VISGRAF LAB WEBINAR 2020-09-23

SIGGRAPH THINK BEYOND

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The leopard never changes its spots: realistic pigmentation pattern formation by coupling tissue growth with reaction-diffusion

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OVERVIEW

- Pigment formation
- Tissue growth
- Pattern enlargement
- Results
- Conclusions

sample code at **mgmalheiros.github.io**

RESEARCH GOAL

- We aim to realistically reproduce animal patterns
  - but we also want to get insights into the underlying biological processes
  - therefore, we look for a plausible explanation for pigmentation pattern formation
  - for that, we have explored the expressiveness of combining simple mechanisms
  - we have found that reaction-diffusion and tissue growth both play crucial roles

PIGMENT FORMATION

- Reaction-Diffusion (RD)
- Implementation
- Exploratory approach

REACTION-DIFFUSION

» OVERVIEW

- Pioneering work of Alan Turing
- Models autocatalytic chemical reactions
- PDEs involving two reagents A and B:
  - *a* and *b* are local concentrations
  - there are reaction and diffusion parts
  - diffusion depends on nearby concentrations
  - D_a and D_b are the diffusion rates

$$\frac{\partial a}{\partial t} = 16 - ab + D_a \nabla^2 a$$

$$\frac{\partial b}{\partial t} = ab - b - 12 + D_b \nabla^2 b$$

REACTION-DIFFUSION

» DISCRETIZATION

- RD is typically solved by numerical methods
- Forward Euler integration is simple and fast
- The domain is a square lattice:
  - a and b are now two matrices
  - $\nabla^2 a$ and $\nabla^2 b$ are the Laplacian operators, implemented by finite differences
  - we use a 9-point stencil, with the given weights around a center cell

$$\Delta a = (16 - ab + D_a \nabla^2 a)\Delta t$$

$$\Delta b = (ab - b - 12 + D_b \nabla^2 b)\Delta t$$

1	4	1	
4	-20	4	/ 6
1	4	1	

REACTION-DIFFUSION

» SIMULATION

- First, define the initial values for *a* and *b*
- Given *Δt*, loop until a final time is reached
- At each iteration:
  - compute Laplacians for all matrix elements
  - evaluate *Δa* and *Δb*
  - calculate a_{next} and b_{next}
  - limit a_{next} by lower bound L_a and upper bound U_a
  - limit b_{next} by lower bound L_b and upper bound U_b

$$a_{next} = a + \Delta a$$

$$b_{next} = b + \Delta b$$

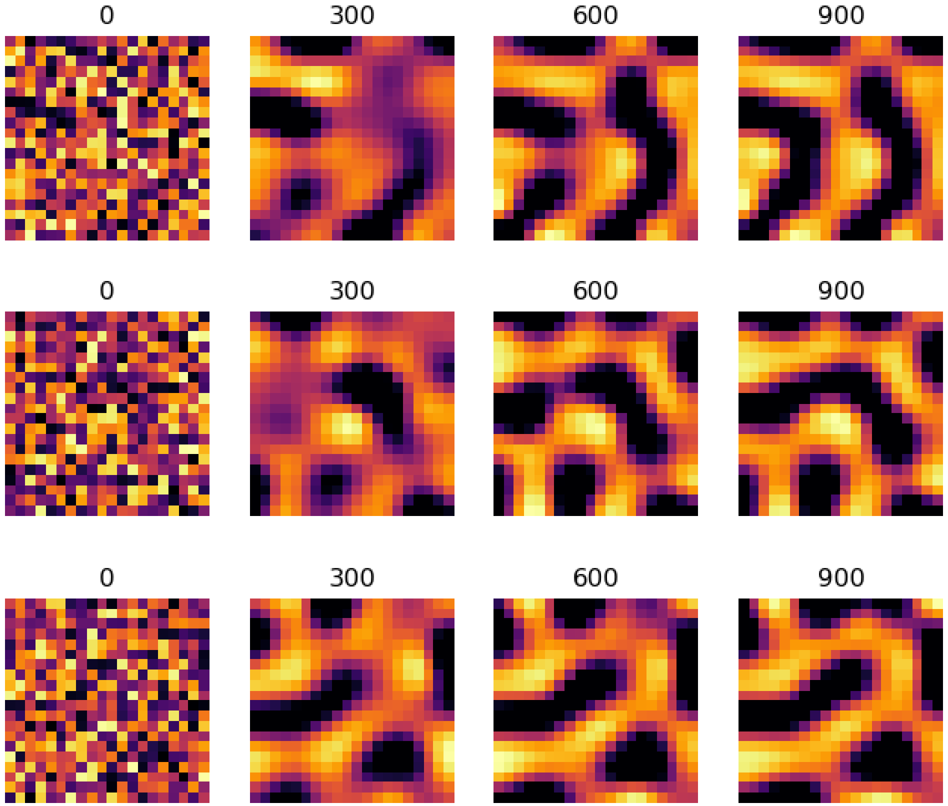
$$a = clip\left(a_{next}, L_a, U_a\right)$$

$$b = clip\left(b_{next}, L_b, U_b\right)$$

REACTION-DIFFUSION

» INITIAL CONDITIONS

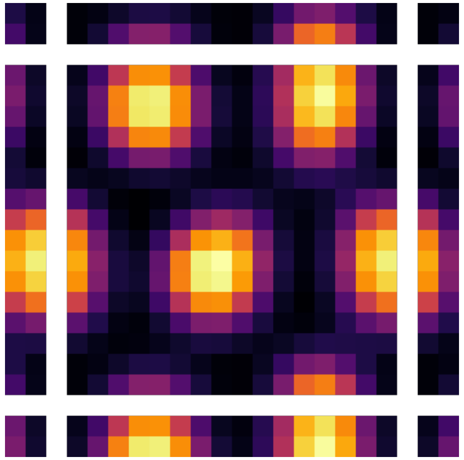
- Reaction-diffusion is sensitive to initial values
- However, pattern formation is also *robust*:
  - small perturbations yield small pattern changes
  - a fixed set of parameters induces the same resulting pattern structure, despite the randomness
- For most experiments we use:
  - $a_{initial} = 4$
  - $b_{initial} = 4$ + uniform random noise in [0, 1]



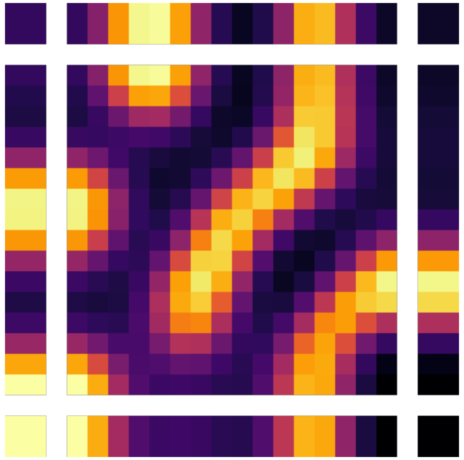
REACTION-DIFFUSION

» BOUNDARY CONDITIONS

- We employ two types of boundaries:
  - toroidal wrapping → matrix borders wrap around



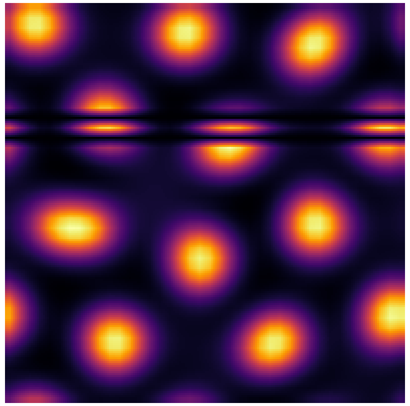
  - no-flux boundary → matrix borders have their concentrations extended outward



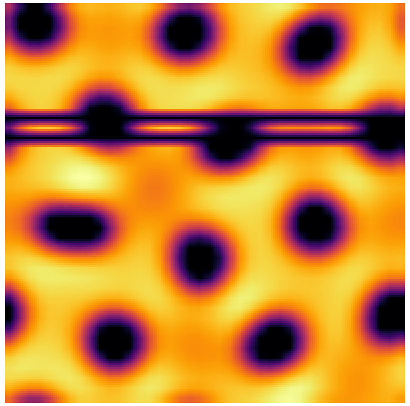
REACTION-DIFFUSION

» VISUALIZATION

- The Turing model exhibits *cross kinetics*, that is, A and B are completely out of phase
- For display:
  - we typically map either the *a* or *b* matrices to a perceptually-uniform color map
  - some experiments also use a simple linear-interpolated color map
  - no further alteration



