Analysis of a Class of Discrete Two-Dimensional Models with Predation and Mutation

BAMC 2016
April 8th

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The General Idea

- Simple discrete two-dimensional predator-prey models based on this form (JM Smith 1968):

$$x_{n+1} = ax_n - \frac{(a-1)}{b}x_n{}^2 - cx_ny_n$$
$$y_{n+1} = \frac{a}{b}x_ny_n$$

- We introduce a constant rate of mutation to study the emergence of a simple ecosystem with stable dynamics from a single initial species.
- Three versions will be considered.

Model Features

Global Features

- Prey x uses logistic growth.
- x produces a child, y, by constant mutation.
- y predates upon x.
- Lotka-Volterra (linear) predator functional response.
- Three parameters:
  - Mutation rate p fixed at 10^{-3}
  - Reproductive control parameter r
  - Predation rate c
  - (c, r) is the 2D parameter space.

Version-specific Features

- In two cases, x and y are similar enough to be in competition for shared resources.
- In two cases, y may survive independently, but it's growth parameter is increased by the availability of x to feed upon.

Two-Dimensional Models

- Model 1

$$x_{n+1} = (1-p)rx_n(1-x_n-y_n) - cx_ny_n$$
$$y_{n+1} = prx_n(1-x_n-y_n) + rx_ny_n$$

- Model 2

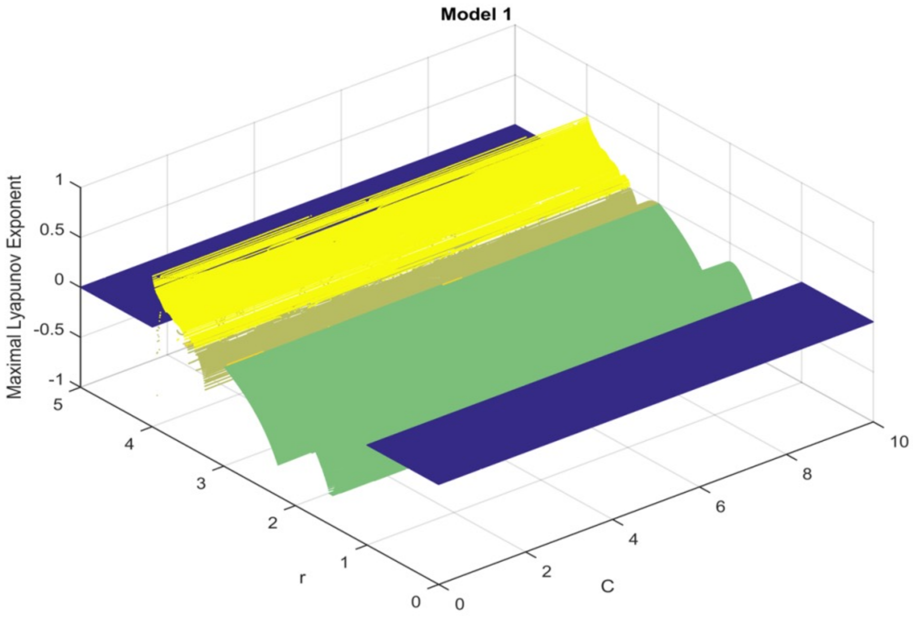
$$x_{n+1} = (1-p)rx_n(1-x_n-y_n) - cx_ny_n$$
$$y_{n+1} = prx_n(1-x_n-y_n) + \frac{2r}{3}(1+x_n)y_n(1-x_n-y_n)$$

