Hydractinia

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Abstract

An agent-based simulation of the Hydractinia colonies and their allorecognition behavior was constructed. We show evidence that the model successfully mimics the phenomenon of colony growth, fusing, rejection (both active and passive), morphological and genotypic mutation, competitive exclusion and the unexpected phenomenon of buffering. We were unable to reproduce the rock-paper-scissors dynamic due to limitations inherent to the model.

1 Introduction

The Hydractinia colonial organism has been studied for its allorecognition properties, which are thought to be a precursor for the MHC immuno-recognition seen in mammalian immune systems. We create a model of Hydractinia colonial growth which incorporates the three morphologies (*stolon*, *fused mat* and *unfused mat*) and the genes (which may occur in the following nine combinations on the two chromosomes: $ff\alpha\alpha$, $fr\alpha\alpha$, $rr\alpha\alpha$, $ff\alpha\beta$, $fr\alpha\beta$, $rr\alpha\beta$, $ff\beta\beta$, $fr\beta\beta$, $rr\beta\beta$,) thought to be primarily responsible for the allorecognition phenomenon.

2 Model Definition

In our conversations about how to design our Hydractinia, we focused on several key questions:

1. Agent-based or cellular automata based simulation?
2. How realistic (both in terms of implementation and model realism) is basing fight-resolution on the global property of colony size?
3. Were we to calculate colony size, how would we determine the size of a colony after it fuses with another?

4. What neighborhood (von Neumann or Moore) should be used for a) counting nearby mat cells b) reproducing and c) fighting?
5. With passive rejection (between two fused mat colonies), should failing to allorecognize the other colony inhibit reproduction, as it does with aggressive rejection?
6. Is dying on a given round considered an 'action', i.e. if a Hydractinia is flagged to die in a given time-step, should it be allowed to do something else before giving up the ghost?

2.1 Agent Based Simulation

In considering the first question, we decided to employ a hybrid model in which each cell of a square lattice is considered an agent in a variety of states. Empty cells are flagged as dead, and may conduct no actions. Alive cells may take *one* of the following actions per turn, checked in the following order:

1. Change to a *dead* agent with probability P_{death} at each timestep
2. In a random order, check each of the cells in the adjacent nov Neumann neighborhood for successful allorecognition. The first failure results in a fight which is immediately resolved.
3. With probability $P_{reproduce}$, spawn. If reproducing, check in a random order the von Neumann neighborhood of adjacent cells for one that is empty. The first empty cell found becomes the location of the new agent.
4. If none of the above actions were taken, do nothing.

2.2 Agent Interactions

Early in our discussions, we agreed that counting the size of a particularly agent's larger community would be both problematic in terms of implementation and was only loosely representative of the real-world characteristics which this model aspect was seeking to represent. In particular, we did not see a simple way to resolve the difficulty of hostile colonies mutually recognizing a third party (i.e. the genotypes $ff\alpha\alpha$, $ff\beta\beta$ and $rr\beta\beta$). Clearly in this case, the two hostile colonies should not be counted as part of the same colony, yet from the perspective of a member of the neutral colony, they should be. Fundamentally, the problem with counting colony membership arises from the fact that allorecognition is not transitive: if colony A recognizes colony B, and colony B recognizes colony C, then colony A does not necessarily recognize colony C. Because the idea of counting colony size is motivated by the sharing of resources among fused colonies, it was not clear how to resolve a situation in which colonies A shares resources with C via B, yet A and C would not normally share resources. One could potentially simply count all cells with which a cell would recognize directly or indirectly (via any number of intermediaries). However, even this approach is problematic, as one may enough up counting all cells as being part of one super colony despite may ongoing internal conflicts! At some point, either arbitrary demarcations must be made, or one must accept the potential that the metric does not truly differentiate colonies in the desired way.

As such, we decided to attempt to subsume the idea that a larger colony has more resources to devote to fights into other aspects of the model and have local interactions dictate all of the model dynamics rather than a mixture of both global and local properties. As a result, we defined a set of model probability parameters which represented the rules given in the assignment description.

- P_{ssuu}, the probability that a stolon-stolon or unfused-unfused fight will be won by the aggressor
- P_{su}, the probability that a stolon-unfused mat fight will be won by the stolon cell

Unfused mat cells obviously have an advantage over all other colonies. They can fight and, due to the increased reproductive potential that comes with nearby mat cells, reproduce faster. Setting $P_{su} > 0.5$ gives the stolon colonies a slight advantage, which is exacerbated by having a larger colony size; however, this advantage should be mitigated by an unfused mat cell colony's greater reproductive rate. Otherwise, our model follows exactly the one described in the assignment.

We also defined the following other paramaters for our model:

- N, the length of an edge of the square lattice on which the agents may move
- t, the number of time steps over which the model runs
- P_{death}, the probability at each time-step that an agent will die. The distribution of lifespans is thus a binomial one centered around $E[lifespan] = \frac{1}{P_{death}}$
- $P_{spawn,base}$, the base probability of reproducing for any morphological cell type at each time step. A binomial distribution with average $E[spawn, base] = \frac{1}{P_{spawn,base}}$
- $P_{spawn,mat}$, the probability added to $P_{spawn,base}$ for each mat cell within Manhattan distance $r = 2$ of the spawning agent.
- $P_{mutate,morph}$, the probability of choosing a random new morphology for the daughter cells when a cell splits
- $P_{mutate,geno}$, the probability of choosing a random new chromosome (for each of the two) for the daughter cells when a cell splits

For visualization, we used the gd libraries to write color PNG image files of the cell-array at each timestep. Using the unix utility *convert*, we collapsed the set of image files into a MNG movie file. You can view the movies of the experiments we cite here at *http://www.cs.unm.edu/~brainsik/cnid/*. The hues *red*, *blue* and *yellow* were assigned to the three morphologies, *stolon*, *unfused mat* and *fused mat* respectively. Combinations of saturation and value were used to differentiate the nine different genotypes possible for each of the three colors.

