

Intransitive fitness interactions, space, and the maintenance of biodiversity: rock-paper-scissors dynamics on a lattice

Level 2 module in “Modelling course in population and evolutionary biology”

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1 Introduction: competitive exclusion and biodiversity

A central problem in ecology is explaining how biodiversity is maintained within communities. It is difficult to reconcile the considerable biodiversity that we can observe in most habitats with some simple and fundamental concepts in ecology. Primary among these is the *competitive exclusion principle*, which states that two (or more) species competing for the same niche (roughly: the same set of resources in the same habitat) cannot coexist, as one species will always have the highest fitness and this should lead to the eventual extinction of all other species within that niche. One of the most obvious violations of the competitive exclusion principle is the paradox of the plankton^a; although all plankton subsist on a very small number of resources (light, CO₂, nitrogen, sulfur, and phosphorous), and do so in an apparently homogenous space (the open ocean), many species of plankton coexist.

Several mitigating factors have been put forth as potential explanations for how biodiversity is maintained. Among these are frequent changes in the habitat (i.e. disturbance) and habitat

^aHutchinson, G.E., The Paradox of the Plankton. *American Naturalist*, 1961. 95(882): p. 137-145.

heterogeneity. Two other possibilities, which we will explore here, are the existence of *intransitive fitness interactions* and spatial structure within habitats.

Intransitive fitness interactions are situations in which species (or type) *A* has a competitive advantage over species *B*, species *B* has a competitive advantage over species *C*, but species *C* has a competitive advantage over species *A*. There are several well-known examples from nature; one of the best studied of these is colicin production in the bacteria *E. coli* (see Kerr et al. 2002^b). Colicins are toxins that are produced by some types of *E. coli*. Due to the nature of colicin production, any cell that produces colicins is at the same time resistant to the toxic effects. However, cells can also be resistant to colicin but incapable of producing it. Due to the metabolic cost of producing colicin and the cost of being resistant to colicin, there is fitness intransitivity. A population of cells that both produce colicin and are resistant to colicin may be invaded by cells that are resistant only (due to the costs of producing colicin). However, a population of resistant-only cells may be invaded by cells that do not have resistance to colicin (due to the cost of resistance). Cells which do not produce colicin nor are resistant can be easily invaded by cells that produce colicin (due to the toxic effects of colicin). Thus the cycle can begin anew.

Another example in nature is the side-blotched lizard (see Sinervo and Lively 1996^c). Male side-blotched lizards have one of three throat colors, each associated with a different behaviour. Orange-throated males defend large territories containing several females. However, this mating strategy can be invaded by yellow-striped “sneaker” males, who defend no territory, and steal copulations. This sneaker strategy may be invaded by blue-throated males, who defend small territories, in which females can be successfully defended from secretive sneaker copulations. Finally, the strategy of the blue-throated males can be invaded by the orange-throated males, simply because they defend larger territories and thus have more matings, and the cycle begins again.

A popular analogy for intransitive interactions is the rock-paper-scissors game, in which rock blunts scissors, scissors cuts paper, but paper wraps (and defeats) rock^d. We will use this analogy to build a simulation model. The model will be built step by step, and the exercises are integrated into the sections describing the development of the model. For the completion of the module, you are required to solve the exercises in Section 2.

2 Basic model setup and exercises

The model will be, for simplicity, a cellular automaton. This will be composed of a grid containing finite number of *cells*; each cell represents part of the habitat, and the state of each cell is either unoccupied, or occupied by one (and only one) of the organisms in the ecosystem. In

^bKerr B, Riley MA, Feldman MW, et al. (2002) Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418: 171-174.

^cSinervo B, Lively CM. (1996) The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380: 240-243.

^dFor an extensive description of the game and its many (often surprising) implications, visit Wikipedia at <http://en.wikipedia.org/wiki/Rock-paper-scissors>.

the simulation, time is discrete and occurs in steps that correspond to one interaction between two organisms or between an organism and an empty part of the habitat (an empty cell).

2.1 Initialization

To begin with, we will create a matrix that will represent the virtual habitat in which the organisms will live (for speed and simplicity, this matrix will be relatively small (e.g. 50×50 , or 2500 cells). The simplest non-trivial ecosystem is one in which there are two species; here we refer to them as *species R* (Rock) and *species S* (Scissors). The first objective is to populate the habitat with individuals of *R* and *S*. The simplest way to do this while maintaining some semblance of realism is to do it randomly. Thus each cell within the matrix will be assigned a state (unoccupied, *R*, or *S*), each at a predetermined frequency; this is implemented in the script `starting.R` such that the initial frequencies of each state can be changed. Once this has been done, the habitat is visualized using pdf output and the `image()` function in R.