a



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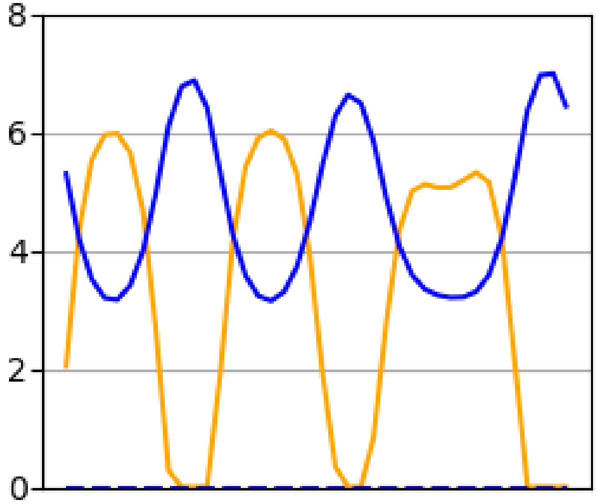
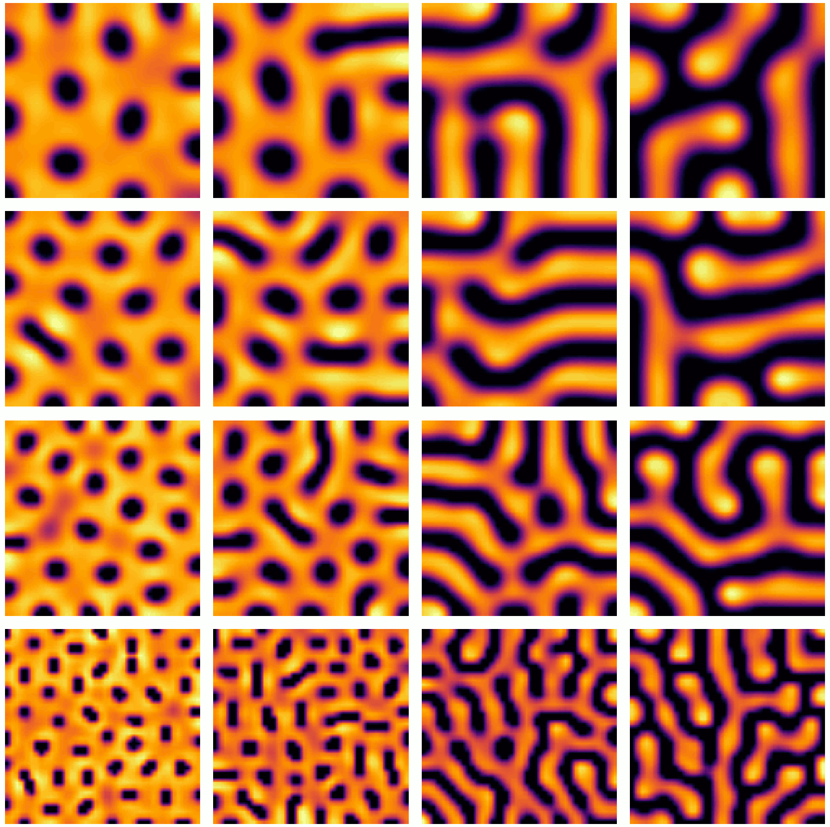


EXPLORATORY APPROACH

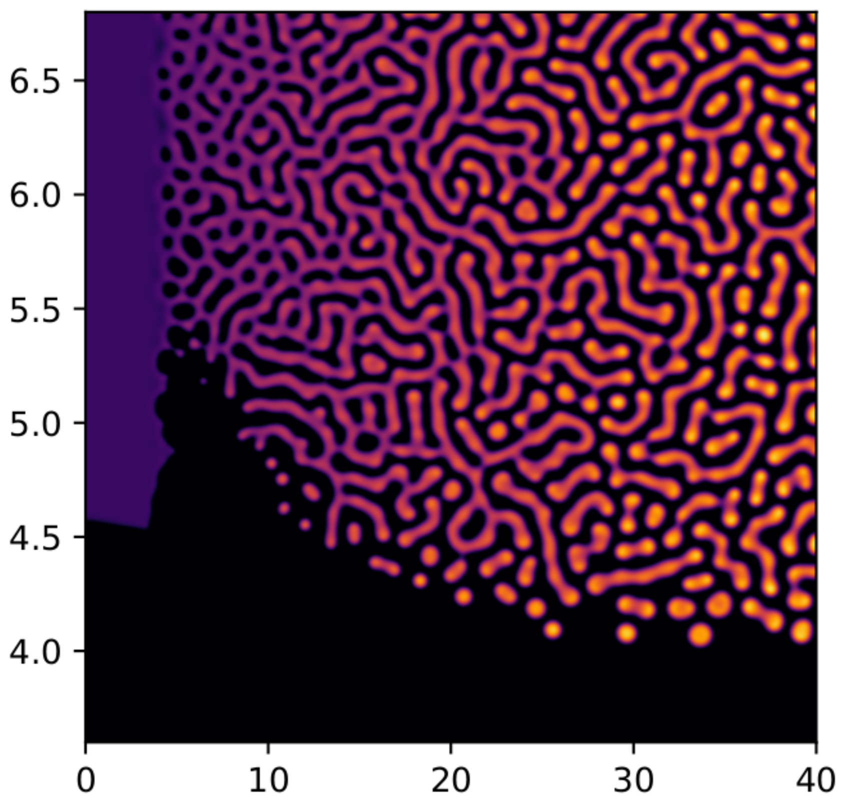
» PARAMETERS

- We have explored the parameter space of the original model, and then proposed extensions to improve expressibility and usage:
  - let $D_a = r\ s$ and $D_b = s$
  - r is the ratio between diffusion rates → structure
  - s expresses the overall pattern scale
  - previously $L_b = 0$, but we found that positive values also alter the pattern structure
  - setting U_a and U_b also changes the dynamics

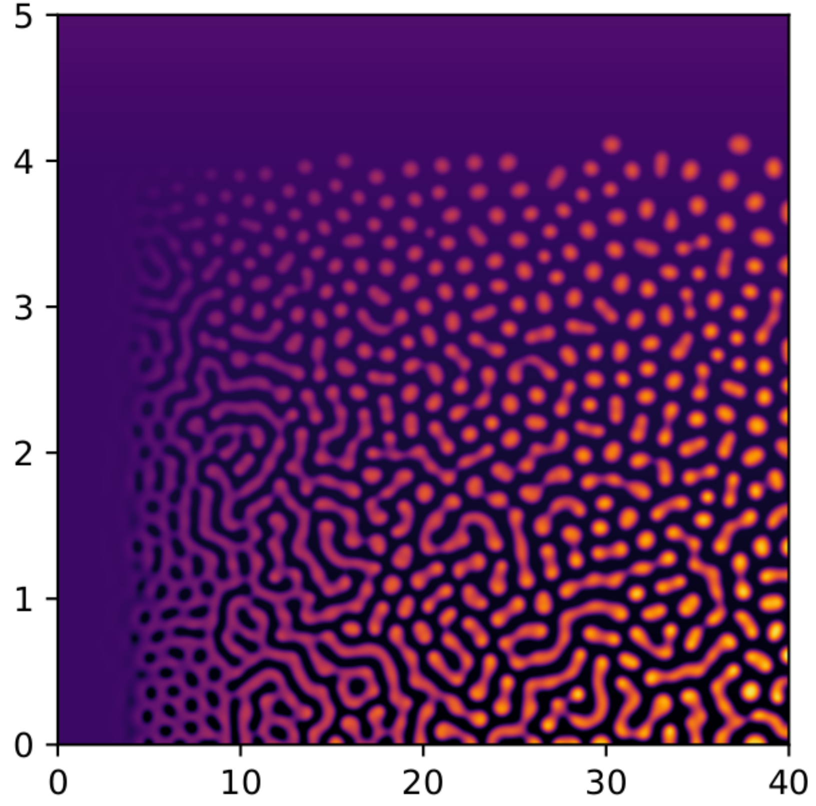


EXPLORATORY APPROACH

» PARAMETER MAPS



ratio (x) × U_a (y)



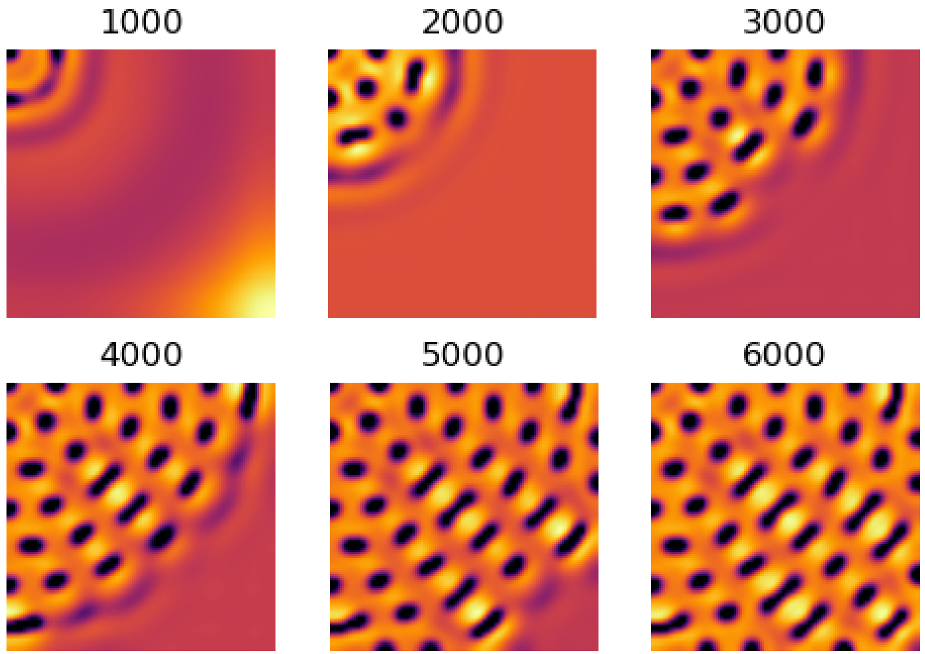
ratio (x) × L_b (y)