A complete listing of the code for our Hydractinia model is included in Appendix A.

3 Experiments

After much tinkering, we settled on the following values for our model parameters:

- N: 150

- t: variable
- P_{death}: 0.03
- $P_{spawn,base}$: 0.30
- $P_{spawn,mat}$: 0.005
- P_{ssuu}: 0.50
- P_{su}: 0.53
- $P_{mutate,morph}$: 0.001
- $P_{mutate,geno}$: 0.001

To establish that our model exhibited the required dynamics, we performed the preliminary experiments outlined in the assignment:

- Single-cell proliferation
- Fusing colonies
- Rejecting colonies (passive and active)

To explore deeper dynamics we conducted the following experiments (which were partially described in the assignment):

- Long-term fusing: What happens after an extremely long period of time to two colonies which recognize each other?
- Competitive Exclusion: What kind of situation results in one colony dominating all others in the area?
- Rock-Paper-Scissors: Is it possible to construct a rock-paper-scissors style dynamical system using the Hydractinia colonies?
- Genotypic Mutation: What role does genotypic mutation serve when activated? What dynamics does it lead to?
- Morphological Mutation: What role does morphological mutation serve when activated? What dynamics does it lead to?
- What other interesting dynamics do we observe in the simulation?

4 Results

4.1 Preliminary Results

Our preliminary results indicated very clearly that our model was indeed behaving as expected. Figures 1 and 2 depict the fusing of colonies which allorecognize each other. Figure one shows a stolon colony (red, $ff\alpha\alpha$) fusing with a fused mat colony (yellow, $ffr\alpha$). Because the fused mat colony began in a corner, its reproductive potential was somewhat hampered. Between timestep 100 and 150, the colonies touch and successfully recognize each other. This recognition is evidenced by the lack of dead or dying cells in the vicinity of the intersection. This experiment was run for 5000 timesteps, the last of which is depicted in the final image in Figure 1. Here we can clearly see the slow diffusion of the two colonies into each other, as shown by irregular border and the splotchiness in that area.

Passive rejection is illustrated in Figure 2, in which two unfriendly ($ff\alpha\alpha$ and $rr\beta\beta$) fused mat colonies are placed in the same vicinity. At time step 140, we can see the small region of passive rejection in which neither reproduction as evidenced by the lack of diffusion seen in the previous figure or fighting as evidenced by the lack of a band of dead cells separating the two colonies. Figure 3 illustrates hostile rejection, in which a stolon colony (red, $ff\alpha\alpha$) rejects a fused mat colony (yellow, $rr\beta\beta$). Because all fights between stolon and fused mat cells result in a dead fused mat cell, the stolon colony quickly overwhelms the fused mat colony.

An interaction between two hostile and aggressive colonies, such as stolon or unfused mat colonies, results in a more dynamic picture. Figure 4 illustrates such an interaction, in which a stolon colony (red, $ff\alpha\alpha$) engages an unfused mat colony (blue, $rr\beta\beta$). The black thread which initially emerges in time step 140 and continues throughout the experiment is evidence of the ongoing struggle for dominance between the two colonies. Here, the balance between the unfused mat colony's higher reproductive rate and the stolon colony's slight advantage in a fight is seen, as this particular dead-zone remains fairly stable between the colonies.

4.2 Deeper Results

Having established that our model correctly mimics the behaviors described in the assignment, we set out on the more complex experiments. One dynamic which we found to be dominate in most heterogeneous simulations in which the genotypes were not predefined, was that of one colony which is neutral to both aggressors colonizing the dead-zone between them. This phenomenon was only seen to occur between two aggressive hostile colonies (fights between stolon and unfused colonies), as the dead-zone is fairly stable in such fights. In fights with fused mat colonies, the winning colony moves the dead-zone away from the potential colonizer too quickly for it to be colonized. However, as we can see in Figure 5, once the colonizer has moved into the niche created by the fight, the fighting ceases as the warring colonies have been buffered by the third party, to which both the aggressors are neutral. This situation is exactly the kind which we were cautious about and motivated us to forego basing cell-fights on the size of their colony.

In some circumstances, one colony will dominate the others; this is particularly true, if the dominating colony is able to exclude several more vulnerable colonies, perhaps fused mat colonies or small stolon/unfused mat colonies. In Figure 6, we see an unfused mat colony (blue, $rr\beta\beta$) colony competitively exclude the other two colonies (red and yellow, $ff\alpha\alpha$ and $ff\alpha\alpha$). The dominating colony is not inherently at an advantage over the other two colonies, but rather is able to first destroy the defenseless fused mat colony, and then slowly whittling away the remaining stolon colony. The fused mat colony, in effect, prevented the stolon colony from growing to a size large enough to hold off the unfused mat colony.

There's no way to feasibly construct a system with a dynamical balance such as that of the game rock-paper-scissors. This failure is due to inherent limitations of the model, namely that fighting is reflexive. In order to have a rock-paper-scissors situation, all three morphologies must have both a weakness and a strength; however, fused mat cells have no strengths, and the weakness of unfused mat cells versus stolon cells is not substantial enough to create the desired dynamic. As suggested in the assignment, we tried a simulation having two colonies that fuse compete against one rejecting colony. Figure 7 depicts the resulting dynamics. The fusing colonies both attack the remaining colony, slowly reducing the defending colony's numbers.

