TEK9010 - Evolutionary Dynamics

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Quasispecies Theory

You need to incorporate three basic principles in order to model evolution; *reproduction*, *selection* and *mutation*. In the world of mathematical biology, we normally assume some sort of asexual reproduction.

$$\dot{x} = \frac{\partial x}{\partial t} = rx$$

The solution of this equation is exponential growth,

$$x(t) = x_0 = e^{rt},$$

but may be checked by resource limitation. Selection arises when different types of individuals reproduce at different rates.

$$\dot{x} = x(a - \phi),$$
$$\dot{y} = y(b - \phi),$$

such that $a \neq b$. The term ϕ ensures that $x + y = 1$, which is only possible if $\phi = ax + by$. We may echange the values a and b with fitness values f_i, in the general case of n types of individuals,

$$\dot{x}_i = x_i(f_i - \phi).$$

Mutation arisis when reproduction is not perfectly accurat, such that an individual of type i can transition to an individual of type j in reproduction. This is is modelled by the mutation matrix $Q = [q_{ij}]$, which is a stochastic $n \times n$ matrix.

The quasispecies equation incorporates all of these concepts of reproduction, selection and mutation,

$$\dot{x}_i = \sum_{j=1}^{n} x_i f_i Q_{ij} - \phi(\mathbf{x}) x_j.$$

This equation gives the rate of change over time $\dot{x}_i$, i.e. the time derivative of the frequency of an individual of species i. The first term on the right-hand side contains the sum of product of all other individual frequencies x_j, the fitness f_j and the mutation rate Q_{ij} from species i to j. The fitness is also called the reproductive rate of the organism, which is determined by phenotype of the organism. The average fitness is given by $\phi(\mathbf{x}) = \sum_i f_i x_i$.

The quasispecies equation describes deterministic evolutionary dynamics in terms of mutation and constant selection acting on an infinitely large population. Generally, the quasipsecies equation has one global equilibrium, consisting of a distribution of genomes in a mutation-selection balance.

Evolutionary Game Dynamics

In game theory, games can be formulated in terms of a payoff matrix, which specifies the payoff for one strategy when interacting with another.

Table 1: Pay-off matrix with interacting strategies A and B, with different payoffs a, b, c and d, dependent on choice.

	A	B
A	a	b
B	c	d

In evolutionary games we interpret the payoffs as fitness - a better strategy would lead to faster reproduction.

In game theory it is absolutely necessary to define the Nash equlibirium. If each player has a chosen strategy, and no player can increase its own expected payoff by changing its strategy while other players keep their unchanged, then the current set of strategy choices consitutes a Nash equilibrium. The Nash equilibrium is related to the evolutionary stable stratgy (ESS). In general, for games with more than two strategies, we can define the two concepts in the following way. If $E(S_i, S_j)$ is the expected payoff for strategy S_i versus S_j, then;

- Strategy S_k is a strict Nash equilibrium if $E(S_k, S_k) > E(S_i, S_k)$ for all $i \neq k$,
- Strategy S_k is a (non-strict) Nash eqmuilibrium if $S(S_k, S_k) \geq S(S_i, S_k)$ for all i,
- Strategy S_k is ESS, if for all $i \neq k$ we have either $E(S_k, S_k) > E(S_i, S_k)$ or $E(S_k, S_k) = E(S_i, S_k)$ and $E(S_k, S_i) > E(S_i, S_i)$.
- Strategy S_k is stable against invasion by selection ("weak ESS") if for all $i \neq k$ we have either $E(S_k, S_k) > E(S_i, S_k)$ or $E(S_k, S_k) = E(S_i, S_k)$ and $E(S_k, S_i) \geq E(S_i, S_i)$.

Note; strict Nash implies ESS implies weak ESS implies Nash.

The replicator equation is the cornerstone of evolutionary game dynamics,

$$\dot{x}_i = x_i[f_j(\mathbf{x}) - \phi(\mathbf{x})].$$

It describes deterministic evolutionary game dynamics. For $n = 2$ strategies, there can be dominance, coexistence, bistability or neutrality. For $n \geq 3$ strategies, there can be heteroclinic cycles. For $n \geq 4$, there can be limit cycles and chaos. The replicator equation with n strategies

$$\dot{x}_i = x_i \left[\sum_{j=1}^{n} a_{ij} x_j - \phi(\mathbf{x}) \right].$$

is equivalent to the Lotka-Volterra equation from ecology,

$$\dot{y}_i = y_i \left(r_i + \sum_{j=1}^{n-1} b_{ij} y_j \right),$$

with the parameters $r_i = a_{in} - a_{nn}$ and $b_{ij} = a_{ij} - a_{nj}$.