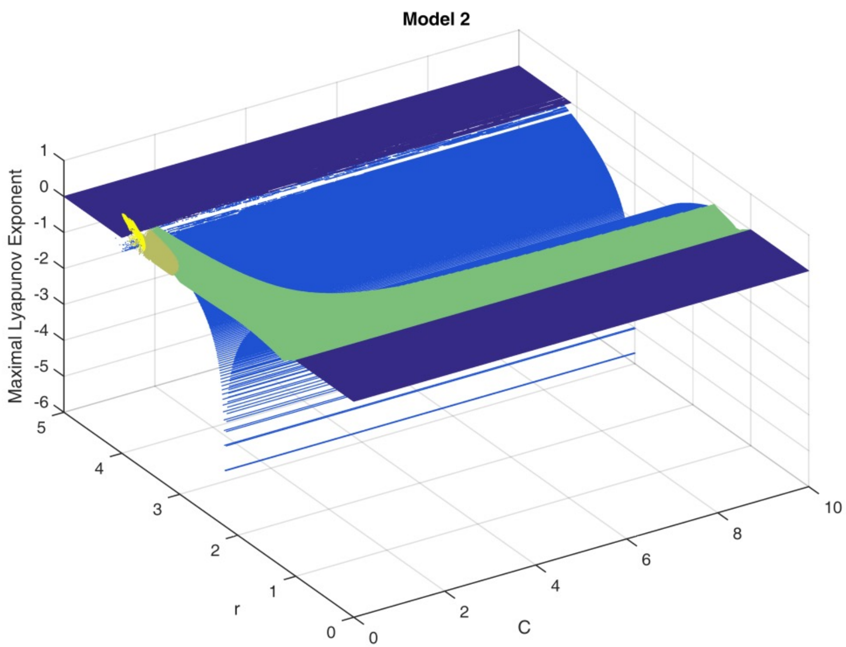
- Model 3

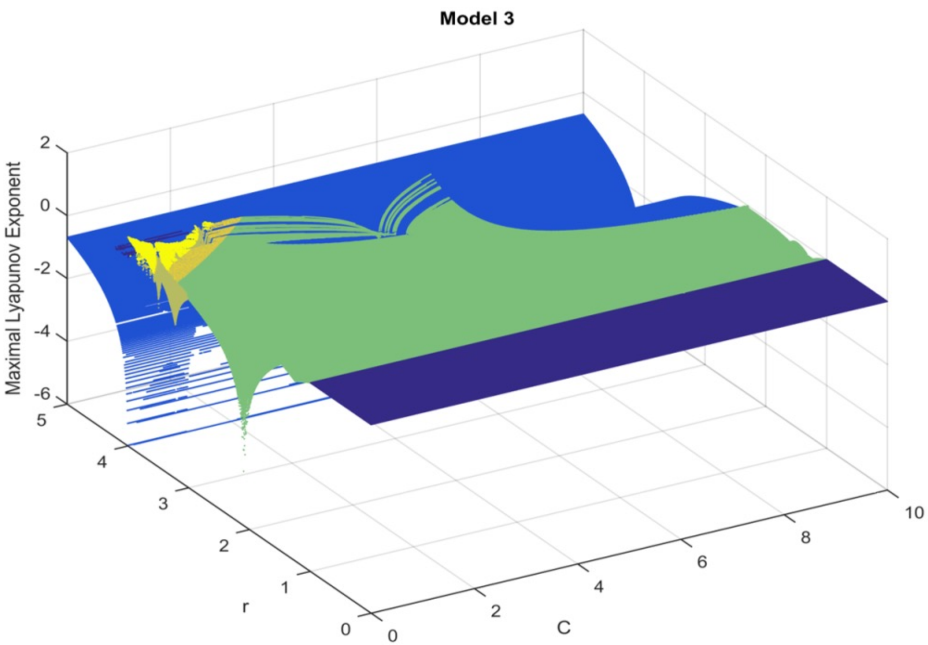
$$x_{n+1} = (1-p)rx_n(1-x_n) - cx_ny_n$$
$$y_{n+1} = prx_n(1-x_n) + \frac{r}{2}(1+x_n)y_n(1-y_n)$$

Results for $p = 10^{-3}$
(Maximal Lyapunov Exponent)