In activating genotypic mutation, we were unsure what to expect. However, the changes in dynamics were significant. Previously, the buffering phenomenon was the most common result between warring colonies in a genotypically diverse environment. Generally, in a prolonged engagement between aggressive colonies, a third party, neutral to both, would colonize the war zone producing a buffered-peace between the aggressive colonies. With genotypic mutation activated, such homogeneous buffer zones were less stable. In particular, a warring colony would generate its own buffer as a result of a genotypic mutation which produces a viable neutral third genotype within the dead-zone. We would frequently see such spontaneous buffers emerge in several locations along the dead-zone, creating a heterogeneous buffer. Further, fused mat buffers were generally unstable, as any mutation which produced an agent hostile to the buffer would destroy it. Figure 8 illustrates an experiment with genotypic mutation activated that resulted in such dynamics. The border between the stolon and unfused colonies first shows the expected dead-zone, but it is quickly neutralized by the emergence of small buffers of neutral cells. Figure 9 illustrates another interesting run using the same parameters as those used in Figure 8. We can see that initially, the aggressive unfused mat and stolon colonies create a buffer to stem their battle, while the fused and stolon colonies fuse peacefully. However, a genotypic mutation results in the hostile stolon subcolony shown in time step 410 eating into the fused colony. Meanwhile, the reproductive advantage of the unfused mat colony allows it to round the tip of the stolon colony and begin attacking the fused colony as well. Genotypic mutation, however, saves the unfused mat colony from complete destruction as patch of fused cells which are neutral to the aggressive stolon subcolony persist (time step 1000).

Activating morphological mutation without also activating genotypic mutation did not lead to an significantly different dynamics. One might think that such additional flexibility might allow the fused mat colonies to defend themselves slightly better (by opening up the possibility of creating stolon or unfused mat cells), but we did not observe this increased flexibility to prevent the fused mat colonies from being engulfed by more aggressive colonies. Further, once the system reached a relatively stable genotypic steady state, the presense of morphological mutation resulted in a *morphological soup* in which a colony became a diverse mixture of the various genetically identical morphologies.

5 Discussion and Conclusion

Generally, we were fairly pleased with the resulting dynamics of our model - they mimicked those described in the assignment to a suitable degree of accuracy, and provided a few interesting and unexpected results. In particular, the buffering phenomenon was an unexpected (though in retrospect, understandable) action in the given model. Even more interesting, however, was the change in the buffering phenomenon with the activation of genotypic mutation. Although it would be presumptuous to claim that the colonies were knowingly doing anything, genotypic mutation provided a clear competitive advantage to all colonies. Those which were stifled by buffering were permitted the opportunity to penetrate the buffer via a mutation which was friendly to the parent colony, but unfriendly to the buffer. Further, colonies being attacked (particularly the fused mat colonies) could survive complete destruction by local mutations which were neutral to both the host colony and the attacking colony.

The model could be improved in many ways, however. First and foremost, the homogeneity of a colony's structure is problematic. In real world Hydractinia colonies are specialized morphological structures which are omitted in our model. The transportation and harnessing of resources was another significant omission. In simulation after simulation, we consistently saw the fused colonies excluded by their less passive morphological counter-parts. Surely, in the real Hydractinia colonies, the fused mat cells serve a more specialized role in conjunction with the other morphologies - the benefits of mat cells promoting increased reproductive potential were not well characterized by the model. In short, while we think that the model did produce some very interesting dynamics, we didn't feel like we were accurately representing the dynamics of real Hydractinia colonies.

Postscript:

Dear Stephanie,

We would like to convey that we've *really* enjoyed the class in general, the projects (which we had many long conversations about), the group discussions and the readings. We even learned that we enjoy working together :)

Sincerely,
Jeremy and Aaron

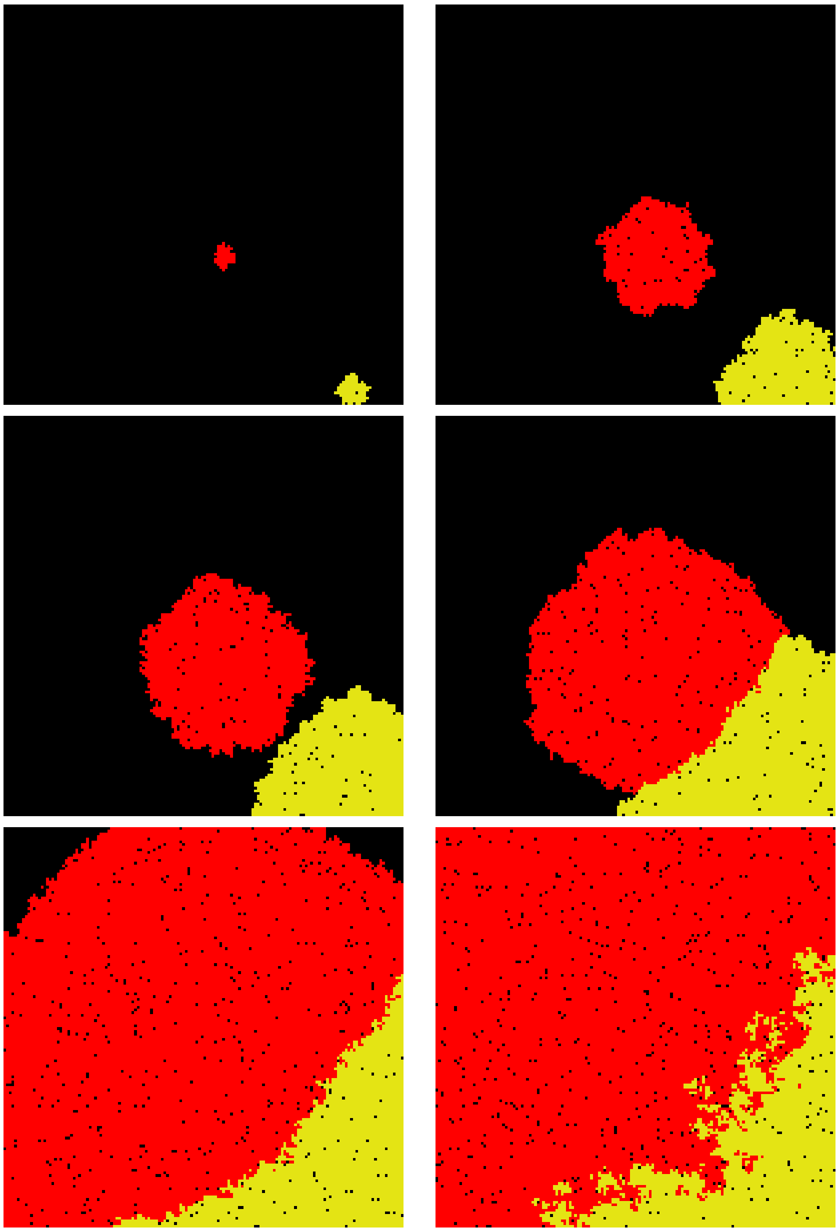

Figure 1: Example of successful allorecognition between a stolon colony (red, genotype: $ff\alpha\alpha$) and fused mat colony (yellow, genotype: $ffr\alpha$). Images are at timesteps 20, 70, 100, 150, 300 and 5000. In the final snapshot, we can clearly see that the two colonies are diffusing amongst each other to some degree, as expected with fused colonies.

