Spatial Ecology - 1

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Sections Covered

- Ball, pp 223-231
- “Spatial Structure and Chaos in Insect Population Dynamics” by Hassell, et. Al.
- “Rethinking Complexity: Modelling Spatiotemporal Dynamics in Ecology” by Bascompte and Solé

Ball—Communities

- Article summarized several models of population.
  - Mostly focusing on Predator vs. Prey models
- The Models
  - Malthus
  - Lotka-Volterra
  - May & Oster
  - Hassel et. Al.

Malthus

- The idea behind the Malthus model was that populations grow with geometrical rapidity until the food runs out, and then famine causes the populations to die out. In the meantime, the food sources replenish, allowing for the cycle to repeat.
- Produces sawtooth and fairly periodic growth patterns.

Malthus

- Drawbacks to the model:
  - Overly simplistic
  - Fails to take into account populations which are in turn the food source for other populations (i.e. rabbits which eat grass, but are in turn eaten by wolves).

Lotka-Volterra

- This model has predators, prey, and the prey’s food source (which is never considered to be a limiting factor).
- Volterra originally dealt with different kinds of fish, but we will use foxes and rabbits.
- Assumes uniform dispersion of predators and prey

Lotka-Volterra

- The model is defined by 3 equations
  1) (Rabbits and Grass) lead to (more Rabbits)
  2) (Rabbits and Foxes) lead to (more Foxes)
  3) (Foxes) lead to (some dead foxes)
- Rules 1 and 2 are autocatalytic since the product is also a reactant.
- Rule 3 states that if the foxes are unable to find food, some will die off.

Lotka-Volterra

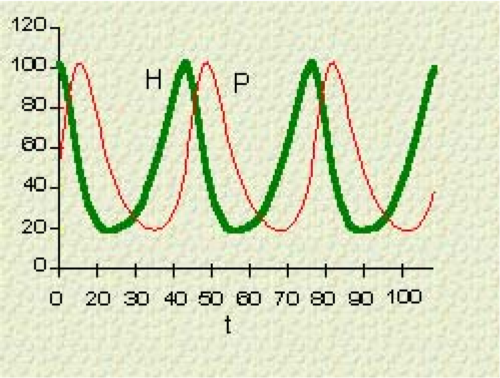
- This is a system of coupled equations (since variables in one equation appear in other equations).
- It is assumed that the populations reproduce at some constant rate in proportion to their population.
- Based off of Lotka’s oscillating chemical reactions.

Lotka-Volterra

- A small range of growth rates allows oscillations in populations to dampen out over time and eventually reach steady states.
- The most common result however is oscillatory population behavior where the population of the foxes seems to follow behind that of the rabbits.

Lotka-Volterra

A General Graph of a Lotka-Volterra Model



Lotka-Volterra

- Drawbacks to the model:
  - If you try and apply to model (i.e. predicting snowshoe hare populations and lynx populations and then comparing them to records), the cycles do not coincide (i.e. sometimes it looks like the rabbits are eating lynxes).
  - Ignores random perturbations to the system (i.e. a freak weather pattern, etc...,)

May & Oster

- Studied a very simple mathematical population model in the 1970’s.
  - Examined a model of populations that breed seasonally to produce generations that do not overlap (i.e. mosquitoes).
- Follows a very basic system of three equations

May & Oster

- Equation 1) $N_{i+1}=aN_i$
- Equation 1 describes the growth of the population is general, where “a” is the average number of offspring produced in each generation

May & Oster

- Equation 2) $N_{i+1}=aN_i(1—N_i/K)$

- However, as the population approaches it's carrying capacity, "K" (i.e. the maximum sustainable population), the growth of the next generation is cut down. Thus, Equation 2 represents the dependence the newest generation on the preceding one.

May & Oster

- Equation 3) $X_{i+1}=aX_i(1—X_i)$
- If you set a scaling factor of $X_i=N_i/K$, you can rewrite Eqn.2) as Equation 3.
- Important to note is that these are non-linear equations!

May & Oster

- I did a couple of runs with the populations, with a starting population of 10, a carrying capacity and varied a. a=4 yielded the most chaotic behavior, while anything bigger than 4 led to complete failure of the system.

Oster & May

- The Implications of this model mean that it is possible to destabilize a population with just overcrowding. This result can also be duplicated with a predator instead, though the point here is that these systems are prone to perturbations and can become wildly chaotic and exhibit highly complex behavior.

Oster & May

- The results of this study demonstrated that the random irregular population fluctuations that Ecologists had been observing (and attributing to random “noise”) can be an intrinsic characteristic of populations regardless of external factors.