TISSUE GROWTH

- Static and growing domains
- Matrix expansion
- Effect of growth

STATIC DOMAIN

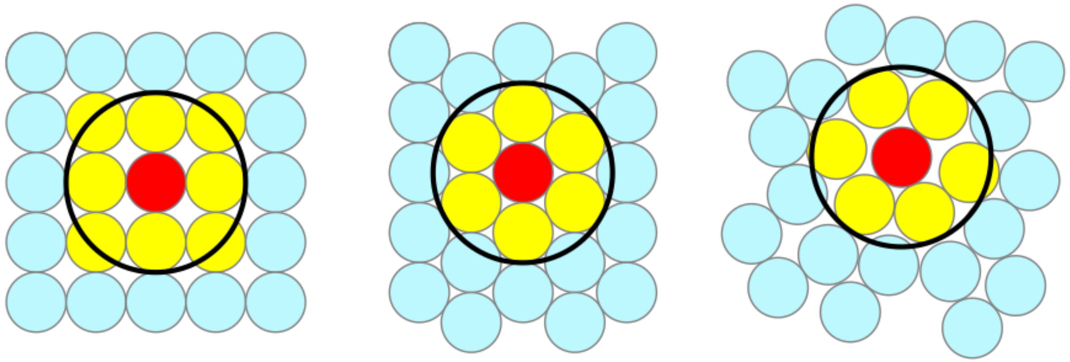
- Normal Turing patterns present a space-filling behavior
- Patterns tend to create equispaced *features*:
  - spots
  - stripes or labyrinths
  - a mix of both
- The average distance between features is called the pattern *wavelength*

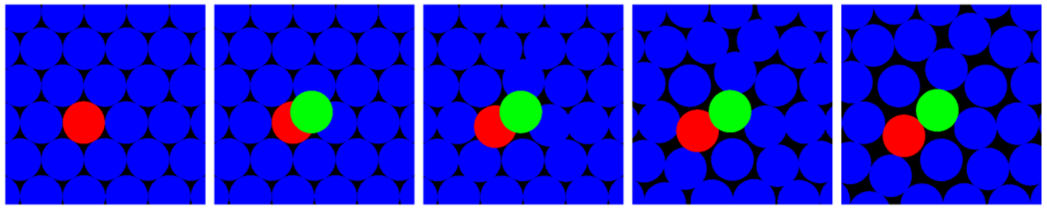


GROWING DOMAIN

» TWO PREVIOUS APPROACHES

- #1 Add continuous growth term to PDEs:
  - simulation still runs over a square lattice
- #2 A point-based cellular model, following the biologic analogy:
  - diffusion occurs only among nearby cells
  - cells divide and push others
- The drawback is being expensive:
  - needs collision mechanics
  - needs repeated Nearest Neighbor Search





GROWING DOMAIN

» A NOVEL APPROACH

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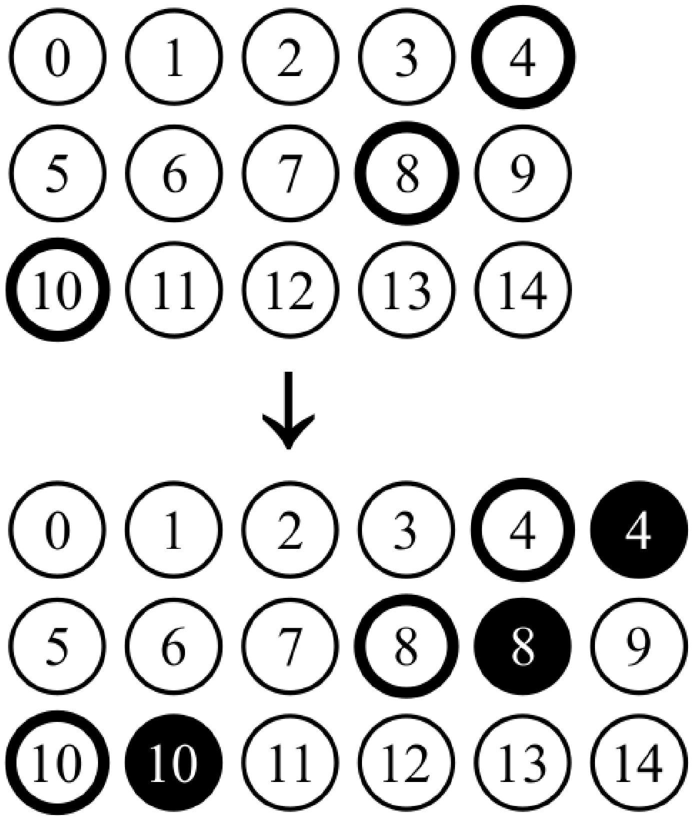
- Here we propose *matrix expansion*:
  - we approximate uniform growth by randomly selecting matrix elements and duplicating them
  - this is performed once for each row → yields a new column
  - then it is performed once for each column → yields a new row
- The domain is always a regular matrix:
  - on average, cell divisions are uniformly spread
  - we define a *growth rate* during simulation