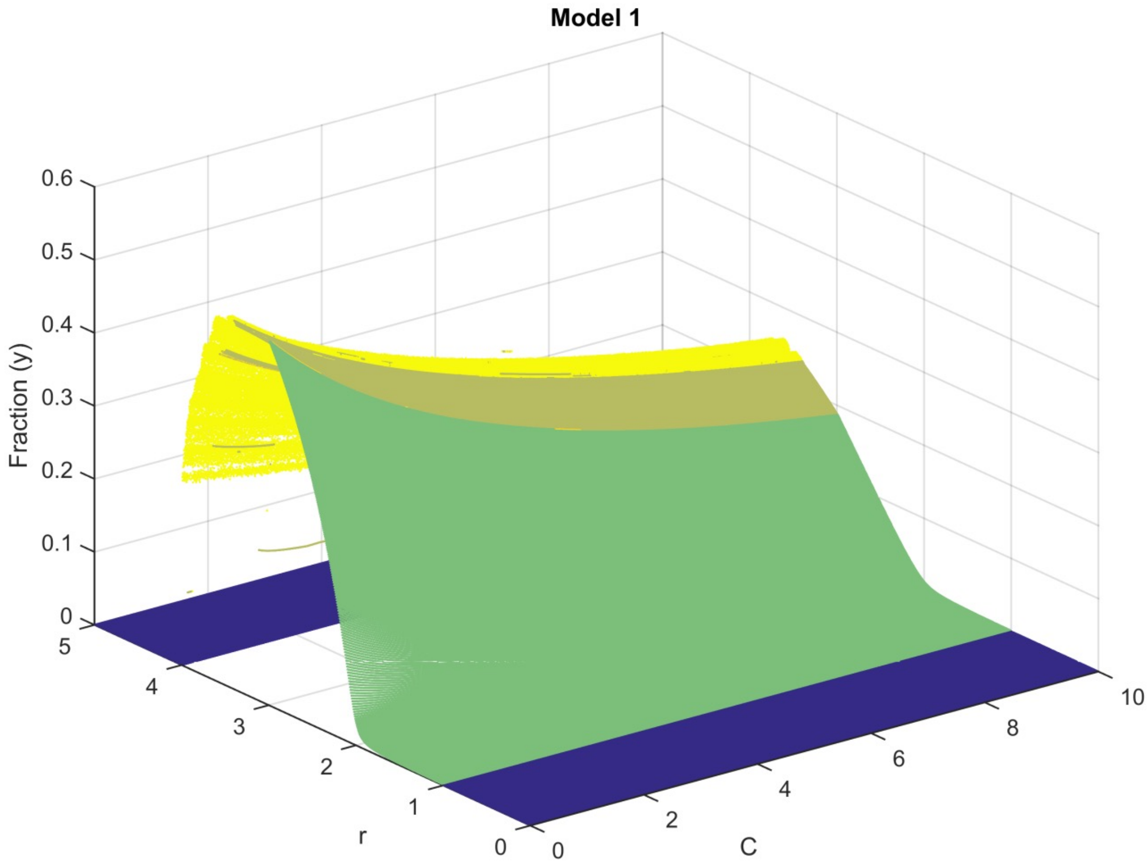
- Purple = Extinction.
- Blue = y-only period 1 (axial fixed point).
- Green = Coexistence period 1 (interior fixed point).
- Orange = 2D quasiperiodicity.
- Gold = 2D periodicity.
- Yellow = 2D chaos.







Model 1 – Predator Fraction of the Population

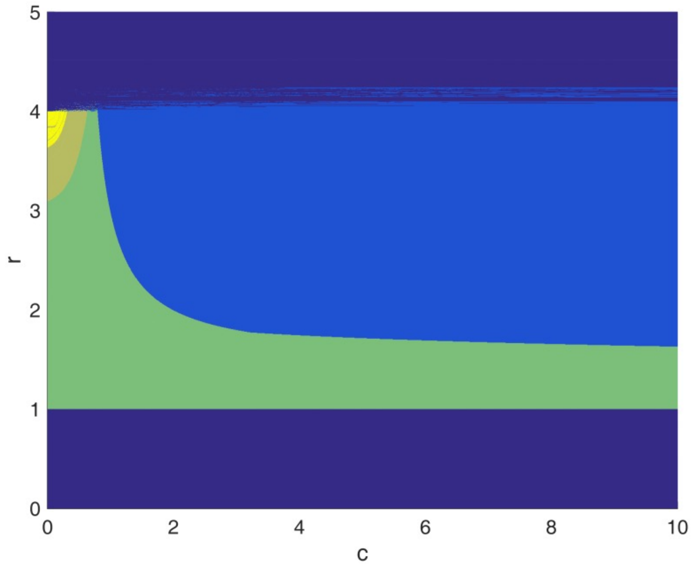


When $p = 0$, interior fixed point has form:

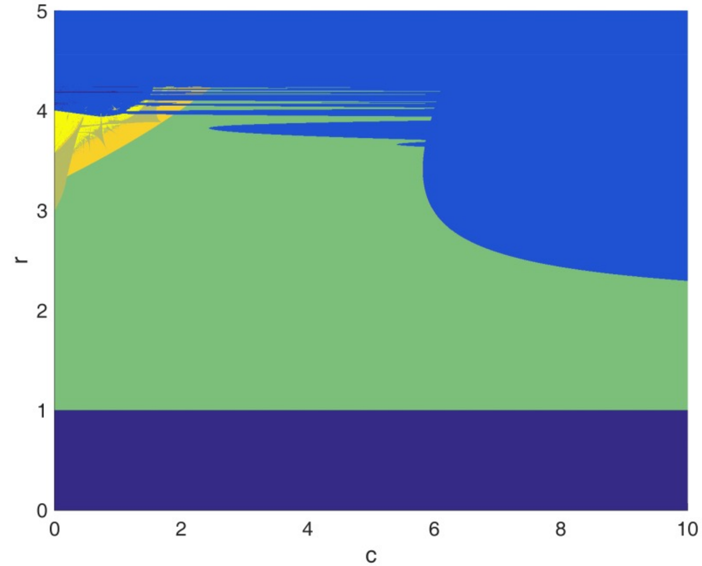
$$(x^*, y^*) = \left(\frac{1}{r}, \frac{r-2}{r+c}\right)$$