2.2 Competition

Next, we can allow competition within the ecosystem. Again, the simplest manner to do this is to allow individuals to interact randomly. Fitness interactions consist of simple win/loss trials. At each time step (one interaction), two individuals are chosen from the habitat and allowed to interact, after which the winner is placed into both cells. For simplicity, we begin with *species R* having a 100% relative fitness advantage over *species S*, i.e. *R* wins 67% of the contests with *S* (and less likely, 33% of the time, Scissors cuts Rock in half). The script `starting.R` shows you how to generate both a plot of the habitat and a plot of the relative frequencies of each species with the `plot()` and `points()` functions. Run multiple simulations. Vary the matrix of competition parameters. Investigate how the strength of competition and the size of the habitat influence the rate at which *species S* goes extinct.

2.3 Intransitive fitness interactions

Few ecosystems contain only two species. Thus, to intensify the realism of the simulation, add another species to the model, the aptly named *species P* (Paper). The addition of a third species allows considerably more complex dynamics, specifically, intransitive fitness interactions. Start by giving each species an infinite fitness advantage over the next (i.e. *R* wins 100% of the contests with *S*, *S* wins 100% of the contests with *P*, and *P* wins 100% of the contests with *R*). This corresponds to the classical game of rock-paper-scissors. Begin the simulations with equal frequencies of each species. Plot both the habitat and the relative frequencies of each species. How does intransitivity influence the diversity maintained in the habitat? How do the initial frequencies of each species influence the outcome? How does the size of the habitat influence the outcome?

2.4 The Paradox of Enrichment

Again, we strive for reality. It is impossible that the fitness advantage of *species R* over *species S* is exactly equal to the advantage of *S* over *species P*; we expect that in many cases the relative fitness advantages of the three species will be vastly different. What happens if *species R* has only a 50% advantage over *S*? Which species generally goes extinct first? Which species increase the most in frequency as a result of the change in relative fitness advantages? How does this influence the expected time to extinction for the various species? How is this similar to the original concept of the “Paradox of Enrichment”^e?

2.5 Spatial structure

It is unrealistic to assume that all individuals can interact with all other individuals within a population. In fact, most interactions that occur will be local interactions, as any organism is only capable of dispersing at a certain rate. This is the next modification to the model. Modify your code such that the second of two interacting individuals is not chosen from the whole lattice randomly; instead it should be chosen such that it lies within a certain neighbourhood (the dispersal neighbourhood) of the first individual. The simplest way to implement this is to allow individuals to interact only with their immediate neighbours. However, we are always striving for both realism and flexibility; thus you should randomly select the second interacting individual from all individuals lying within a certain dispersal radius of the first individual (i.e. a certain number of cells). Cells on the “edge” of the habitat should not be treated any differently (i.e. they should have just as many neighbours as other cells in the habitat). Thus *periodic boundary conditions* must be implemented^f. Generate both a plot of the habitat and a plot of the relative frequencies of each species. How does the dispersal radius influence the time to extinction? Can you observe spatial patterns?

3 Additional exercises (and complications)

3.1 Additional species

Again, it is of course unlikely that there are only three species in the habitat. This model is easily expandable to more species, although equal levels of intransitivity are not always possible (e.g. a possible configuration with four species is: $D > A > B, C$; $B > C, D$ and $C > D$. C and D appear to be at a disadvantage as they can only beat one other species (is this true?)). This imbalance does not exist for some slightly more complicated scenarios (which are these?). What happens to the stability of the ecosystem when more species are added? Does the average

^eThe original paradox referred to the phenomenon that increasing the input of a prey species increases the abundance of its predator instead of the abundance of the prey itself in simple Lotka-Volterra models.

^fPeriodic boundary conditions (a.k.a. infinite periodic tiling) are implemented such that when one goes off the top of the grid, one comes in at the corresponding position on the bottom, and when one goes off the left of the grid, one comes in on the right. This creates a situation in which no cells exist at the “edge” of the grid.

time (or minimum time) to extinction of all but one species increase or decrease? Is it possible to obtain stable coexistence of several species? Is there a similar paradox of enrichment as was observed previously? What happens if one species has an advantage over only one other species?

3.2 Differential dispersal

Species are not identical in their forms of dispersal; for example, some plants utilize wind for dispersal, others use mammals, and others depend on insects. Each of these obviously has different inherent average dispersal radiuses. How does this affect the diversity that is maintained in the system? Is it more stable if species with large fitness advantages disperse locally or globally?

3.3 Death

No habitat is immune to disturbance. In fact this has been proposed as one simple way in which diversity is maintained. Perhaps there are periodic disturbances in the habitat, such as forest fires. A simple way to implement this is that cells at a random location and within a certain radius are vacated after a specific (or random) number of updates to the habitat. How does implementing such a regime influence the expected time to extinction for each species?

3.4 Mixed strategies

So far, each individual had a fixed “species”. However, in many real cases, the interacting individuals (often belonging to the same species) can choose from a number of “strategies”, and the combination of the strategies in an interaction will determine who wins and who loses (or the chances thereof). In our example, let the individuals “decide” in each encounter which strategy to use. The type of the individual will then not be a fixed strategy, but can be described with the set probabilities with which it will choose each strategy. Store this vector of probabilities as the “genotype” of each individual; let mutations occur, and see how the strategies evolve. You can also implement strategies that depend on the history (previous interactions) of the individual.