Hassel's Model

- Hassel et. Al. proposed a model that was much more realistic than the preceding models.
- As mentioned earlier, the fundamental assumption was that predators and prey were uniformly mixed.
- However, really populations are patchy, with clustering occuring (i.e. Bluegill Sunfish).

Hassel

- Studied Insects (prey/hosts) and Insect Parasitoids (predators/parasites).
  - The parasitoids lay their eggs on/in/or near a host. At this point the host is “infected” or “parasitized”. When the parasitoid eggs hatch, they will feed on and kill the host.
- Both predator and prey only travel locally

Hassel

- The system is modeled by the following equations:

1) $N_{t+1}=\lambda N_t f(N_t,P_t)$

2) $P_{t+1}=qN_t(1-f(N_t,P_t))$

Where N_t, P_t are the populations of Host and Parasitoid, respectively. λ is the amount of offspring produced by an unparasitized host (which is independent of the population density). $f(N,P)$ is the fraction of hosts escaping parasitization, assumed to be e^{-aP}. q is the number of female parasitoids emerging from each host parasitized.

Hassel

- A key feature of the model is that it allows for μ_N, μ_P, specified fractions of the host and parasitoid populations respectively to move to adjacent patches on a square grid.
- So in each step, the first equation is applied to find out how many hosts and parasites are in the current generation, and then a fixed fraction of each population migrates locally

Hassel

- If the patches in the n x n array are "too small", both host and then parasite will head to extinction.
  - "too small" depends on the dispersion fractions and the hosts intrinsic growth rate.
- Note: no matter how large the array is, the system goes extinct if $\mu_N \to 0$ or $\mu_P \to 0$.

Hassel

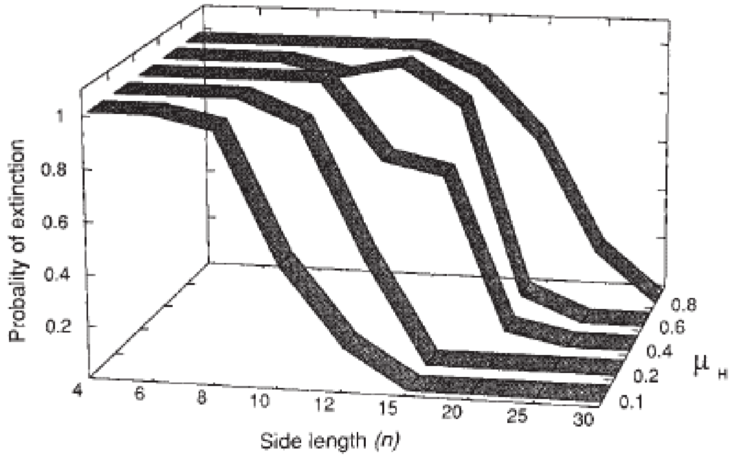


FIG. 1 Extinction probabilities for the specific model described in the text, in relation to the numbers of patches in a square grid of side length (n) and the fractions of hosts dispersing to neighbouring patches (μ_N) ($\mu_P = 0.89$, $\lambda = 2$, reflective boundaries). Extinction is measured as the proportion of 20 replicates failing to persist over 2,000 generations. Each replicate is started by setting nonzero population densities in only the third patch from the left in the top row. The same 20 pairs of initial host and parasitoid densities are used for all the parameter combinations. Local extinction occurs by numeric underflow (densities less than about 10^{-45}); however, the results are robust when local extinction thresholds for both hosts and parasitoids are modelled explicitly.

Hassel

- Persisting populations tend to take the form of Spiral Waves, Crystal Lattices (if λ is small enough), or Chaos.
- These look like the BZ-reaction, and in this case the hosts can be thought of as activators with the parasites acting as long-range inhibitors.
- These patterns persist since it takes time for the results of local interaction to travel to the remainder of the grid.

