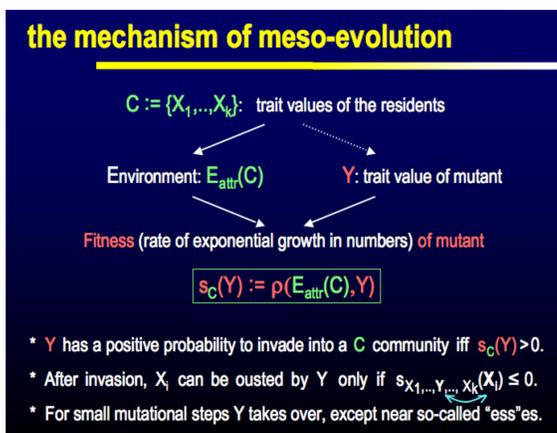


## An ecology-based theory of meso-evolution with practical applicability

The theory of structured populations is a mathematical framework for developing and analyzing ecological models that can take account of relatively realistic detail at the level of individual organisms. This framework has given rise to the theory of adaptive dynamics (AD), a versatile framework for dealing with the evolution of the adaptable traits of individuals subject to ecologically driven selection.

By concentrating on general features of ecologies AD can be used to make general predictions about meso-evolutionary patterns. Moreover, AD has produced a general toolbox for dealing efficiently with eco-evolutionary processes of any level of complexity.

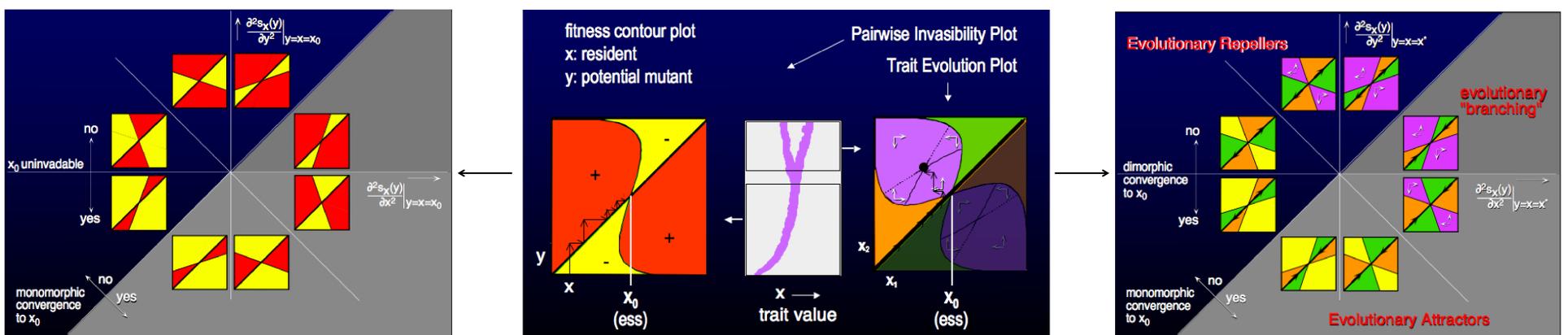


## Evolution proceeds by repeated mutant substitutions

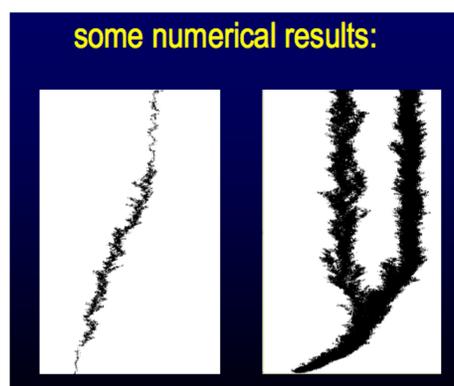
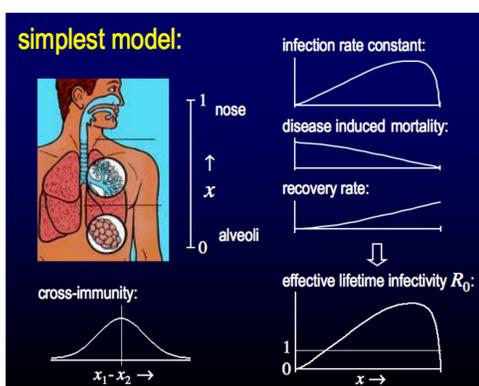
Let the environment be defined as anything that influences the population dynamical behavior of individuals. Populations can then be represented as frequency distributions over the possible states of individuals, the movement of which depend on the environment. In a given trend-free environment populations grow on average exponentially. Fitness is the rate constant  $\rho$  of this growth.

Real populations influence their environment and as a result stay bounded. Hence their dynamics moves towards an attractor which produces a trend-free environment  $E_{attr}$ . If we characterize different sorts of individuals with a trait vector,  $X$  for the resident populations and  $Y$  for potential mutants, then whether a  $Y$  mutant can invade depends on its fitness in the environment engendered by the traits  $X_1, \dots, X_k$  of the resident populations.

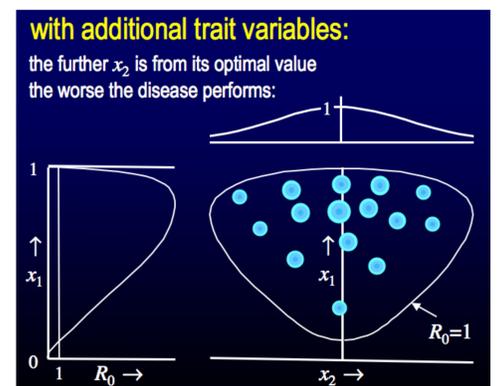
## Some graphical tools, applicable to one-dimensional trait spaces



## Applying AD ideas to the evolution of respiratory diseases



More deeply seated respiratory diseases are both less infective and more harmful. They should therefore evolve in the direction of the nose. Close to the tip they are hampered by lack of space, making for an "optimum depth". There limited cross-immunity can lead to evolutionary branching.



## Some robust predictions

1. The larger the population density, the larger the variety of respiratory diseases circulating in a population.
2. The variety of diseases of the upper airways that circulate will be far larger than the variety of those of the lower airways.
3. Since the target of a respiratory disease will primarily evolve upwards, and subsequent diversification in the vertical direction is slow, there will in general be room at the bottom. Therefore, emerging respiratory diseases will usually have a deep target, be highly virulent, but not overly infective, and hence easier to contain than the already circulating ones would be.