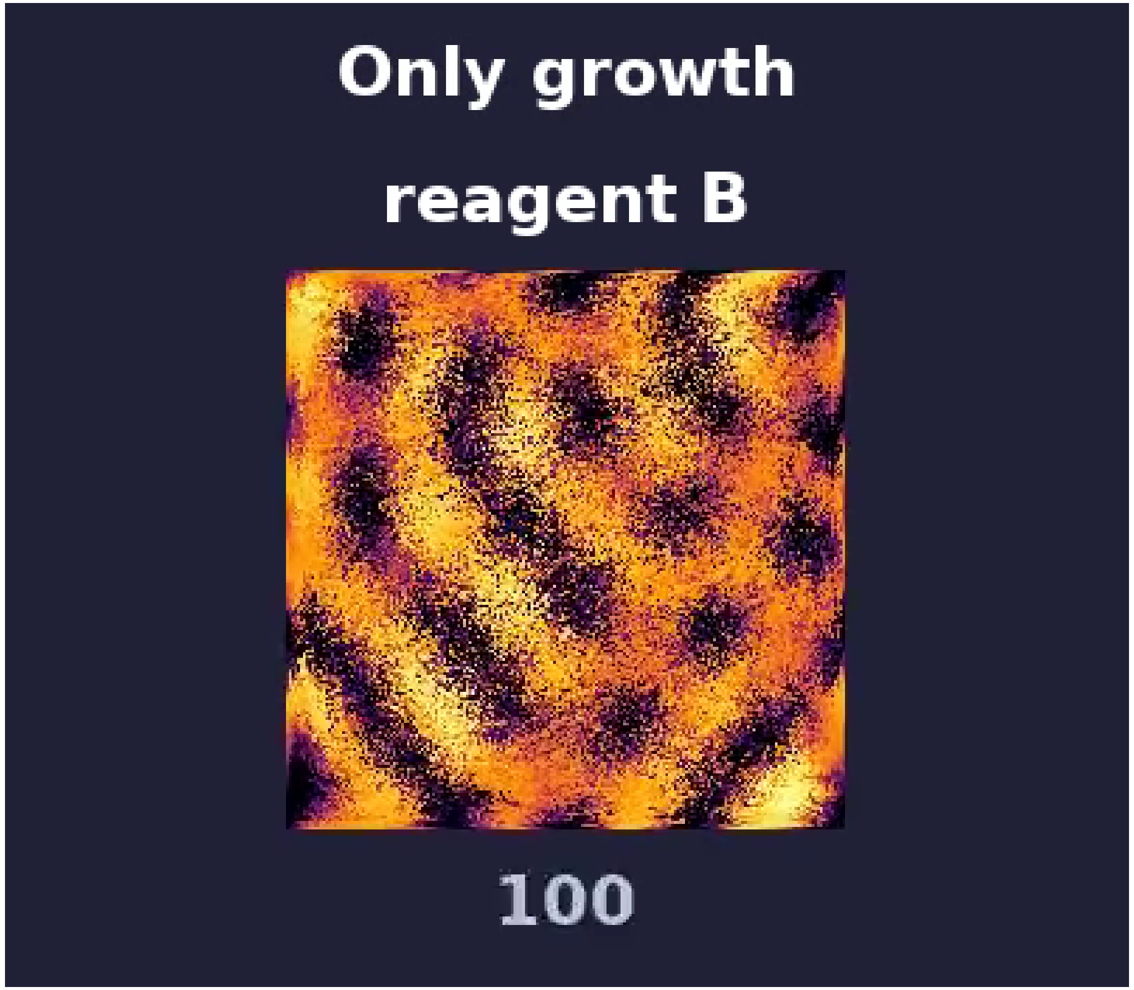


EFFECT OF GROWTH

» INITIAL STATE

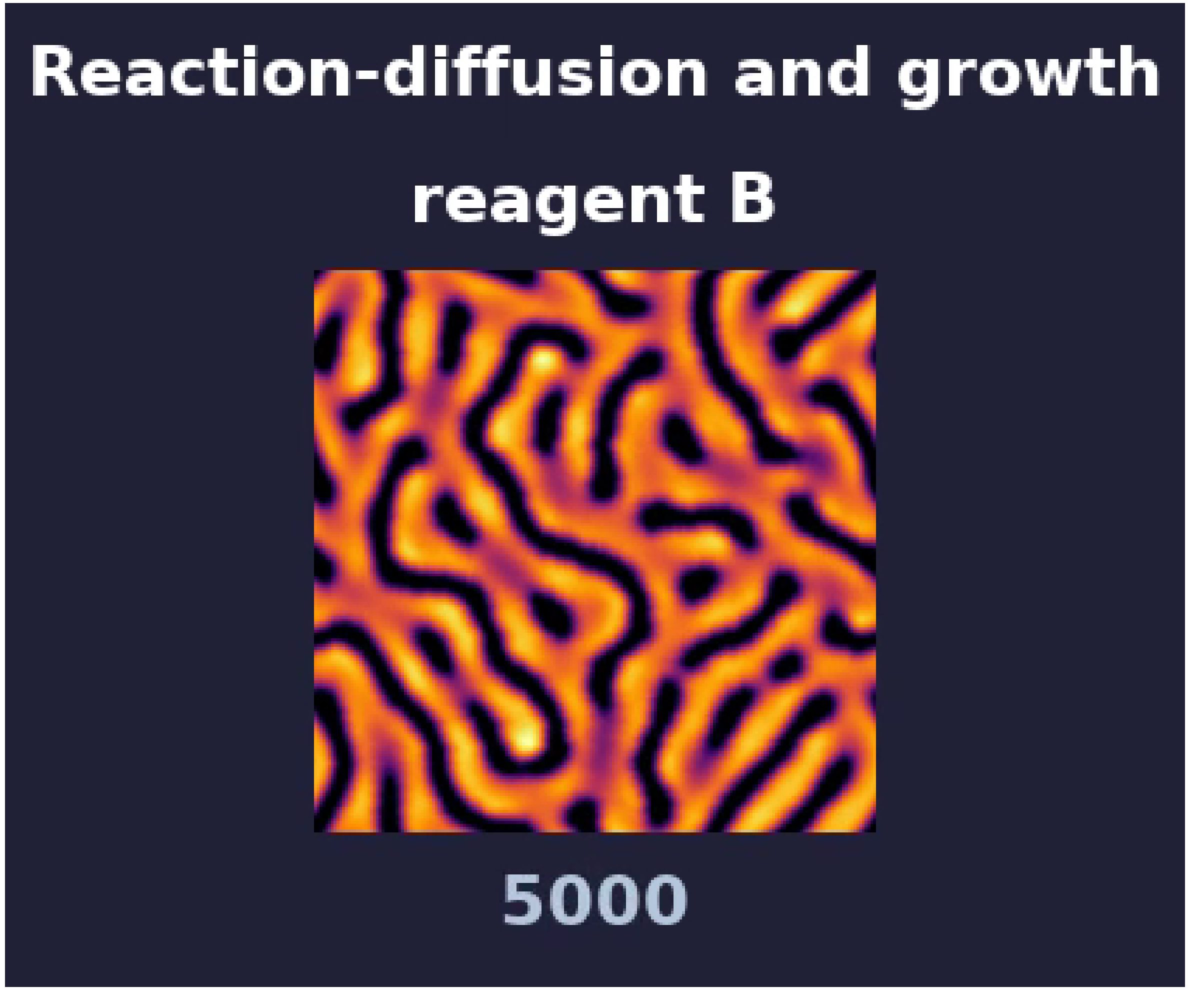
EFFECT OF GROWTH

» ONLY GROWTH, NO DIFFUSION



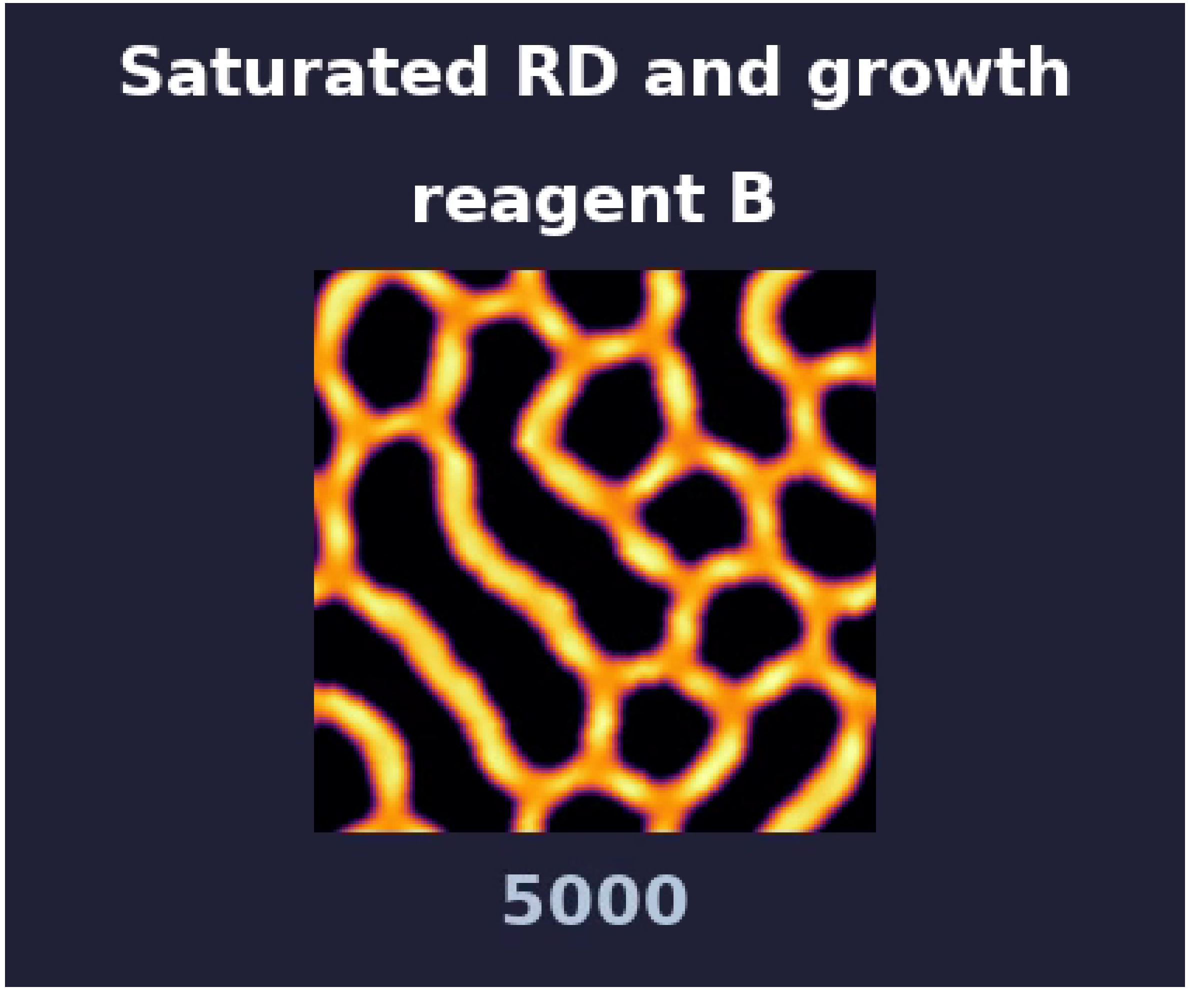
EFFECT OF GROWTH

» GROWTH AND REACTION-DIFFUSION



EFFECT OF GROWTH

» GROWTH AND SATURATED REACTION-DIFFUSION



PATTERN ENLARGEMENT

- Problem
- Continuous reinforcement
- Effect of growth

PROBLEM

- How to maintain the overall pattern appearance during growth?
  - cell division adds noise!
  - large constant areas need to expand
  - borders must be kept well-defined: sharp, not blurry
- Reaction-diffusion does not have these properties, but a similar model can achieve this

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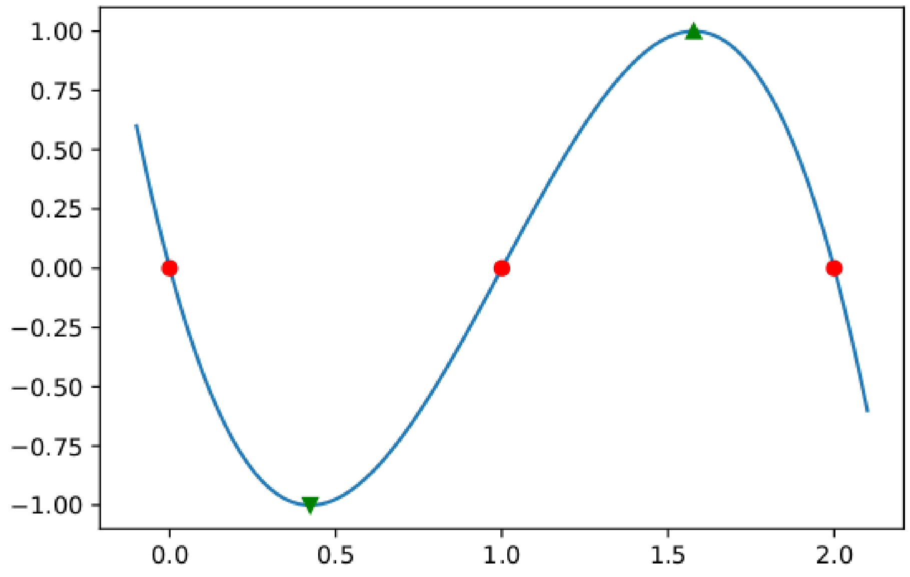
CONTINUOUS REINFORCEMENT