Hassel

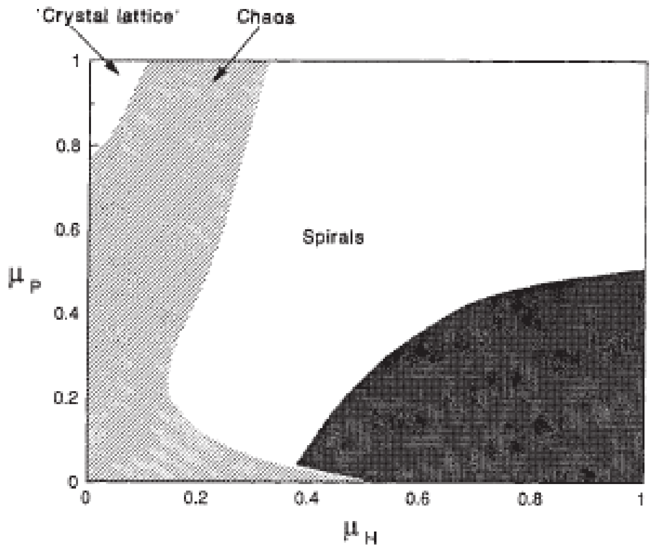


FIG. 3 Diagram showing the dependence of the type of persistent spatial pattern observed on μ_N and μ_P, for $n=30$ and $\lambda=2$. The boundaries are obtained by simulation, and are approximate (and partly subjective). The shaded area represents parameter combinations for which the persistent spatial pattern is unlikely to be established by starting the simulation with a single non-empty patch (as described in Fig. 1 caption). Spirals may be established in these cases by starting with a lower μ_N and increasing it after 100 to 200 generations. Non-persistence occurs for some combinations with very small μ_N or μ_P; this area is imperceptible in the figure.

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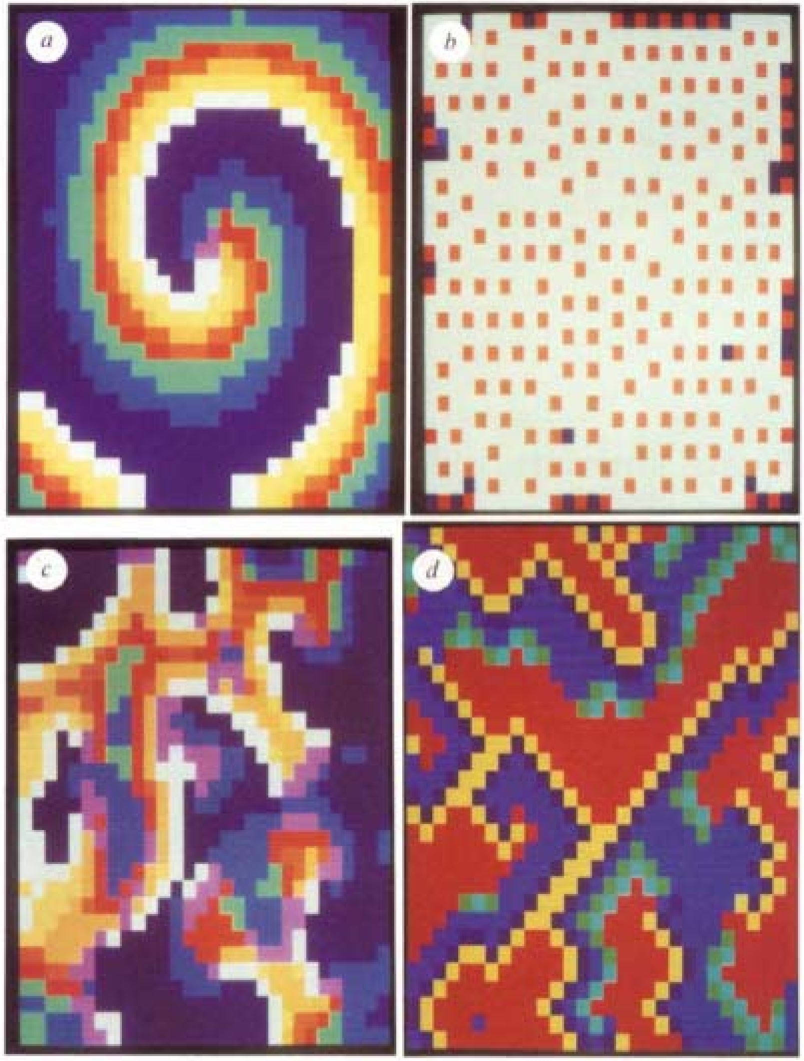