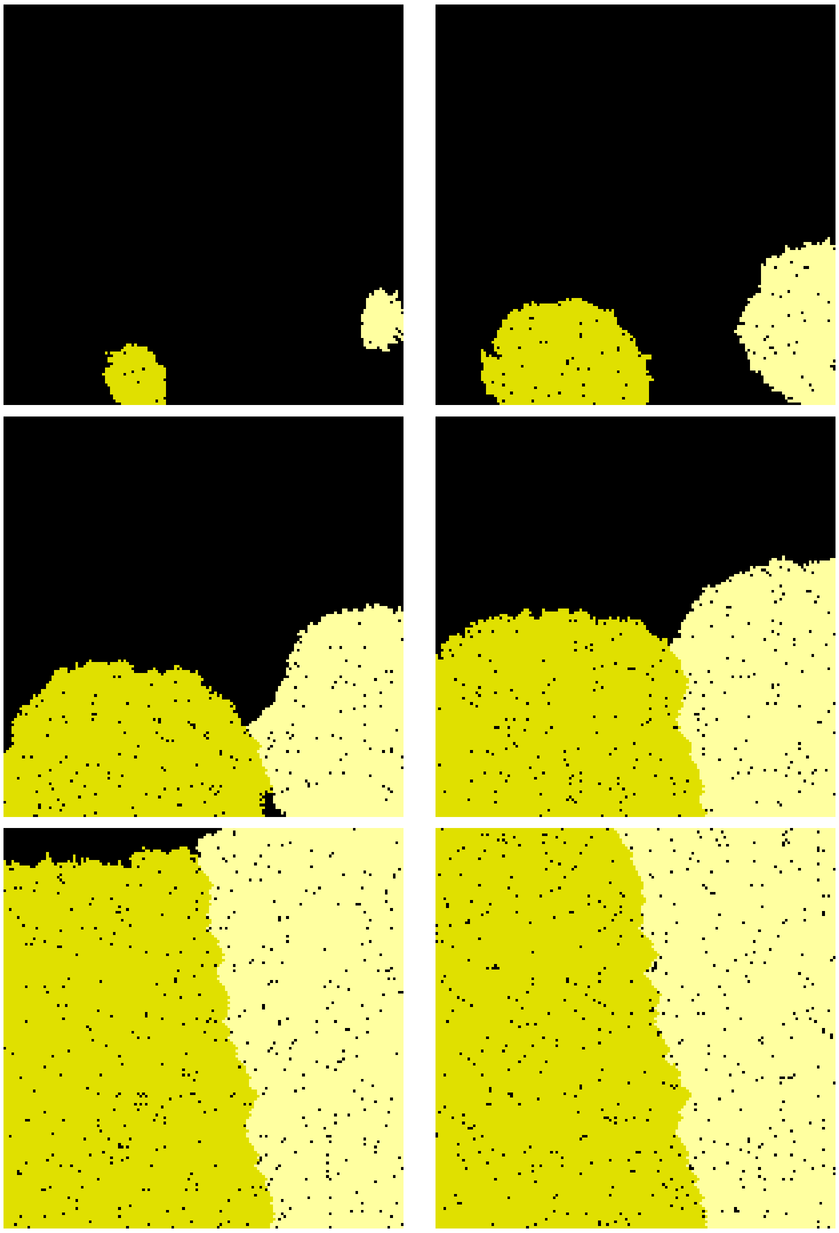

Figure 2: Example of passive rejection by two fused mat colonies (genotypes: $ff\alpha\alpha$ and $rr\beta\beta$). Images are from timesteps 40, 90, 140, 190, 250 and 600. Not the lack of dead cells (black) at the intersection of the two colonies - this indicates that there is no fighting between the colonies.

