Coexistence of Toxin-Producing and Sensitive Micro-Organisms

Project Module Associated with
Introduction to Computational Science:
***Modeling and Simulation, 2^nd^ Edition* by**

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Prerequisites: "Probability" section from Module 13.4, "Probable Cause—Modeling with Markov Chains"; and one of Module 10.3, "Spreading of Fire"; Module 10.4, "Movement of Ants–Taking the Right Steps"; or Module 10.5, "Biofilms: United They Stand, Divided They Colonize."

Introduction

A scientist has stock cultures of two species of Paramecium, designated as species A and species B. Paramecium is a one-celled organism that may reproduce two to three times daily. Cultured separately, following a short lag period, both populations expanded exponentially for about 10 days and then leveled off. As an experiment, the scientist adds equal numbers of the two species to the same, fresh culture medium. Population counts are made daily, and the culture medium is changed regularly for a month. After a lag, both species grow exponentially for awhile, but after a week, species B begins to decline, while species A continues to expand and eventually plateaus. After a month, only species A remains. Species B has died out.

This experiment is modeled on the experiments performed by G. F. Gause in the1930's (Gause 1934) and served as the basis for the **Competitive Exclusion Principle (CEP)**. This principle states no two species living in the same area, occupying the same niche (competing for the same resources) can coexist. One of the species will be eliminated or excluded from the area. This principle is supported by mathematical models and laboratory experiments, with carefully controlled conditions. In the Paramecium experiments, species A was more efficient at utilizing the resources in the medium for faster reproduction.

Exclusion is only one outcome when species that compete for the same resources occur in the same area. Over time, natural selection may work to reduce competition. Species may evolve so that they use a different portion of the resources available. They, in effect, subdivide the resources to avoid direct competition. This outcome is referred to as **resource partitioning**. For instance, in tropical rainforests, there are many animal species (e.g., birds, bats, primates, etc.) that feed on fruit. With the tremendous variety of fruits available, animals can avoid competing with other species by specializing on the fruits they eat. Even in more unstructured environments, resource partitioning may take place among members of the same species. In experiments using a single clone of *Escherichia coli*, cultured for long periods of time in nutrient-limited conditions, the bacteria develop into a stable community of three clonal types that differ metabolically, have diverse growth rates and glucose uptake, and utilize different metabolic products for energy (Rosenzweig, et al. 1994).

Competition may be indirect, where a resource is utilized by one species more efficiently, so that it is not available for a competitor (**resource depletion**). Or, competition may be direct, where one species interferes with or denies access to a resource (**interference**). In the experiments using Paramecium species, species A outcompetes species B by a more efficient use of the resource (e.g., food), thus by resource depletion. If we set up an experiment using two bacterial species, we might find that one of the species produces a toxic product, which kills the second species (interference). A major benefit of reducing either form of competition is survival of a diverse community.

Torvisk, et al. (1990) took topsoil from a Norwegian Beech forest and performed DNA analysis of the bacteria in the sample. Their results indicated tremendous phenotypic and genotypic diversity. Using their data, Dykhuizen (1998) estimated 500,000 species in just 30 grams of soil. It is difficult to understand how there could exist 500,000 non-overlapping niches in that much soil, even if we assume that the soil is highly structured. How can all of these species coexist successfully in this upper layer of soil? If we turn to modeling of a simpler community, we may be able to gain some insight as to the incredible bacterial biodiversity.

Killer and Sensitive Populations

Czárán and Hoekstra (2003) presented a cellular automaton simulation of two hypothetical organisms inhabiting an area, where killer organisms produce toxins that can kill sensitive organisms. Their model, which can represent a number of systems of micro-organisms, illustrates the conditions under which such populations can live together, reaching equilibrium numbers without extinction to either group.

For the simulation, we consider five abundance states:

- **0** – absent
- **s** – sparse sensitive strain
- **S** – abundant sensitive strain
- **k** – sparse killer strain
- **K** – abundant killer strain

Killer and sensitive strains can inhabit the same cell in all combinations of abundance, from absent to abundant. Thus, a cell can be in one of nine states: 00, 0k, 0K, s0, sk, sK, S0, Sk, and SK. State transitions are as follows:

- **Local Extinction:** With probability e, a catastrophe can occur in a cell causing extinction, so that the state (other than the empty state of 00) changes to 00 at the next generation, or time step. Notice that both organisms have the same probability of extinction.
- **Internal Transitions:** In a cell having only one species and where no catastrophe occurs, a sparse population becomes abundant (s to S, k to K) in one generation, so that s0 $\rightarrow$ S0 and 0k $\rightarrow$ 0K. However, in locations where sparse populations of both organisms occur, the sensitive strain has the advantage of a faster growth rate, so that sk $\rightarrow$ Sk $\rightarrow$ SK; in a cell sparsely cohabited by both populations, the sensitive organism becomes abundant in one generation, while the killer organism

takes two time steps. Although not having the advantage of growth rate, the abundant killer organism does have the advantage of toxin production, shrinking an abundant sensitive strain to sparse and killing a sparse sensitive strain. Thus, in one time step, SK $\rightarrow$ sK and sK $\rightarrow$ 0K.

- **Colonizations:** Abundant populations, S or K, have the potential of colonizing neighboring cells that do not contain sensitive (s or S) or killer (k or K) populations, respectively. Specifically, if any of the eight neighbors in its Moore neighborhood has abundant killers (K), with a dispersal probability of d, a cell in state s0 or S0 will transition to sk or Sk, respectively. However, sensitive organisms cannot propagate in a similar manner into cells that contain killers.

