

# Evolutionary Suicide in Spatial Host-Pathogen Systems

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## Goal

To investigate the phenomenon of evolutionary suicide in spatial host-pathogen systems.

## Background and motivation

Evolution can sometime lead populations to extinction (Darwin, 1859 and 1871; Matsuda, 1994a and 1994b). This is possible because some individual advantages (gained by the mutation of traits) can have disastrous effects on the population as a whole (Hardin, 1968). For example, a predator the traits of which mutated toward extreme voracity is likely to abound initially, but when its prey becomes too scarce, it is going to starve and could even go extinct. We refer to *evolutionary extinction* as evolution toward trait values at which a population can no longer persist. There exists a distinction between '*evolutionary suicide*' and '*evolutionary murder*,' depending on whether an evolutionary extinction is caused, respectively, by the mutation of the extinguishing population itself, or by the mutation of another population in the same environment. It turns out that evolutionary suicide is a quite frequent phenomenon under frequency-dependent selection (Ferrière, 2000).

My interest in the field of spatial evolutionary dynamics is recent, but motivated by my Ph.D. studies on spatial dynamics and synchronization of oscillators.

## Research questions

My project is to investigate evolutionary suicide in a spatial host-pathogen system where one or more traits of the populations are allowed to evolve. Previous work (Rand *et al.*, 1995; Keeling, 2000) has shown that in a spatial explicit PCA (Probabilistic Cellular Automaton) model pathogens are at risk of extinction when their transmissibility is too high. In other words, if a pathogen "burns out" too quickly all the hosts it can reach, it will go extinct. Also using the so-called PATCH (Partitioning, Allocation, Transmission, and Coalescing of Habitats) model it has been shown that the evolving transmissibility of the pathogen tends to a critical value, beyond which the pathogen cannot persist.

However, it is not yet clear if evolution of the pathogens will lead the population to hover just below the critical value of transmissibility, or whether evolution will take it all the way to extinction. The former could happen in spatially extended host-pathogen populations through cluster-level selection: pathogens that transmit too efficiently remove themselves from the pathogens by eradicating their host clusters. In the first case I will turn my attention to elucidating the mechanism of cluster-level selection in more detail, possibly by using the PATCH model, or by developing another suitable model approximation. In the latter case, instead, I will focus on the extinction process, investigating the extinction bifurcation: according to Gyllenberg *et al.* (2000) this would have to involve a discontinuous transition to extinction.

## Methods and work plan

My work will be primarily based on two models.

- One model is a spatially explicit PCA (Probabilistic Cellular Automaton) composed of a square lattice of sites with periodic boundary conditions. Each site can be in one of three states: empty, occupied by a healthy host, or occupied by a parasitized host (i.e., occupied by a host and a pathogen that eventually will kill the host). At each step of the simulation, a site can change its state with a probability determined by the configuration of its four nearest neighbours. In particular, if a healthy host is located near one or more parasitized hosts, it can in turn become infected, with a probability that increases with the pathogen's transmissibility.
- The other, spatially implicit, model is called PATCH model, because simulation steps are broken up into a sequence of four macroscopic steps: Partitioning, Allocation, Transmission, and Coalescing of Habitats. The model's dynamical variables are the number of patches of different size, and the simulation steps involve interactions between patches and within patches. The PATCH model offers two advantages compared with the PCA model: first, it remove stochasticity from the simulations, and second, simulations are much faster, because the PATCH model is based on a set of deterministic equations. Of course, because the PATCH model is an approximation only concerned with large-scale patterns, it cannot describe small-scale dynamics due to local correlations.

Based on these models, I will investigate the question whether or not evolutionary suicide occurs when the transmissibility of the pathogen is allowed to evolve in the PCA model. There are two possible scenarios:

- On the one hand, the pathogen could go extinct because it causes excessive host infection. Should this happen, I would continue with the following problem. A work by Gyllenberg *et al.* (2000) investigated evolutionary bifurcations in a structured metapopulation model in which the dispersal rate of an organism is allowed to mutate and showed that for evolutionary suicide to occur the population has to undergo a discontinuous transition to extinction. I would therefore try to understand whether this conclusion holds for the PCA and the PATCH models, too.
- On the other hand, it is also possible that extinction does not happen, so that pathogens that are slightly beyond the critical value of transmissibility will kill themselves by locally "burning out" their host clusters, while pathogens that are slightly below the critical value will persist. This would result in an interesting example of group selection to focus on, since evolution, instead of being driven by individual fitness only, would be driven by cluster-level fitness, too.

If time permits, the following extensions of the project could be considered:

- To introduce the evolution of other pathogen strategies in addition or instead of transmissibility;
- To consider also evolution of the host (specifically, by allowing for adaptive variation in the host's resistance or dispersal rate); and

- To investigate more complex mechanisms of spatial spread, like infections occurring over longer distances or the possibility for the pathogens to travel through host-free environment.

### **Relevance and link to ADN's research plan**

This project aims at establishing further insight into the phenomenon of evolutionary suicide, which has already been a focus of ADN's studies (Ferrière, 2000). In particular, this work will help understanding whether a spatial model composed of hosts and pathogens, as proposed by Rand *et al.* (1995) and Keeling (2000), can evolve toward host extinction, and under which general ecological conditions this can happen. Additionally, this project is putting a result previously obtained by ADN (Gyllenberg *et al.*, 2000; on discontinuous transitions to extinction) to a test in a more complex ecological scenario.

### **Expected output and publications**

The study envisaged here is expected to be published in at least one jointly authored paper and will be integrated as one chapter in my Ph.D. thesis.

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