The Benefits of Self-Limitation

Model 2

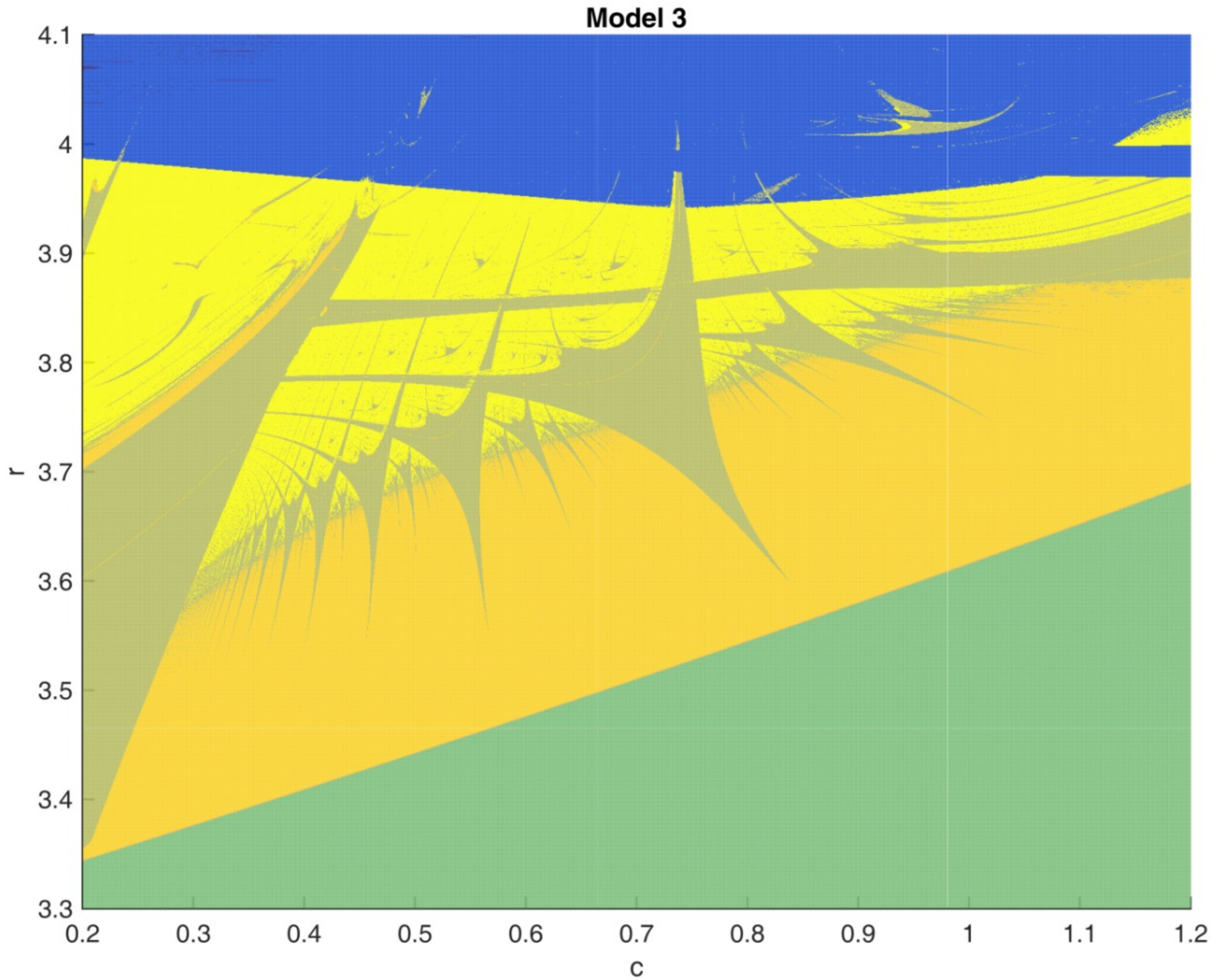


Model 3



For $0.63 < c < 0.79$, period-1 coexistence (green) extends to $r = 4$, where if the predator did not exist, x's population would chaotically oscillate and visit values arbitrarily close to zero. E.g. at $(c = 0.64, r = 4)$, $x^* = 0.105$.

