. It also manages to form a regular (3-fold) morphology. (xi.-xv.) start from an initial rectangular shape and in (xi.) a regular (4-fold) morphology emerges, while in (xii.-xv.) organic shapes are visible.

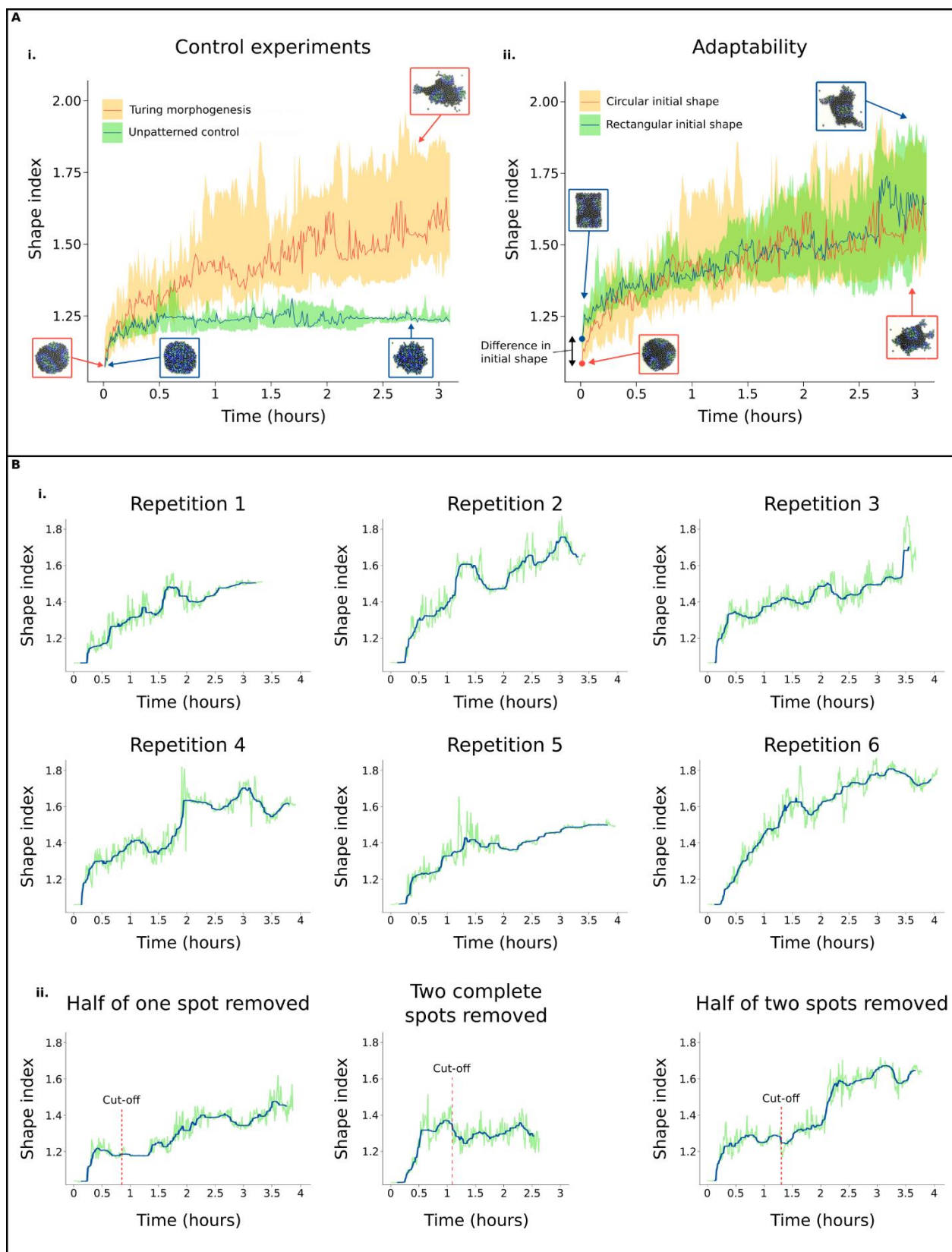


Figure S3. Quantitative analysis of emergence, adaptability and robustness. (A) Emergence and adaptability graphs showing the median, absolute maximum and absolute minimum shape index every forty seconds of six repetitions of the Turing morphogenesis algorithm starting from a circular shape and three repetitions of morphogenesis with random concentrations, i.e., no Turing patterning (control) (i), and starting from a circular shape and five repetitions of the same Turing morphogenesis algorithm starting from a rectangular shape (ii). (B) Individual

graphs showing the median of a moving window of thirteen minutes (centered at the current time on the x axis) and real shape index of the six repetitions of the Turing morphogenesis algorithm starting from a circular shape **(i)**, and three regeneration experiments where half of a Turing spot was removed (left), two complete Turing spots were removed (center) and half of two Turing spots were removed (right) **(ii)**.