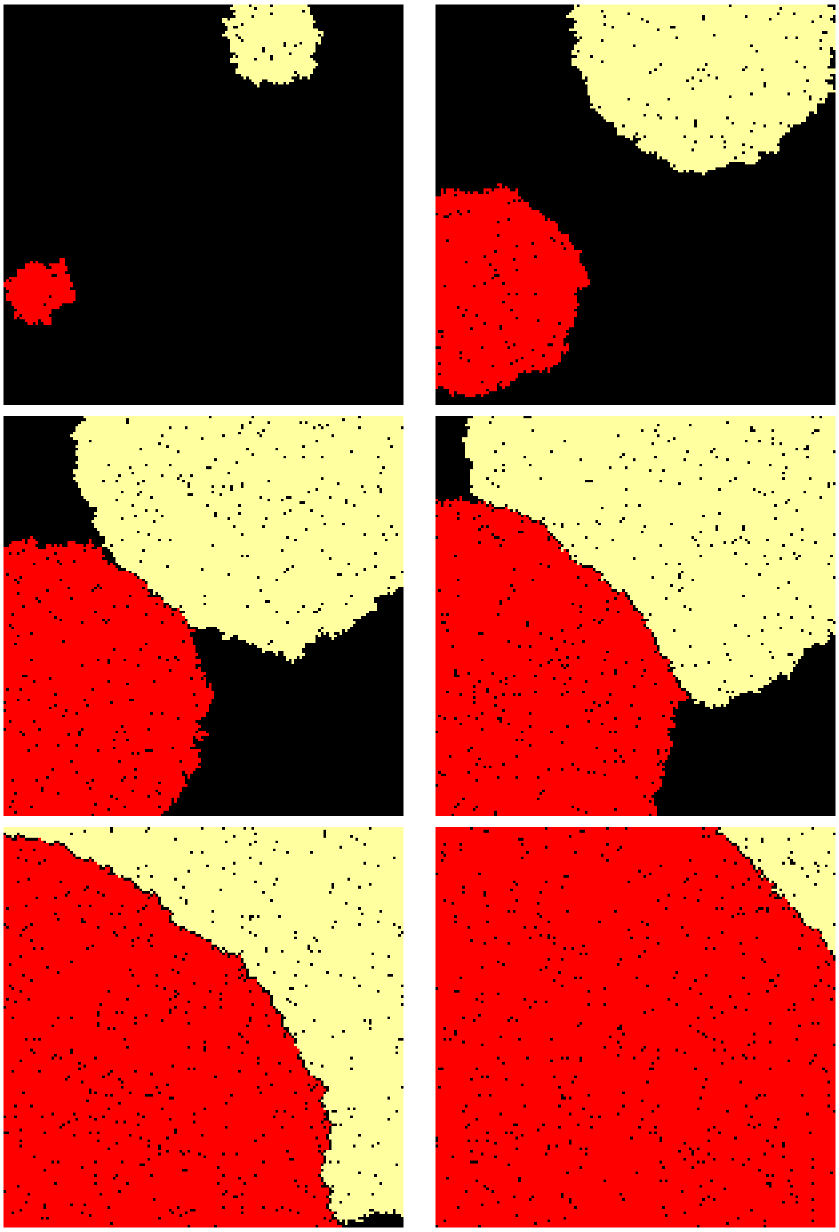

Figure 3: Example of active rejection by a stolon colony (red, genotype: $ff\alpha\alpha$) and a fused mat colony (yellow, genotype: $rr\beta\beta$. Images are from timesteps 50, 130, 190, 230, 350 and 600. Note the thin region of dead cells (black) which persists at the intersection of the two colonies; this region indicates active rejection resulting in the death of cells (fused mat cells, in this case).

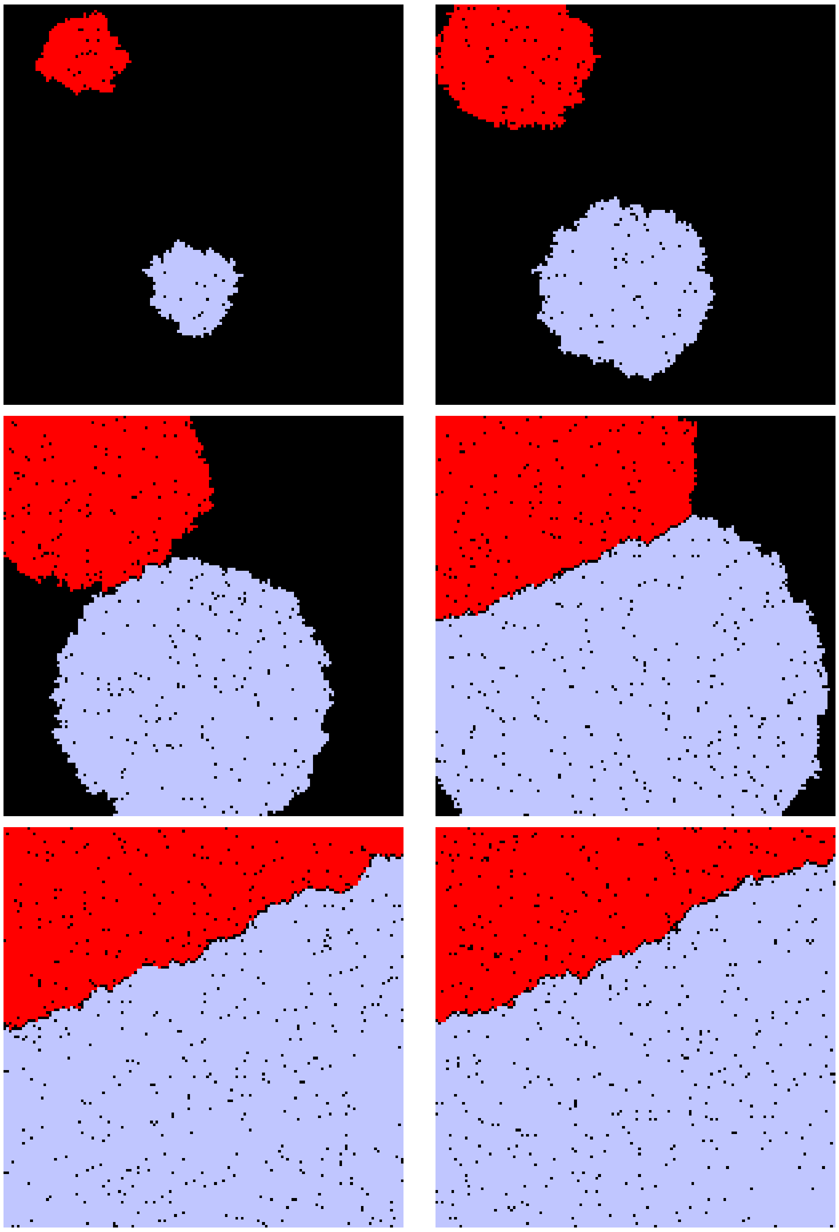

Figure 4: Example of active rejection between a stolon colony (red, genotype: $ff\alpha\alpha$) and an unfused mat colony (blue, genotype: $rr\beta\beta$). The unfused mat colony grows at a higher rate than the stolon colony as a result of the presence of other mat cells increasing the probability of reproduction. Images are from timesteps 50, 90, 140, 200, 500 and 920.