Similarly, the mutant predator stabilises the dynamics for subregions of $1.5 < c < 6, 3.6 < r < 4$. Dependent on I.C.'s and the precise value of r, there may also be stable coexistence for $r > 4$, where x alone would perish.



Model 3 Zoom

Blue = y-only period 1 (axial fixed point $(0, y^*)$).

Yellow = 2D chaos.

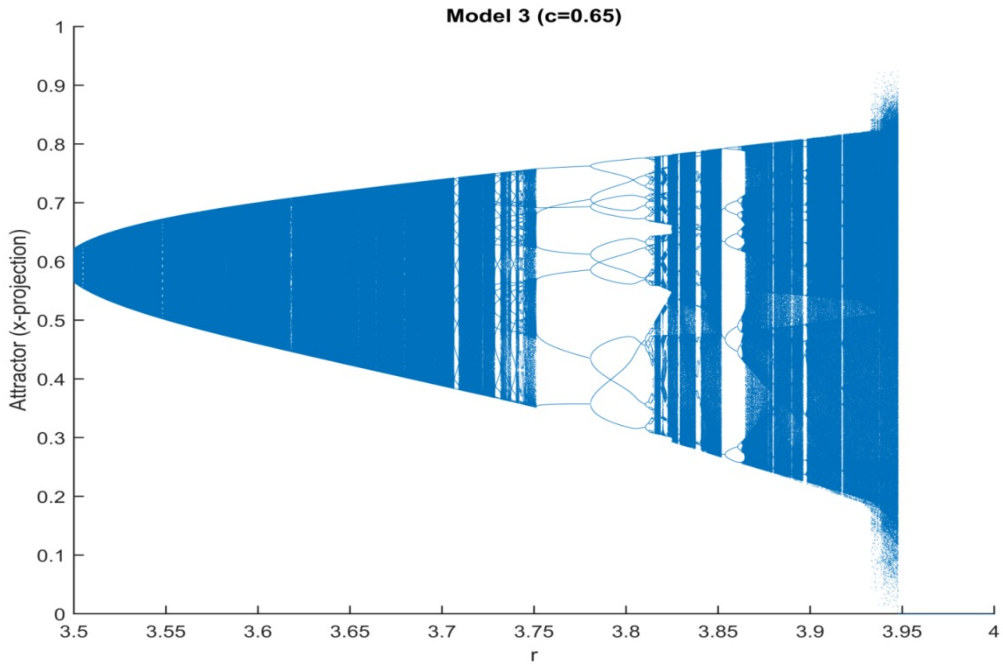
Gold = 2D periodicity.

Orange = 2D quasiperiodicity.

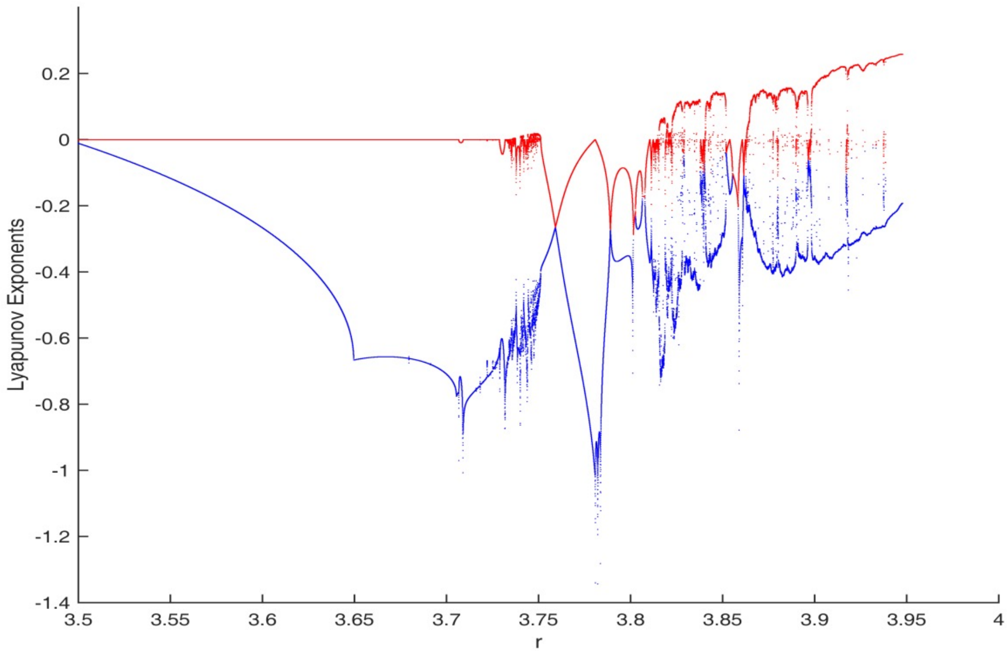
Green = Coexistence period 1 (stable interior fixed point).