» OVERVIEW

- Models an autocatalytic reaction
- Has a dual effect: smoothing and maintenance
- PDE involving reagent C:
  - *c* is the local concentration
  - there are reaction and diffusion parts
  - diffusion depends on nearby concentrations
  - D_c is the diffusion rate

$$\frac{\partial c}{\partial t} = \gamma(t-w-c)(t-c)(t+w-c) + D_c \nabla^2 c$$



CONTINUOUS REINFORCEMENT

» GROWTH AND REINFORCEMENT

RESULTS

- Impact of initial state
- Simulated biologic patterns

RESULTS

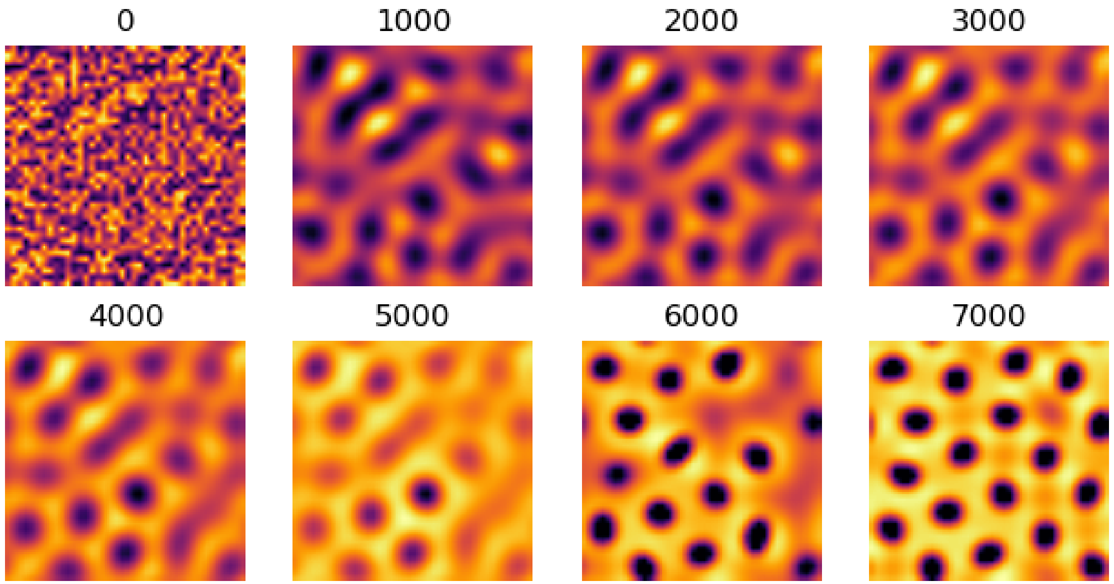
» PREPATTERN

- The initial state of the simulation is called a *prepattern*
- We employed two types of prepatterns:
  - random initial concentration
  - local random production
- Simulations have two or more phases
- The resulting concentrations of a phase are directly fed into the next phase

RESULTS

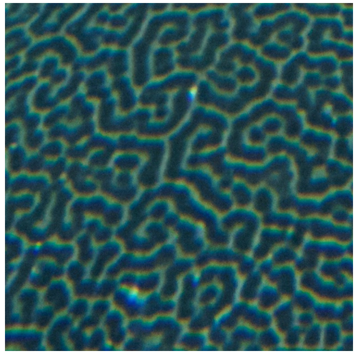
» RANDOM INITIAL CONCENTRATION

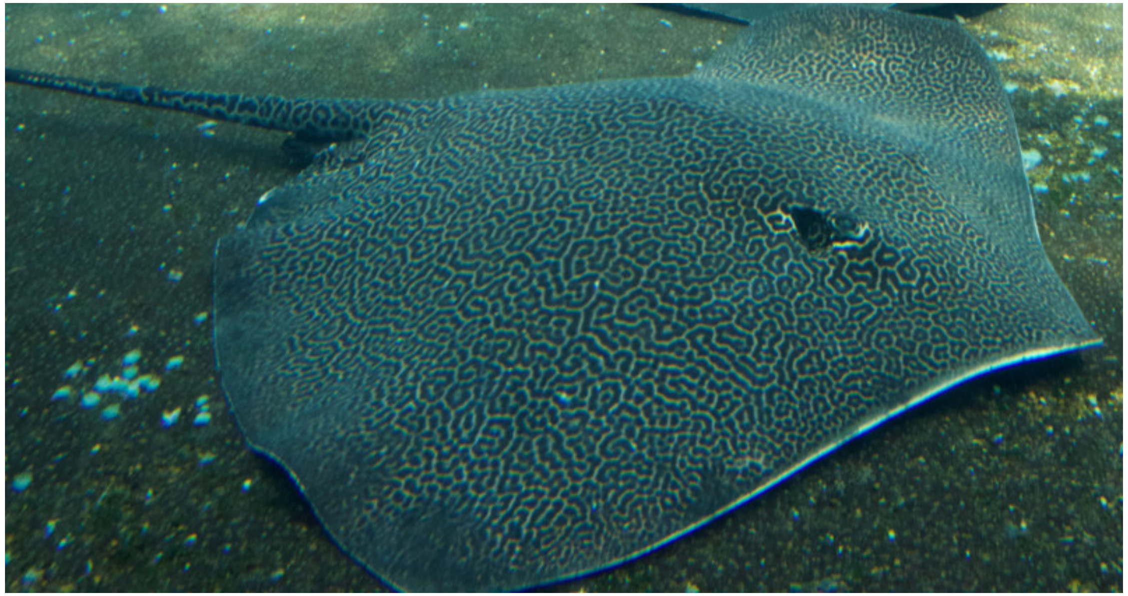
- Prepattern:
  - reagent A starts constant
  - reagent B starts constant plus a small random variation
- The first phase usually develops into spots
- Many works state the ubiquity of spots in early embryonic development