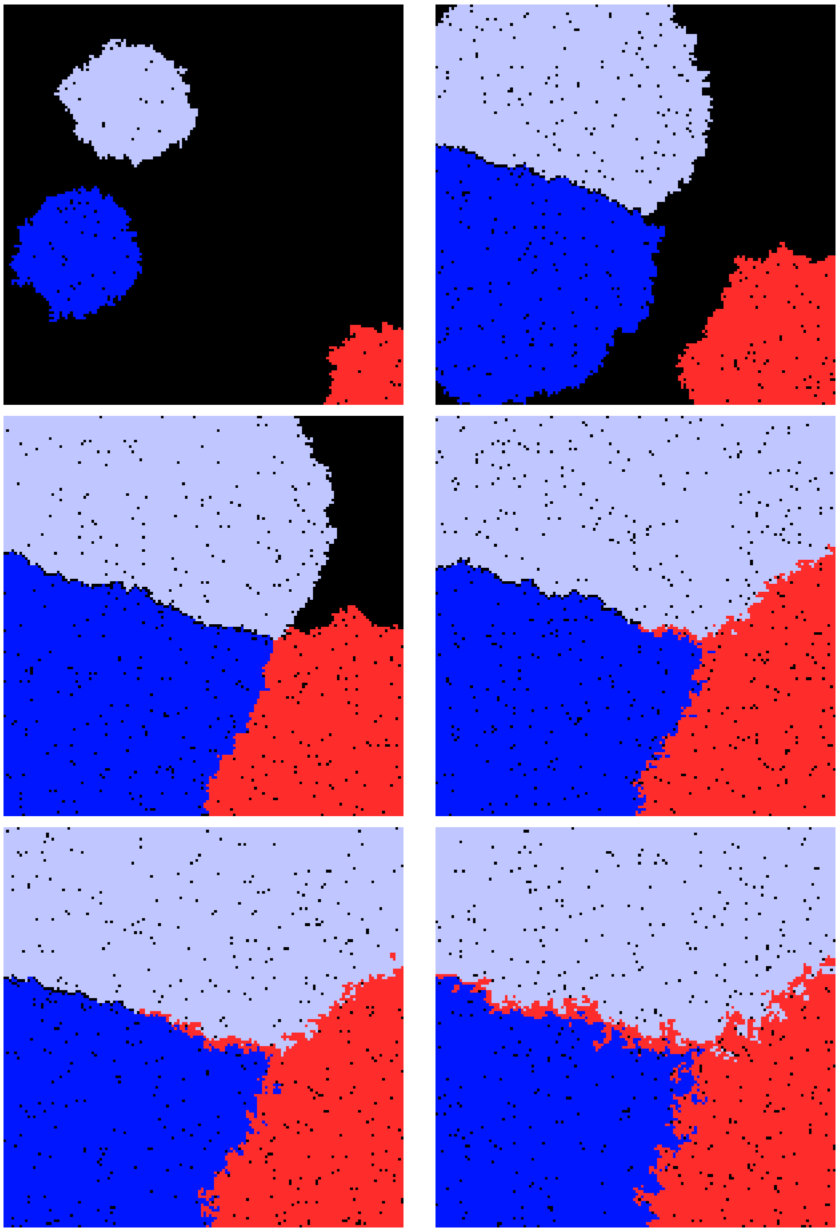

Figure 5: Example of the buffering phenomenon, in which the fighting region between two hostile colonies is colonized by a third colony which is neutral to both aggressors, resulting in a stable, non-hostile arrangement of cells. The two hostile colonies are unfused mat colonies (light and dark blue, genotypes: $ff\alpha\alpha$ and $rr\beta\beta$, while the buffering colony is a stolon (red, genotype: $ff\beta\beta$). Images are from timesteps 70, 150, 200, 350, 700 and 1500.

