生物数理の理論とその応用
ミニシンポジウム「進化動態の数理」
進化動態の数理的記述について－概説

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1   Evolution

Evolution is a dynamical process that inherited phenotype of a population changes through generation. Genotypes underlies phenotype and genetic constitution of a population also changes by evolution. Evolution is driven by natural selection and genetic drift. Natural selection includes sexual selection, kin selection, etc. and is accompanied by adaptation. Individuals with some phenotype reproduce more offspring than others and if the phenotype is genetically inherited, the fraction of such individuals with the phenotype will finally dominate the population. This is "adaptation". Individuals with higher fitness increase in frequency and finally dominate the population.

Evolution is also driven by statistical effect of random events even if the trait in focus is neutral. This is called genetic drift and neutral genes which confer no advantage to the bearer can be fixed or lost simply by chance.

In this paper I deal only with adaptation as a major force of evolution. But the effect of stochasticity of neutral traits could be relevant as I mentioned in the last section.

2   Models to deal with evolution by adaptation

Adaptation is a process that maximizes individual's fitness. But this is not simply "optimization" as is often used in engineering because individual's fitness is likely affected by how other individuals behave. This is a game theoretic situation and we have to define individual fitness as dependent on the target individual as well as other individuals in focus. To model evolution by adaptation, we define 1) fitness of a population along hypothetical phenotypic traits or genetic constitution. This is called "adaptive landscape". Through

evolution the population will climb on the adaptive landscape to reach a local fitness maximum. But the adaptive landscape often changes its shape as the population evolves because the change of the population status usually results in the change of individual's fitness. The most major case is frequency dependency.

If the population reaches a state where no other traits can invade, the population is said to be at evolutionarily stable strategy, ESS [1].

3 Adaptive dynamics

Although the concept of ESS has greatly contributed to understand evolution of many traits/behaviors of animals and plants, ESS itself does not indicate that a population will converge to the state. In this sense ESS is based on a "static" view. To better understand the dynamic process of evolution, adaptive dynamics has been proposed in the last decade and is now widely used in various theoretical study of evolution [2] [3].

Adaptive dynamics is a framework of phenotypic evolutionary dynamics. It just focuses on phenotype. In adaptive dynamics, we first define "invasion exponent" as the fitness of mutant m in a resident population r, $S_r(m)$.

Once the invasion exponent $S_r(m)$ is defined, the dynamics of trait r can be traced as follow.

- Selection gradient defined as

$$\left. \frac{\partial S_r(m)}{\partial m} \right|_{m=r}$$

determines the direction of evolutionary change.

- Evolutionarily singular strategy $r*$ satisfies

$$\left. \frac{\partial S_r(m)}{\partial m} \right|_{m=r=r*} = 0$$

- An evolutionarily singular strategy $r*$ is ESS iff

$$\left. \frac{\partial^2 S_r(m)}{\partial m^2} \right|_{m=r} < 0$$

, i.e., at ESS $r*$ is fitness maximum.

- An evolutionarily singular strategy $r*$ is convergence stable strategy CSS iff

$$\left. \frac{\partial^2 S_r(m)}{\partial r^2} \right|_{m=r=r*} > \left. \frac{\partial^2 S_r(m)}{\partial m^2} \right|_{m=r=r*}$$

which indicates that the selection gradient points to $r*$.

Topology of the invasion exponent $S_r(m)$ determines the trajectory of evolution.

We should note that ESS and CSS are mutually independent concept and evolutionarily singular strategy, a candidate of an end point of evolution, can be either ESS or non-ESS, either CSS or non-CSS. Intriguing trajectory like evolutionary branching and evolutionary suicide has been reported [4].

4 Evolutionary dynamics build up from individual level

Adaptive dynamics starts with defining the invasion exponent $S_r(m)$ for each target system. And it is defined as an expression under a certain biological assumptions. Recently, thanks to the advance of computer technology, quite a realistic model called individual-based model, IBM, is widely used to explore biological phenomena. In IBM, individual is the unit and all birth and death events of individuals are inherently stochastic.