FIG. 2 Photographs illustrating the different patterns of spatial dynamics obtained from the specific model (*a*–*c*) and the cellular automaton model (*d*) discussed in the text. Each photograph is a snapshot in time with the colour coding representing different relative abundances of hosts and parasitoids within a patch. *a*, Typical 'spiral waves' obtained in the spiral region of Fig. 3. *b*, The 'crystal lattice' pattern obtained for $\mu_P \to 1$ and small μ_N (top left of Fig. 3). This pattern settles to a completely static mosaic of high density and low density patches; there is variation within the high and low density categories, although this variation does not show up with our colour-coding. *c*, Spatially erratic ('chaotic') patterns obtained in the chaos region of Fig. 3. *d*, A typical spatial pattern generated from the cellular automaton in which the movement rules correspond qualitatively to the specific model. The automaton has nine states, labelled A to I; movement to the next state in cyclic order is automatic, except that state A (empty) moves to state B only in the presence of at least one neighbouring B (modelling host colonization), and state D moves to state E only in the presence of an F neighbour (modelling parasitoid colonization). Only the four orthogonal nearest neighbour cells are used. Variant automata (exhibiting spirals, crystals and other behaviour) are generated by using eight nearest neighbours, and by changing the required neighbours for $A \to B$ to C or D and for $D \to E$ to D, F, G or H. These changes affect the velocities of the colonization wavefronts of hosts and parasitoids, and are analogous to changes in μ_N and μ_P in the specific model.

Hassel

- Hassel et. Al. used cellular automata to test the robustness of their results instead of just testing different functions for $f(N,P)$.
- Actual population numbers were replaced by nine categories taken by dividing each population density into “very low”, “medium”, or “high”.
- Then movement rules were established for each automata that defined what color each square would be based on its present color, and that of it’s neighbors (i.e. BZ-Reaction).

Hassel

- A significant product of this research was that it showed that “patchiness” enables both hosts and parasites to persist is stable patterns that normally would have become extinct if there were global dispersion.

Bascompte

- The basis behind this paper was to describe different ways to introduce ‘space’ into a model, and what effects Chaos has in preventing metapopulation extinction in such spatiotemporal systems.
- Finally, they talk about a method of detecting spatiotemporal chaos.

Bascompte

- The fact that simple non-linear functions are able to produce chaos is not very surprising.
- However, there is no proof that natural populations produce deterministic chaos. Due to this lack of conclusive proof, a number of ecologists have argued against the idea of deterministic chaos since it seems to imply that the system has an increased probability of extinction.

Bascompte

- However, the introduction of a spatial dimension can not only in a sense “allow” chaos…it seems to “like” chaos.
- This is because “chaos can enhance persistence. Spatially induced stability needs asynchronous dynamics among patches to compensate for buffer crashes.
- In essence, the overall populations of competing species can persist even though local populations may become extinct.

Bascompte

- In studying the three spatial patterns of coupled reaction & diffusion (stationarity, spiral waves, and chaos), 3 lessons arise:

1) Since the same restricted patterns can arise in different models, it implies that the way the elements react is important, and not detail (at least not as important.

Bascompte

2) The structures produced are “emergent”, and arise only from simple rules applied locally.

3) The spatiotemporal phenomena arise from very simple causes.

Finally, Bascompte notes that these patterns are largely influential on the persistence of populations.

Bascompte

- Despite the fact that systems developed from these simple rules have intrinsic chaos, arguments against chaos are that:
  - Since chaotic dynamics imply large unstable fluctuations, some populations will approach or go below extinction threshold.
  - There are periodic windows in a chaotic domain, so feasibly some small perturbations can make a system switch from chaotic to periodic.

Bascompte

- However, spatiotemporal chaos is structurally stable due to spatiotemporal intermittency and supertransients.
  - Transient time is the number of iterations required to reach the long-term dynamics necessary to be captured by the attractor.
  - When the space is introduced, the transient time is much higher than in an uncoupled map, and is called supertransience.

Bascompte

- The different types of supertransients either make it seem like the system is not at a steady state, or make it impossible to detect whether or not the system is in it’s attractor.
- Also, spatiotemporal systems have to deal with multiple attractors. Thus, even with identical parameters, different initial conditions may diverge to different attractors.

Bascompte

- The study of spatiotemporal chaos argues against a reductionist view, since it the system generated by the simple-rule based elements modifies the boundary conditions in which the elements operate (feedback).

Bascompte

- An important result of this study is that it shows that if the amount of space falls below a certain threshold, extinctions will occur.
- This means that habitat destruction can cause a selective extinction of most successful competitors, or that extinction can occur generations after perturbations.

Bascompte

- The study implies that the traditional views held by Ecologists (i.e. asymptotic behavior of models) may not be an accurate way of viewing the natural world.
- Instead, a spatiotemporal view may be more relevant/accurate in describing the natural world.

Bascompte

- Overhead of Box #3

Conlusions

- Patchiness in simple rule systems can create a chaotic system. This may imply that the wide variation of Ecological data is not caused by random noise, but is potentially intrinsic.
- This Chaotic behavior increases the probability of survival of competitive species if the spatial array is large enough.

Questions or Comments?