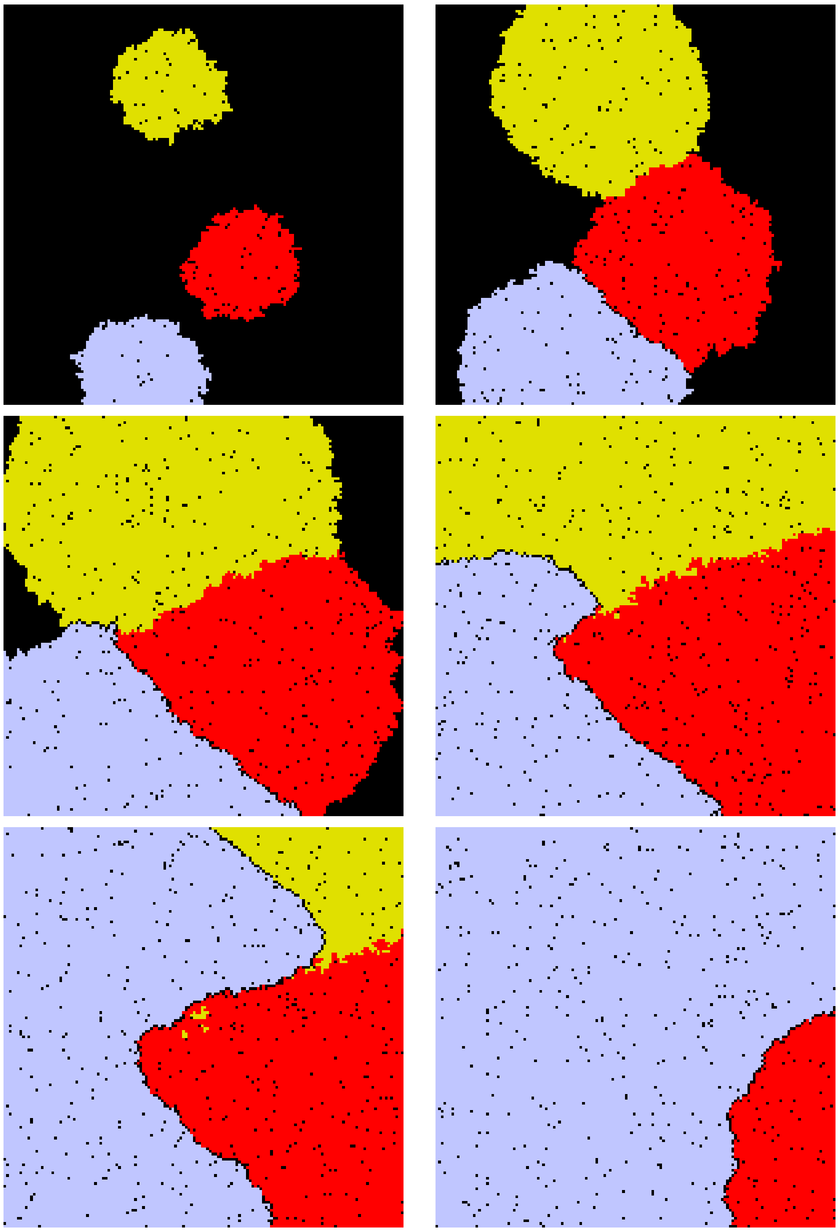

Figure 6: Example of a single colony (unfused mat, blue, genotype: $rr\beta\beta$) dominating others (stolon and fused mat, red and yellow, genotypes ($ff\alpha\alpha$ and $ff\alpha\alpha$) via competitive exclusion. The unfused mat colony, being significantly larger, is able to slowly whittle down the resistant stolon colony. Images are from timesteps 70, 120, 180, 300, 600 and 5000.

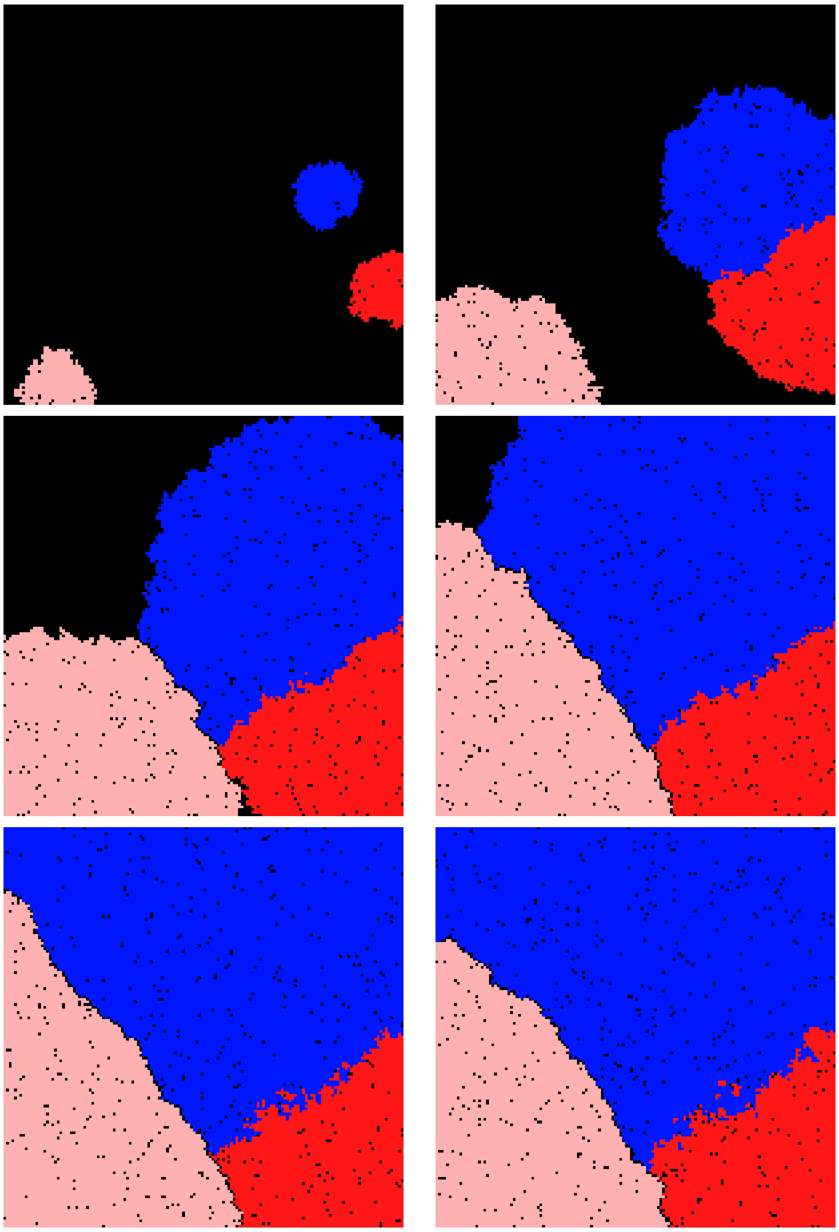

Figure 7: Rock-Paper-Scissors experiment (as suggested in the assignment), in which two colonies fuse (unfused mat and stolon, blue and red, genotypes: $ff\alpha\alpha$ and $ff\alpha\beta$), while one rejects (stolon, red, genotype: $rr\beta\beta$).