RESULTS

» RETICULATE WHIPRAY





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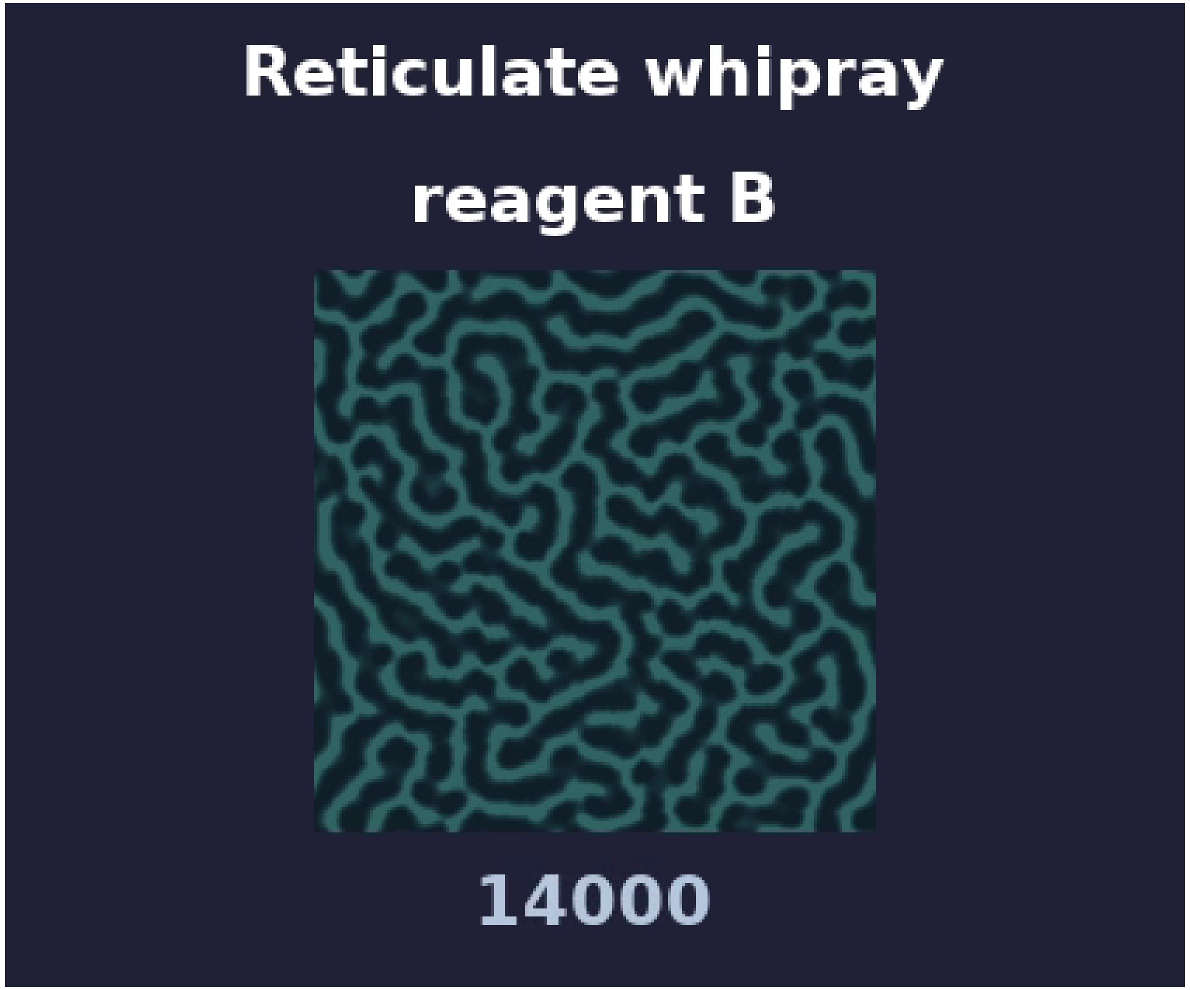
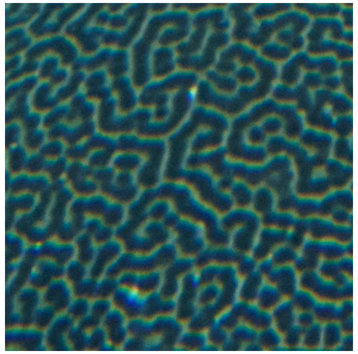
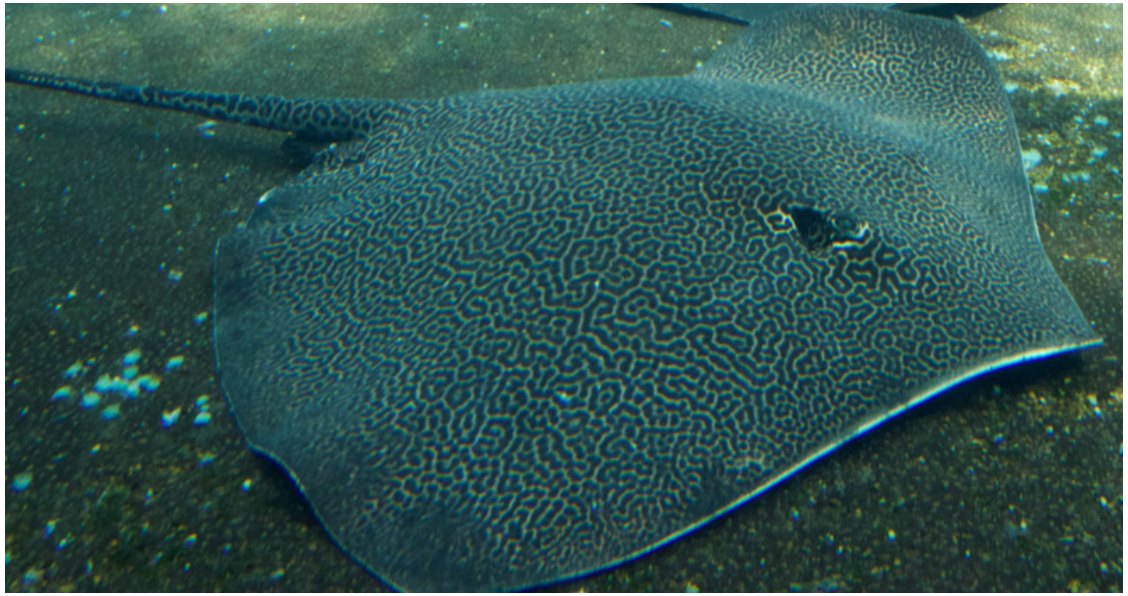
RESULTS

» RETICULATE WHIPRAY







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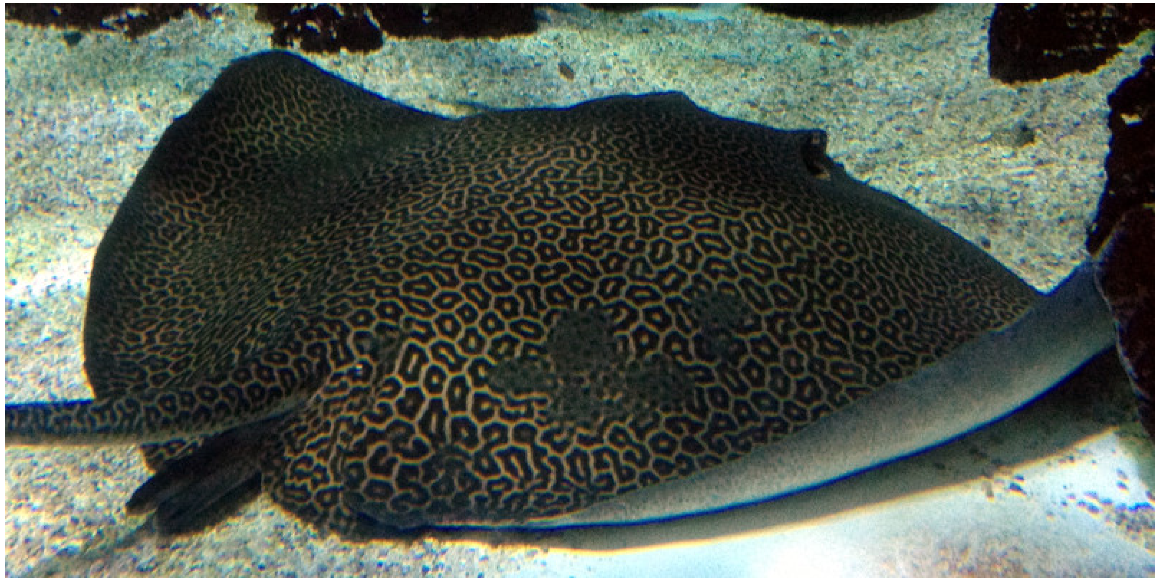
RESULTS

» HONEYCOMB WHIPRAY



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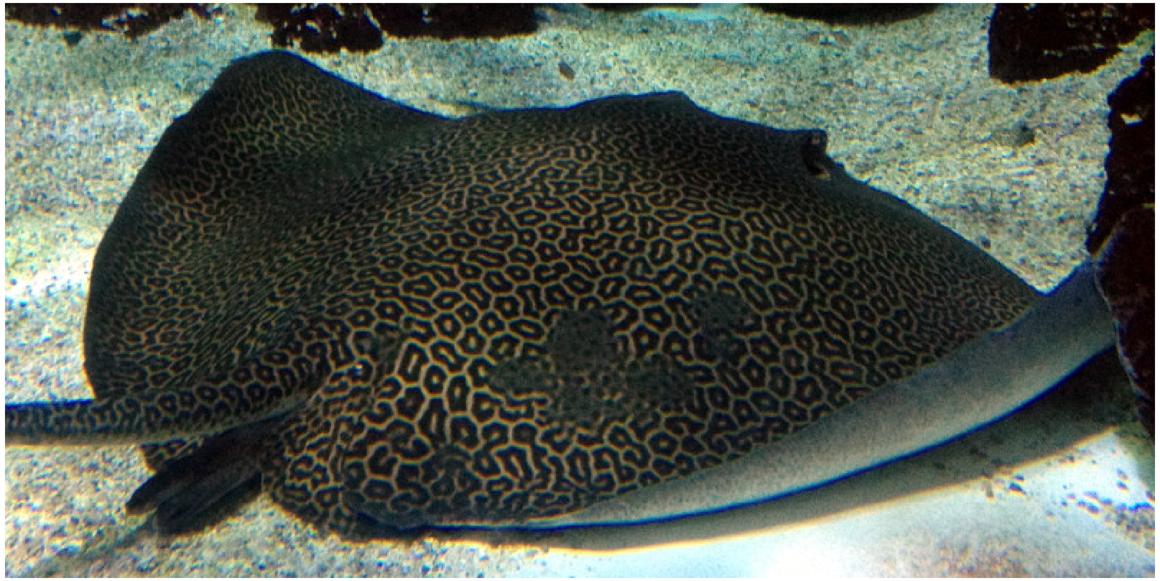
RESULTS

» HONEYCOMB WHIPRAY



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RESULTS

» YELLOW-BANDED POISON DART FROG

photo by Adrian Pingstone (Wikimedia Commons, public domain)