Model 3, $c = 0.65$

Feigenbaum Diagram

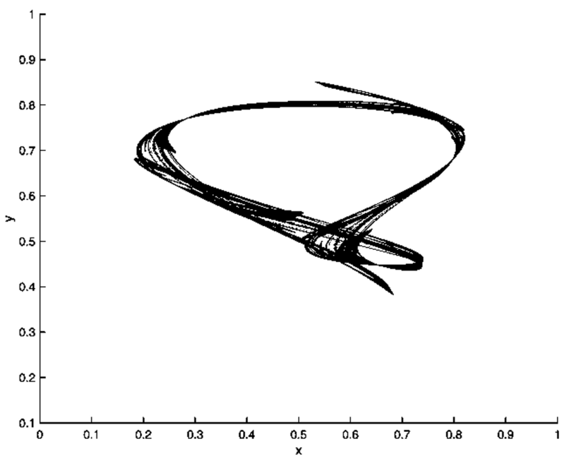


Lyapunov Exponents

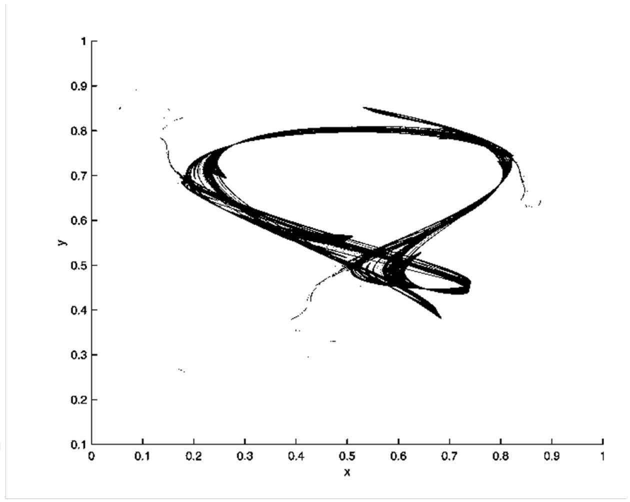


Model 3, $c = 0.65$

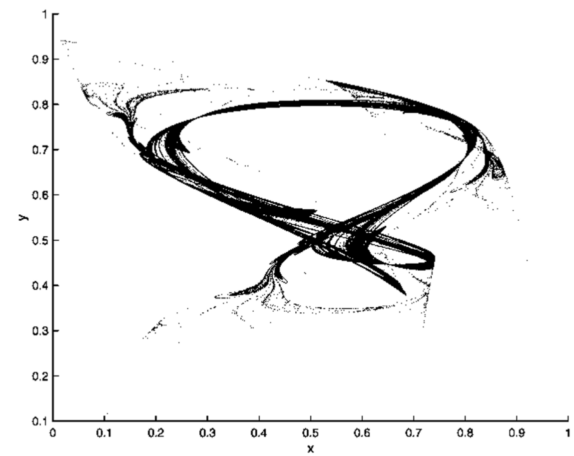
Example Strange Attractor



$r = 3.9300$



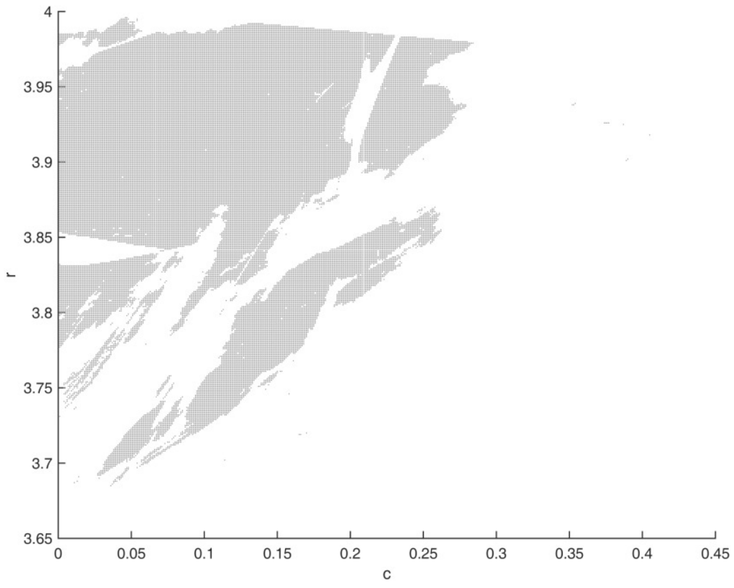
$r = 3.9325$



$r = 3.9350$

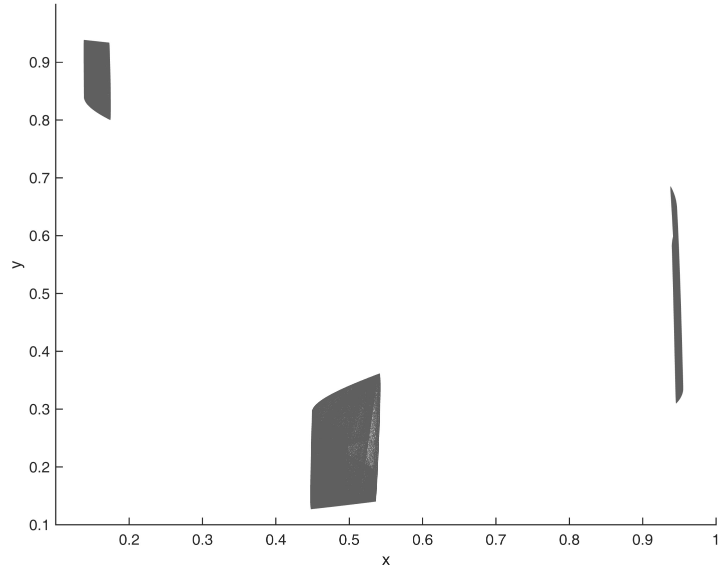
Hyperchaos (Model 3)

Region of Hyperchaos



(c, r) parameter space, with
$\lambda_1, \lambda_2 > 10^{-3}$

Example Hyperchaotic Attractor

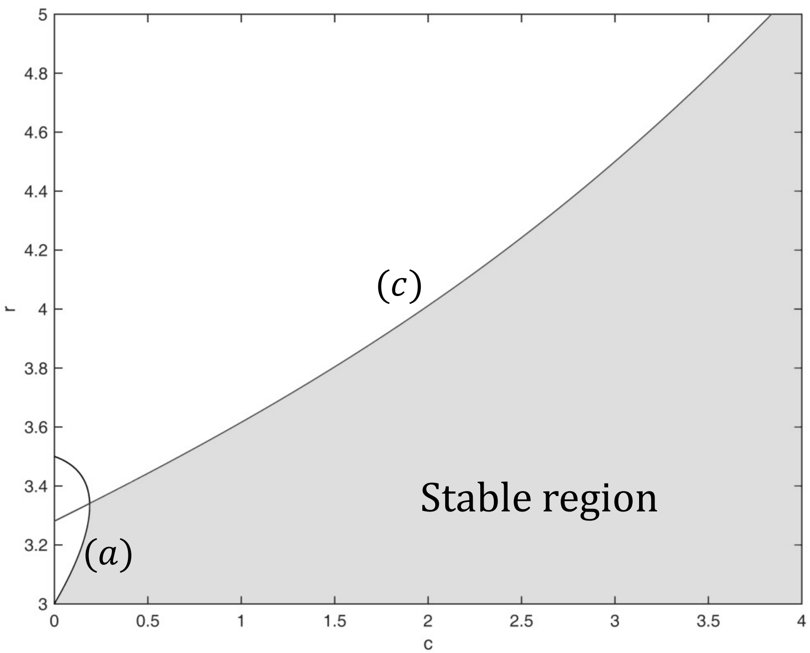


$c = 0.082, r = 3.846$
$\lambda_1 \simeq 0.153, \lambda_2 \simeq 0.102$

Analytic Results for Model 3

- Analytic results are obtained in the limiting case $p \to 0$:
  - $x_{n+1} = rx_n(1 - x_n) - cx_n y_n$
  - $y_{n+1} = \frac{r}{2}(1 + x_n)y_n(1 - y_n)$
- Using the Jury conditions, plot the boundaries of the interior fixed point's stable region (6th order polynomials):
  - (a) $1 + tr(J(x^*, y^*) + det\big(J(x^*, y^*)\big) > 0$
  - (b) $1 - tr(J(x^*, y^*) + det\big(J(x^*, y^*)\big) > 0$
  - (c) $1 - det\big(J(x^*, y^*)\big) > 0$
- Along with the boundary of $x_3 = 0$ given our I.C.'s (for $p = 0$: $x_0 = y_0 = 0.1$), they align with the edges of the region where the fixed point (x^*, y^*) is the post-transient result of numerical simulations.