  Additionally, one or both types of organisms can colonize empty (00) cells. Each S (or K) in a neighboring cell has a probability d of colonizing the site and, consequently, a probability of $(1 - d)$ of not colonizing the site. For example, suppose $d = 0.2$ and a site has neighbors Sk, SK, SK, sk, 0k, and three 00's. Therefore, the number of neighbors with S, *numS*, is three, and the number of neighbors with K, *numK*, is two. The probability that none of these abundant neighbors will colonize the site at the next time step is the product of the independent events of no colonization by the *numS* abundant sensitive neighbors and no colonization by the *numK* abundant killer neighbors, $(1 - d)^{numS}(1 - d)^{numK} = (1 - d)^{numS + numK} = (1 - d)^5 = (1 - 0.2)^5 = 0.8^5 = 0.328$.

  The probability that no neighboring S (or K) colonizes the surrounded 00 cell is $(1 - d)^{numS}$ (or $(1 - d)^{numK}$). Thus, the probability of the opposite situation, that at least one S (or K) propagates into that site, is $(1 - (1 - d)^{numS})$ (or $(1 - (1 - d)^{numK})$). Thus, the probability that the independent events of S and K in the Moore neighborhood colonizing a 00 site so that the site transitions to sk is the product of the two probabilities, $(1 - (1 - d)^{numS})(1 - (1 - d)^{numK})$. For example, with Sk, two SK's, sk, 0k, and three 00's as neighbors and $d = 0.2$, the probability of 00 $\rightarrow$ sk is $(1 - (1 - d)^3)(1 - (1 - d)^2) = (1 - 0.8^3)(1 - 0.8^2) = 0.176$.

  For the probability of the independent events of S invading and K not invading a surrounded 00 site so that the site transitions to s0, we take the product of $(1 - (1 - d)^{numS})$ and $(1 - d)^{numK}$. Thus, with Sk and two SK's as the only neighbors with abundant populations, the probability of 00 changing to s0 is $(1 - (1 - d)^3)(1 - d)^2 = (1 - 0.8^3)0.8^2 = 0.312$.

  Symmetrically, the probability of S not invading and K invading so that 00 becomes 0k at the next time step is $(1 - d)^{numS}(1 - (1 - d)^{numK})$. Using the example above, the probability of 00 $\rightarrow$ 0k is $(1 - d)^3(1 - (1 - d)^2) = 0.8^3(1 - 0.8^2) = 0.184$. Notice, that the sum of the four probabilities for 00 transitioning to the only possibilities, 00, sk, s0, or 0k, is 1: $0.328 + 0.176 + 0.312 + 0.184 = 1.000$.

Quick Review Question 1 Suppose the dispersal probability is 0.3 and the values in the Moore neighborhood of a site with value 00 are sK, sk, sK, sk, 0K, 0K, S0, and SK. Determine the probability of each of the following situations:

a. 00 $\rightarrow$ 00

b. 00 $\rightarrow$ sk

c. 00 $\rightarrow$ s0

d. 00 → 0k

Project

1. **a.** Develop a cellular automaton simulation with periodic boundary conditions for the killer-sensitive system of section "Killer and Sensitive Populations." The simulation function should have parameters for the size of a square grid, the probability of dispersal (*d* above), the probability of a catastrophe (*e* above), and the number of time steps, or generations. Upon initialization, have a 0.86 probability of a cell being empty, 00, and have equal probabilities for the other possibilities.

b. Plot the number of sensitive organisms and the number of killer organisms versus time.

c. Develop an animation function to visualize the simulation with empty cells (00) in white, cells with only sensitive cells in one color (or grayscale), cells with only killer cells in another color (or grayscale), and cells with sensitive and killer cells in a different color (or grayscale).

For each of the situations in Parts d-k, with d *representing probability of dispersal and* e *representing the probability of a catastrophe, run the simulation for at least 100 time steps on grids of size 100, and plot the numbers of sensitive and killer organisms versus time. Optionally, also produce an animation of the simulation. Discuss the results, considering disturbance, dispersal ability, growth rate, and coexistence.*

d. $d = 0.5$ and $e = 0.3$
e. $d = 0.5$ and $e = 0.1$
f. $d = 0.7$ and $e = 0.7$
g. $d = 0.9$ and $e = 0.2$
h. $d = 0.7$ and $e = 0.8$
i. $d = 0.7$ and $e = 0.6$
j. $d = 0.7$ and $e = 0.8$
k. $d = 0.8$ and $e = 0.4$

l. For intermediate values of e, $0.2 \le e \le 0.5$, discover values of d in which the sensitive and killer populations can coexist. Discuss the results, considering disturbance, dispersal ability, growth rate, and coexistence.

m. For higher values of e, $0.6 \le e \le 0.8$, discover values of d in which the sensitive population survives and killer population becomes extinct. Discuss the results, considering disturbance, dispersal ability, growth rate, and dominance.

References

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Answers to Quick Review Questions

1. **a.** $(1 - d)^{numS + numK} = (1 - 0.3)^7 = 0.082$

b. $(1 - (1 - d)^{numS})(1 - (1 - d)^{numK}) = (1 - (1 - 0.3)^2)(1 - (1 - 0.3)^5) = (1 - 0.7^2)(1 - 0.7^5) = 0.424$

c. $(1 - (1 - d)^{numS})(1 - d)^{numK} = (1 - 0.7^2)0.7^5 = 0.086$

d. $(1 - d)^{numS}(1 - (1 - d)^{numK}) = 0.7^2(1 - 0.7^5) = 0.408$