RESULTS

» YELLOW-BANDED POISON DART FROG

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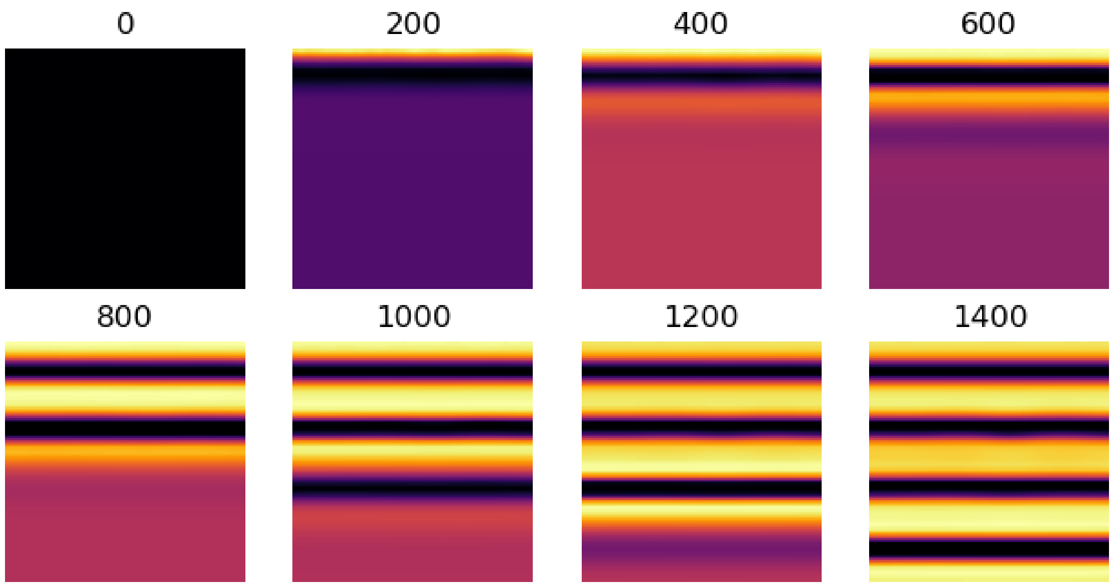
RESULTS

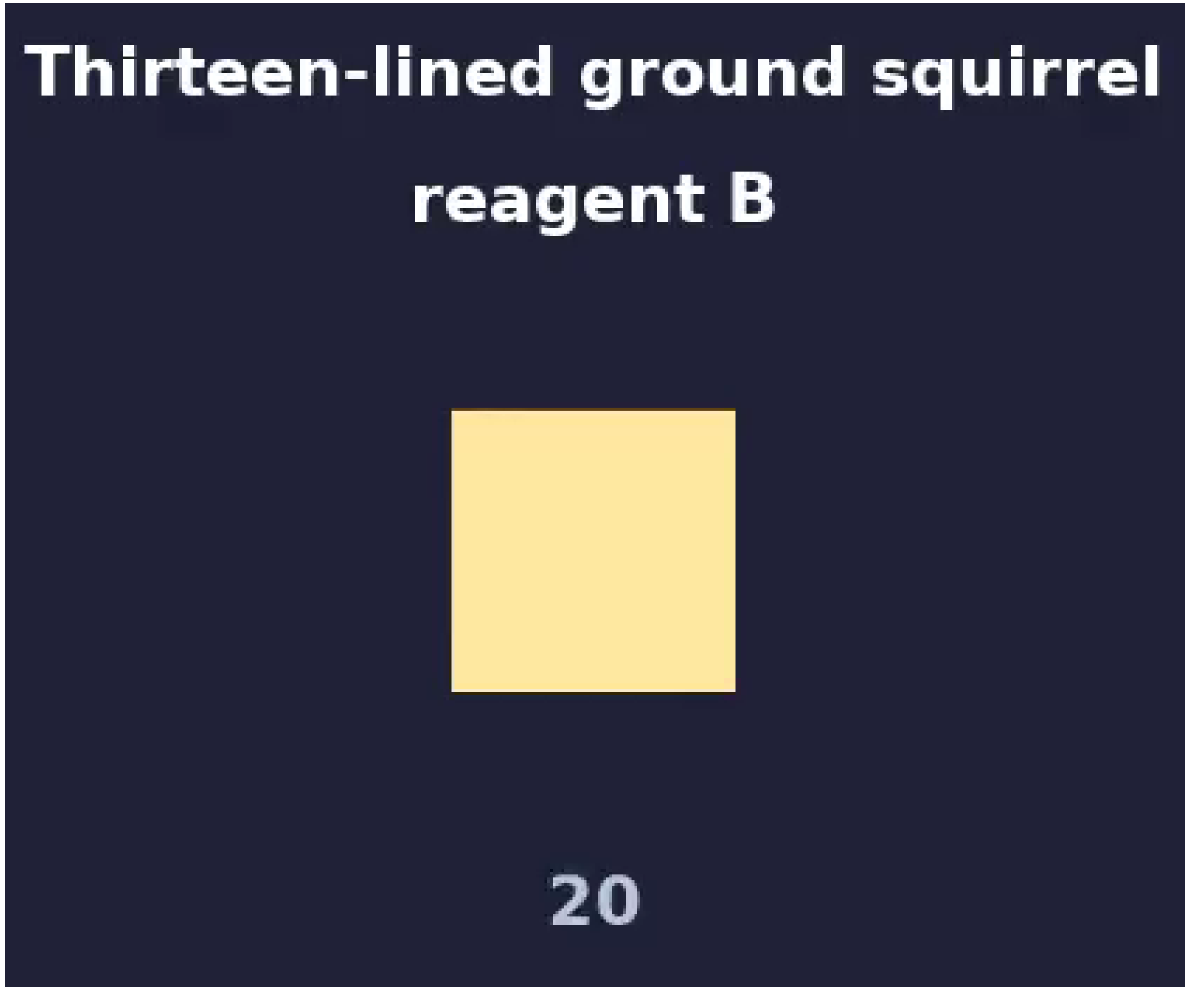
» LOCAL RANDOM PRODUCTION

- Prepattern:
  - reagent A starts constant
  - reagent B starts constant
  - B is produced in small random amounts, along the *dorsal spine*
- The first phase usually develops into straight stripes
- Growth noise disrupts the stripes in very interesting ways



RESULTS

» THIRTEEN-LINED GROUND SQUIRREL



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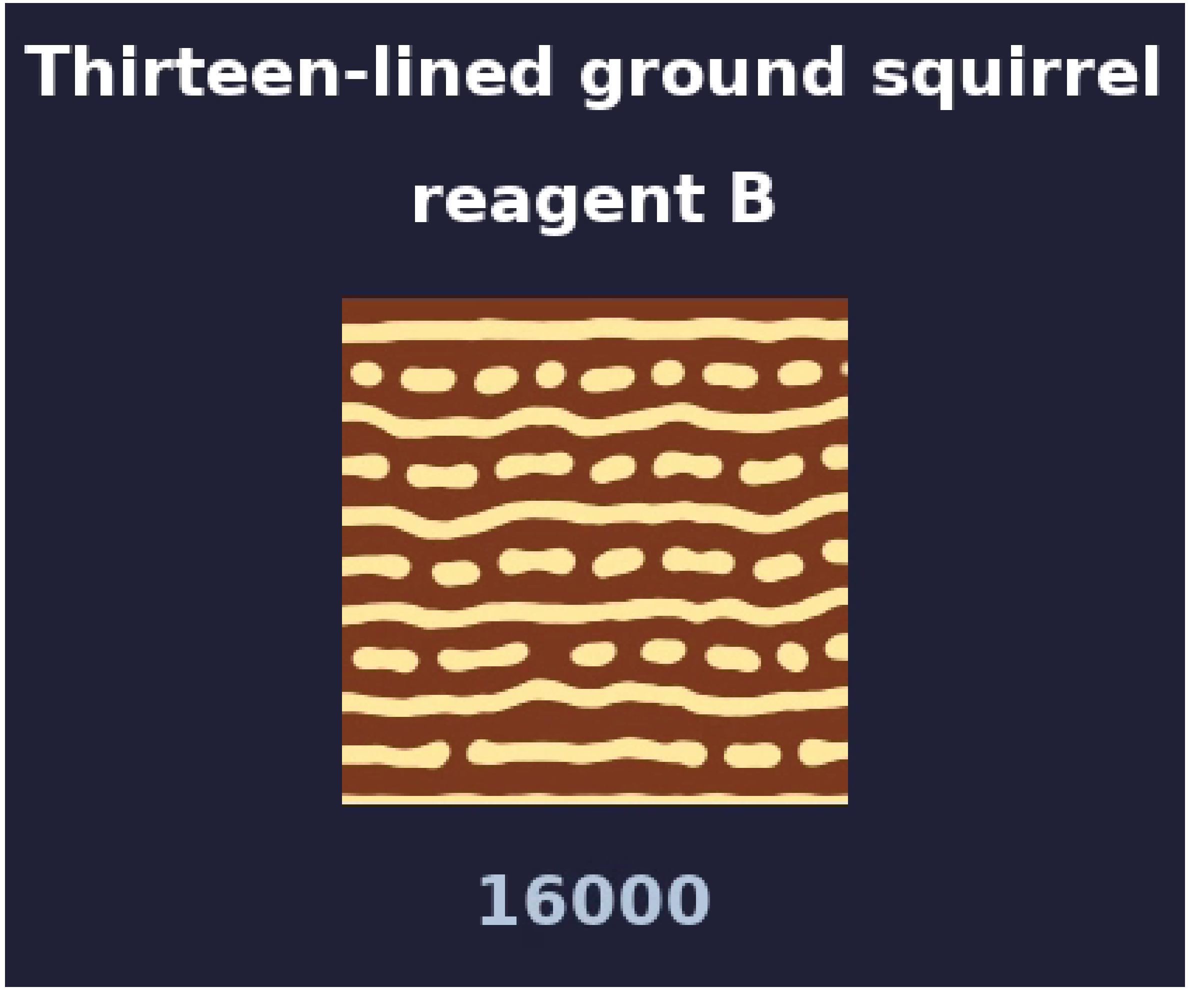
RESULTS