Jury condition boundary curves ($p = 0$)



Conclusion

- Simple discrete 2-d models display dynamic phenomena including hyperchaos, Neimark-Sacker bifurcation, quasiperiodic orbits and Arnol'd tongues.
- Such models also show examples of beneficial self-limitation for the parent-prey species - producing a mutant predator can stabilise the population dynamics where there would otherwise be chaotic fluctuations or extinction.
- A stable two-dimensional predator-prey relationship can be established, starting from a single species.
- The analytic intractability of the model suggests that this concept would be best scaled to larger systems through computational stochastic eco-evolutionary models of food web assembly (Drossel et al 2001, Loeuille and Loreau 2005, Yoshida 2003, Allhoff et al 2015).

Acknowledgements

- Supervisors: Dr Mark McCartney, Dr David Glass
- Funding by Department of Employment and Learning (DEL)

References

- This work:
  - McCartney and Abernethy, Cannibalism and Chaos in the Classroom, accepted for publication in *Int. J. Math. Educ. Sci. Technol.*
- Similar styles of study:
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- Using ideas from:
  - J. M. Smith. Mathematical Ideas in Biology. Cambridge University Press, 1968.
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Appendix I – Effect of parameter variation:

- Other values of p: increasing p (tested 0.1 and 0.25) compresses the region of co-survival, and begins to flatten these regions against the axes. Quasiperiodicity is introduced to Model 1.
- The effect of no mutation – have also tested p=0 to see if mutation really has an effect (and how reasonable it is to look at the limiting case). This results in smoothing of the fractured boundaries, the creation of new extinction regions beyond $r = 4$, and separation of the fixed-point region to create an intermittent region where x alone survives.
- Other initial conditions: tested $x_0 = 0.3$, kept y_0 at 0 (in keeping with the nature of the model). This has little effect except non-qualitative alterations to the broken boundary of coexistence in Model 3.
- Did also test predator reproductive ratios of $^2/_3$ for Model 3 and ¾ for both Models 2 and 3 for consistency. Changing Model 2 further has little effect of interest, but some things happen to model 3 as this parameter increases: mainly, the encroaching blue ovals of 1d collapse become wider and better defined in r and move closer to the axes (hence the smaller region of coexistence for Model 2 in the presented results), and ovals of extinction move into this interface and become much more prominent. We do not focus on these versions.

Appendix II – Model justification:

- Inspiration for model justification: JM Smith's textbook "Mathematical Ideas in Biology" 1968, also used as an example in YA Kuznetsov's textbook "Elements of Applied Bifurcation Theory" 2013.

Appendix III – Lyapunov exponent algorithm:

- From Sprott's "Chaos and Time-Series Analysis":
  - $x_{n+1} = f(x_n, y_n);\ y_{n+1} = g(x_n, y_n)$
  - ${y'}_{n+1} = \frac{C+D{y'}_n}{A+B{y'}_n}$, where $J_n = \begin{pmatrix} A & B \\ C & D \end{pmatrix} = \begin{pmatrix} f_x & f_y \\ g_x & g_y \end{pmatrix}\Big|_{(x_n, y_n)}$
  - Then $\lambda_1 = \lim_{n\to\infty} \frac{1}{2n} \sum_{k=1}^{n} \log\left(\frac{(A+B{y'}_k)^2+(C+D{y'}_k)^2}{1+{y'}_k^2}\right)$

Appendix IV – More realistic model:

- Model improvements (although just a “pure predator” model:
  - A Ricker-based two-species bioenergetic consumer-resource predator-prey model with Holling Type II response, a constant rate of mutation, and y feeds on the eggs of x
  - $x_{n+1} = \max\left(0, (1-p)\left(1 - \frac{cy_n}{1+x_n e^{r(1-x_n)}}\right) x_n e^{r(1-x_n)}\right),$
  - $y_{n+1} = \max\left(0, x_n e^{r(1-x_n)}\left(1 + \frac{cy_n(\lambda-p)}{1+x_n e^{r(1-x_n)}}\right)\right),$

    where λ is ecological efficiency.

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