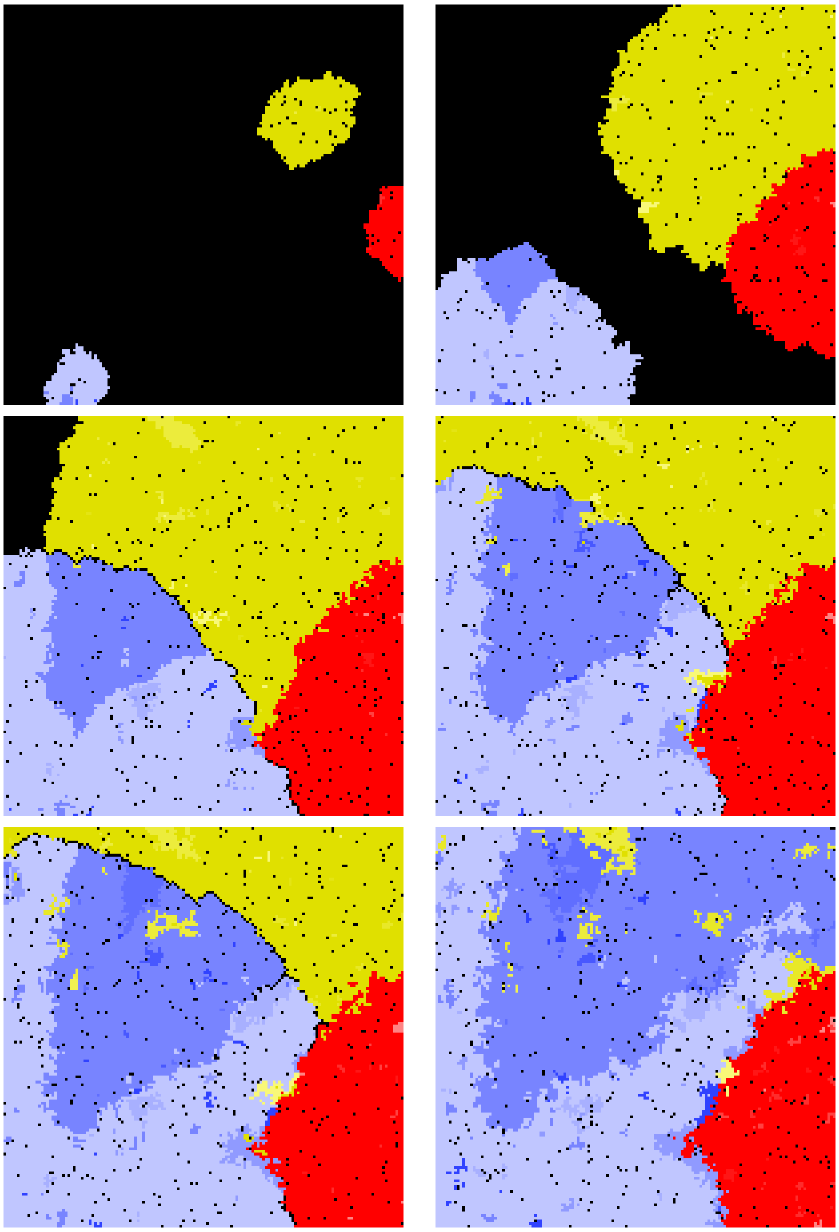

Figure 8: Activating genotypic mutation for the system used in Figure 6 (example 1). Images are timesteps 50, 140, 250, 380, 450 and 800.

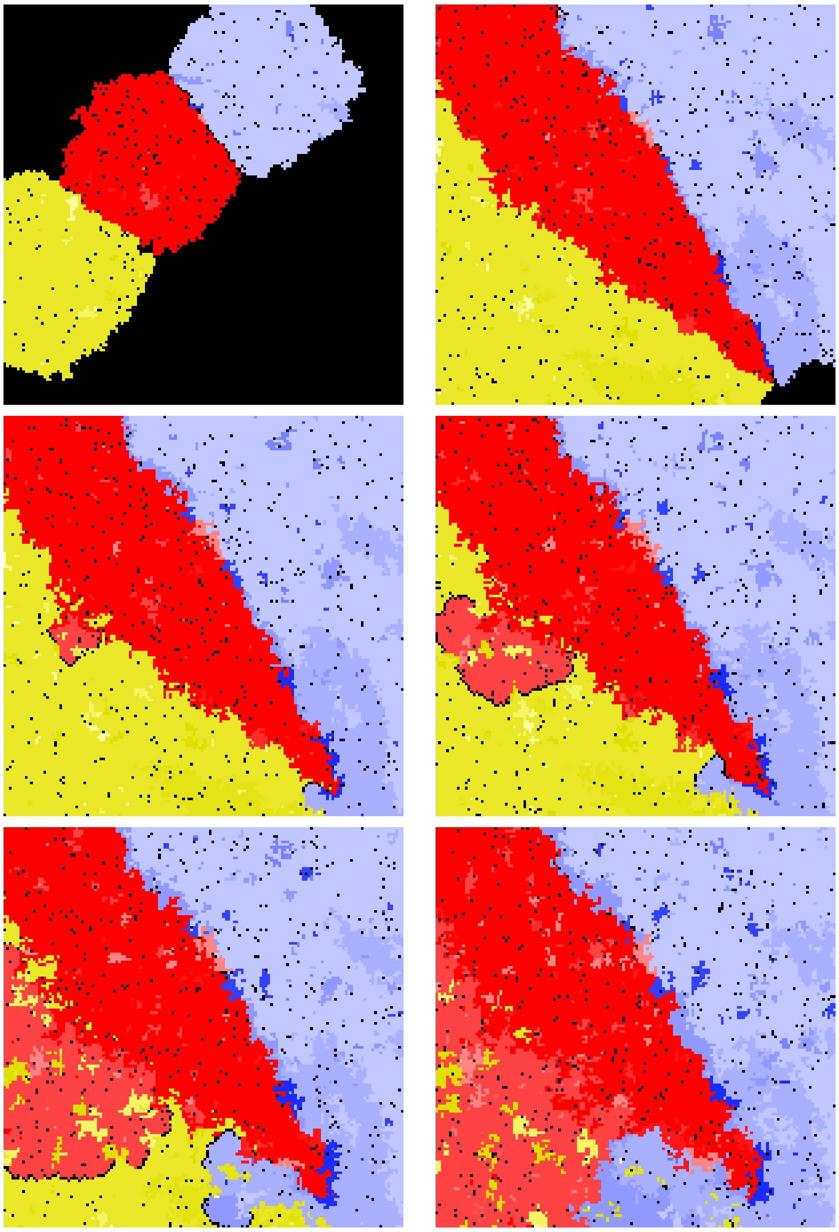

Figure 9: Activating genotypic mutation for the system used in Figure 6 (example 2). Images are timesteps 110, 320, 410, 500, 640 and 1000.