» THIRTEEN-LINED GROUND SQUIRREL



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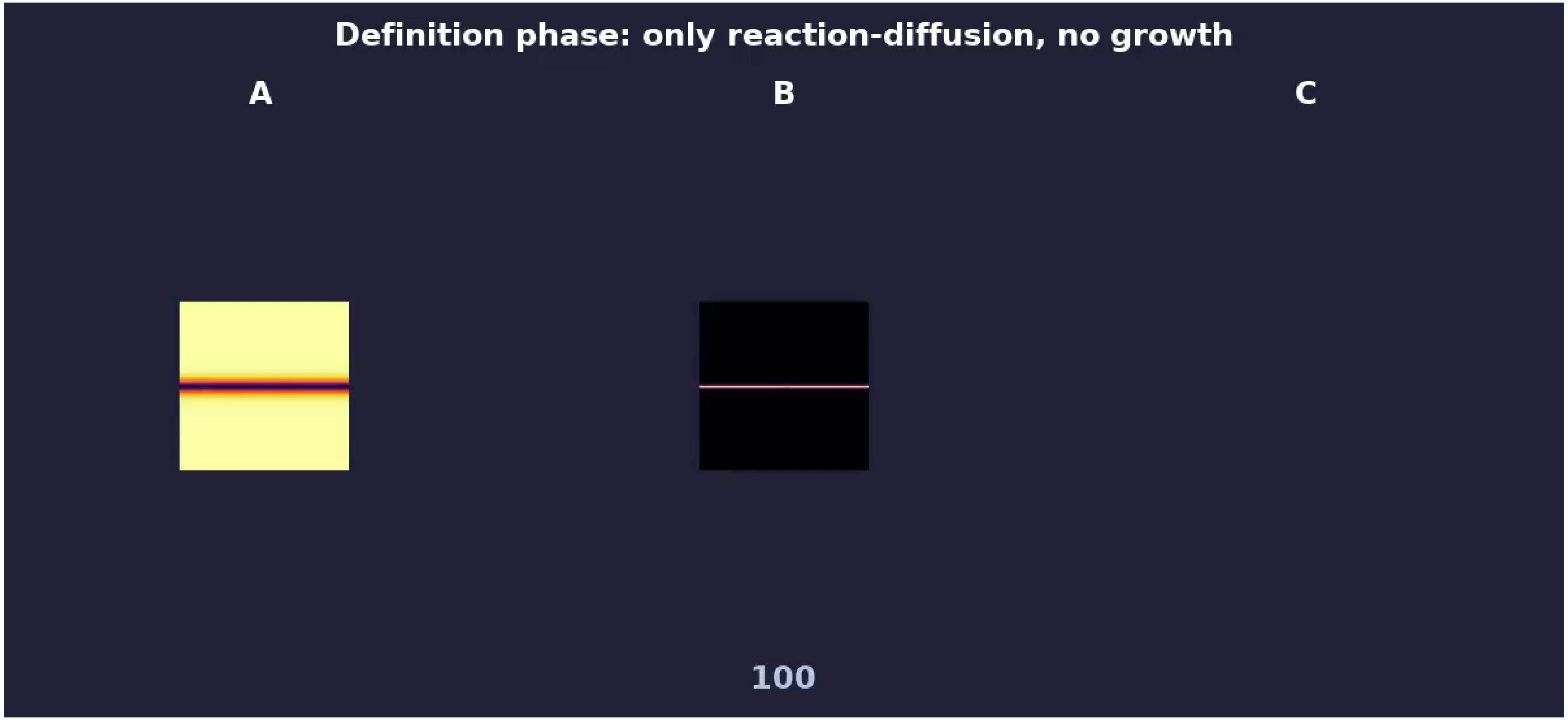
RESULTS

» LEOPARD



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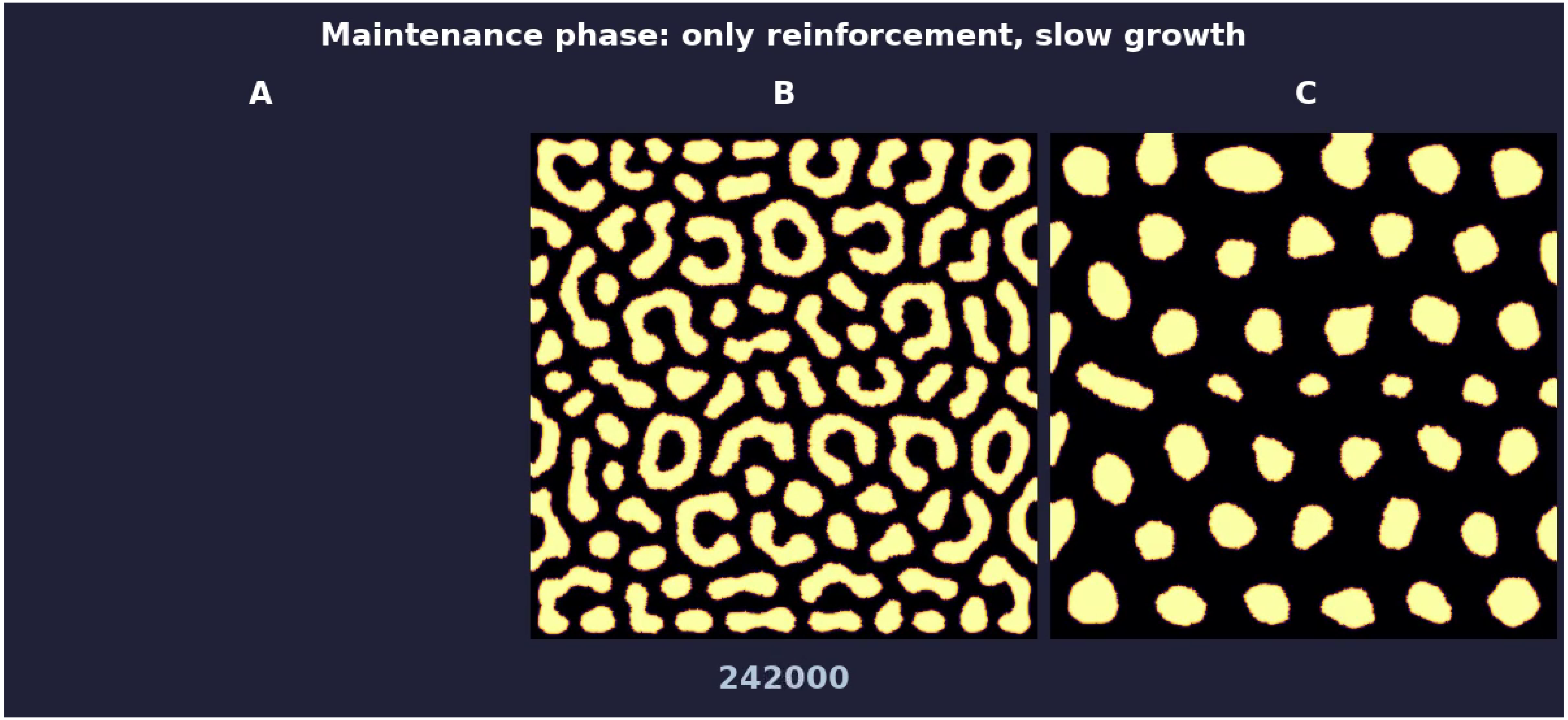
RESULTS

» LEOPARD



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RESULTS

» LEOPARD

- With a single set of parameters:
  - stripes develop into spatially-organized spots
  - due to growth, spots split into rosettes
  - limited growth in the dorsal spine produces deformed rosettes
  - shorter growth phases provide continuous variation of rosettes on other parts of the body

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RESULTS

» LEOPARD

- Important insights:
  - the residual pattern before growth provides the brown spots
  - pheomelanin (reddish pigment) and eumelanin (black pigment) are induced by the same process
- 3D rendering:
  - simple mapping from final concentrations to pigmentation, using a specialized fur shader
  - visual complexity arises from fur orientation and self-shading

CONCLUSIONS

- Contributions
- Future work

CONCLUSIONS

» CONTRIBUTIONS

- Tissue growth can be successfully approximated by matrix expansions
- The extended RD model provides great expressiveness and more intuitive controls
- A continuous reinforcement equation is demonstrated
- We emphasize the importance of the careful definition of the initial state
- We have generated a few unprecedented 2D patterns matching real species

CONCLUSIONS

» FUTURE WORK

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- Simulate pigment formation over a developing 3D surface
- Evaluate other mechanisms to couple geometric modification and localized pattern change
- Provide a deeper mathematical analysis
- Implement an artist-oriented pipeline for pattern design
- Develop a technique for pattern similarity comparison and visual characterization, able to automate classification and recognition
- Perform new experiments to reproduce more species

THANK YOU!

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The leopard never changes its spots: realistic pigmentation pattern formation by coupling tissue growth with reaction-diffusion

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