Prisoner's Dilemma and Cooperation

Table 2: A payoff matrix depicts a prisoner's dilemma game if $T > R > P > S$.

	C	D
C	R	S
D	T	P

In a prisoner's dilemma game you can either cooperate (C) or defect (D). Defection is "rational", because it maximises the payoff. But, if my opponent analyses the game the same way that I do, the we both choose defection which leads to a suboptimal payoff. The social optium does not provide the highest payoff for the individual. Thus, the prisoner's dilemma captures the essence of cooperation and how defection can dominate.

The repeated Prisoner's dilemme is a tool for studying direct reciprocity, which represents a mechanics for the evolution of cooperation. In a series of "tournaments", Robert Axelrod invited participants to submit strategies for a repeated game. The clear winner in these tournaments was the simple Tit-for-Tat (TFT) statetegy. TFT starts with a cooperation, then does whatever the oponent did the previous round. TFT has a couple of weaknesses.

Table 3: Tit-for-Tat (TFT) payoff against Always Defect (ALLD). The expected number of rounds played is given by $\bar{m}$.

	TFT	ALLD
TFT	$\bar{m}R$	$S + (\bar{m} - 1)P$
ALLD	$T + (\bar{m} - 1)P$	$\bar{m}P$

TFT cannot prevent netutral drift leading to Always Cooperate (ALLC) and it cannot correct mistakes.

An improvement on TFT is the Generous TFT (GTFT). This strategy cooperate whenever the oponent has cooperated and sometimes even cooperates when the oponent has defected. It is therefore able to correct mistakes.

In a repeadted PD game where one allow for evolution of reactive strategies, it is revealed that TFT is a catalyst for cooperation, but will be replaced by GTFT. Both of these strategies are outcompeted by Win-stay, lose-shift (WSLS), which can correct mistakes and is stable against neutral drift to ALLC.

Stochastic Description of Finite Populations

The Moran process: Pick one individual for reproduction and one for death. The offspring of the first individual replaces the second. The individual can be the same. We typically have two types of individuals, A and B.

An interesting process to model is the one where the initial state is one A individual and N - 1 B individuals. The probability that A takes over the whole population is called the fixation probability. We are interesting in studying if a mutation can take over the whole population.

Introducing fitnes to this kind of model would make things more interesting, as we could model a situation where the mutation is favoured.

One may also introduce random mutations, introducting the molecular clock of neutral evolution.

Games in Finite Populations

Computing fixation probabilities can determine if a selection one strategy over another.

There is surprising $\frac{1}{3}$ law.

There are ESS that hold for finite population size N, i.e. ESS_N.

Geme dynamics of TFT and ALLD changes for finite populations.

Evolutionary Graph Theory

A graph can represent the spatial configuration of a population, the differentiation hierarchy of cells in a multicellular organism, or a social network. Individuals are placed on the vertices of the graph and the edges of a graph determine competitive interaction. All invividuals of the population are labelled $i\ in[0, N]$, at each time step, an individual is chosen for reproduction. The probability that the offspring of i replaces j is w_{ij}, i.e. the process is determinded by an $N \times N$ matrix W, where all entries are probabilities. The Moran process is given by the *complete graph* with identical weights.

Other simple ones:

- The (directed) cycle,
- The line and the burst,

The temperature of a vertex is given by,

$$T_j = \sum_{i=1}^{N} w_{ij}.$$

If all vertices have the same temperature, then the fixation probability is equivalent to the Moran process. This is called the isothermal theorem.

The cycle and directed cycles are isothermal. All symmeric graphcs $w_{ij} = w_{ji}$ are isothermal.

Suppressing and Ampllifying Selection

There are graphs that can do both these things. One-rooted vs multiple-rooted graphs. (Super) star,funnnel

Games on Graphs

Games on graphs can be studied by assuming that individuals interact with their nearest neighbors an thereby acumulate payoff. Some games are the birth-death, death-birth and imitation process games.

Spatial Games

This is just pretty pictures.