In IBM, a set of strategies (traits, genetic structure, etc.) is assigned to individuals and all individuals reproduce or survive according to a certain rules. IBM has been recognized as a powerful tool to simulate and explore the consequence of complicated set of birth- and death-rules on the population-level phenomena.

Figure 1 show a snapshot of an IBM where hosts and parasites interact. Both hosts and parasites are located in two-dimensional torus space and a parasite parasitized any hosts within a certain radius R. If a host is parasitized, a parasite offspring emerges and disperse a certain distance to land in the space. If a host escapes parasitism, a certain number of host offspring emerges and disperse a certain distance to land in the space. All hosts and parasites dies after reproduction. This corresponds to the Nicholson-Baily model of host parasite population dynamics.

By extending the IBM to include the evolution of host resistance to parasitism and parasite virulence to overcome the host resistance, we have very interesting simulation results (Takasu in prep.).

Until now, most theoretical study on evolutionary dynamics has been based on a deterministic description of the invasion exponent. As I showed IBM simulation shows a variety of interesting phenomena worth to be "mathematically" explored.

Most mathematical models have been "analytical models" which describes the population-level phenomena, i.e., population density, etc. However, IBM is based on "algorithm" that rules birth and death of each individual. Exploring mathematical link between the analytical models and algorithmic models is worth to challenge.

References

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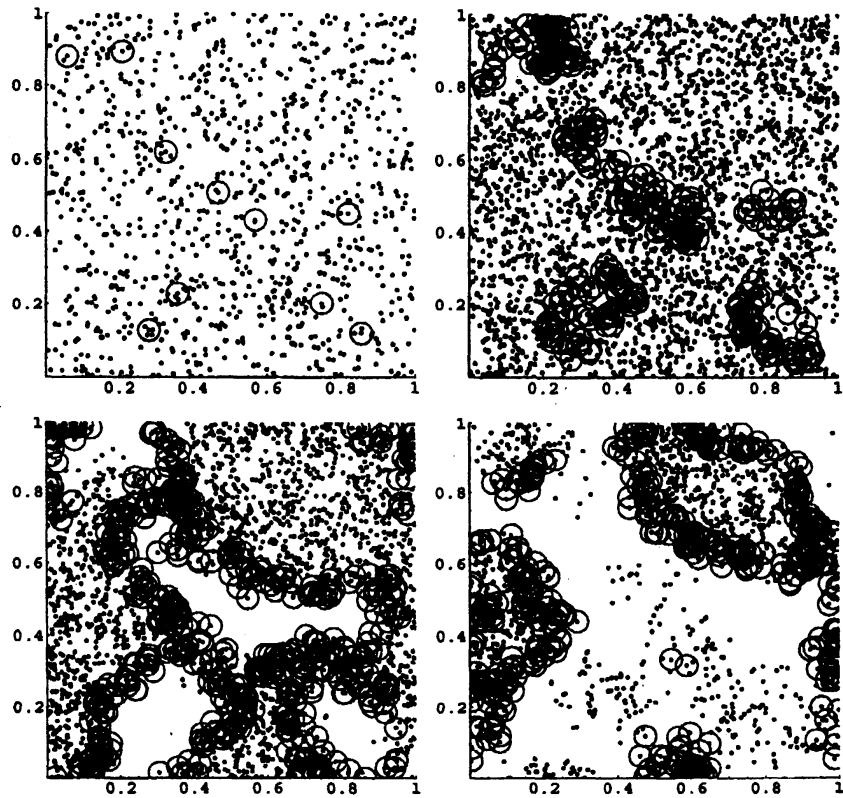
Figure 1: Snapshots of the host-parasite IBM in two dimensional space. Hosts are shown in dots and parasites are in dots with radius.

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