

Diffusion approximations for matrix games in group-structured populations

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THE
GENETICAL THEORY OF
NATURAL SELECTION

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Fundamental Theorem of Natural Selection

The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time. (Fisher 1930, p.35)

- ▶ **Increase of mean fitness under weak selection**
(Nagylaki 1976, 1977, 1987, 1989, 1993)
- ▶ **Partial change in mean fitness**
(Price 1972, Ewens 1989, Lessard 1997)
- ▶ **Stochastic effects**
(Wright 1931, Malécot 1948, Kimura 1964)

Group selection

The average adaptiveness of the species thus advances under intergroup selection, an enormously more effective process than intragroup selection. (Wright 1932)

By all odds the most important cases of interdeme selection are those in which the character that increases the probability of survival of the deme as a unit is itself being selected against within the population. (Lewontin 1965)

Kin selection

Species ... should tend to evolve behaviour such that each organism appears to be attempting to maximize its inclusive fitness. (Hamilton 1964)

$$\tilde{w}_J = 1 + s \sum_I \rho_{J \rightarrow I} a_{J \rightarrow I}$$

for some coefficient of relatedness $\rho_{J \rightarrow I}$

Evolutionarily stable strategy

Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness. (Maynard Smith and Price 1973)

Stable state of the replicator dynamics (Taylor & Jonker 1978)

$$\dot{x}_k = x_k((A\mathbf{x})_k - \mathbf{x} \cdot A\mathbf{x})$$

for a game matrix $A = [a_{kl}]_{k,l=1}^n$, and conversely if A symmetric.

Evolutionary stability for finite populations

For finite N , we propose that B is an ESS ... if two conditions hold: (1) selection opposes A invading B ,... and (2) selection opposes A replacing B . (Nowak et al. 2004)

$$P(\text{fixation of single } A \text{ among } N) < \frac{1}{N}$$

Selection favors a strategy if its abundance (average frequency) exceeds $1/n$... in the stationary distribution of the mutation-selection process. (Antal et al. 2009)

$$E(\text{frequency of strategy } A \text{ among } n) > \frac{1}{n}$$

Questions

- Can we ascertain **diffusion approximations** for matrix games in finite group-structured populations?
- What is the relationship with **game dynamics** in well-mixed populations?
- What are the roles of **relatedness** and **group selection**?
- What **coefficients of relatedness** come into play?
- Is an **inclusive fitness** formulation possible?

Population structure

D groups of N individuals

n strategies S_1, \dots, S_n

ordered group type $(S_{i,1}, \dots, S_{i,N})$

with strategy frequency vector $\mathbf{x}_i = (x_{1,i}, \dots, x_{n,i})$

frequency $z_i(t)$ in generation $t \geq 0$

Life cycle

Reproduction: infinite number of offspring

Migration: proportional dispersal of a fraction m of offspring

Selection after migration : **viability** of S_k in a group of type i

$$w_{k,i} = 1 + \frac{(A\mathbf{x}_i)_k}{ND}$$

Life cycle

Reproduction: infinite number of offspring

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Selection after migration : **viability** of S_k in a group of type i

$$w_{k,i} = 1 + \frac{(A\mathbf{x}_i)_k}{ND}$$

Mutation: from S_k to S_l with probability

$$u_{kl} = \frac{\mu_{kl}}{ND}$$

Sampling: group of type j from type i with probability

$$P_{ij}^D(\mathbf{z}(t))$$

Key Lemma

When $D = \infty$, there is *uniform convergence* of the frequency

$$z_j(t+1) = \sum_i z_i(t) P_{ij}(\mathbf{z}(t))$$

to

$$\hat{z}_j(\mathbf{x}) = \sum_{\mathbf{r}} c_j(\mathbf{r}) x_1^{r_1} \cdot \dots \cdot x_L^{r_L}$$

with $c_j(\mathbf{r})$ the number of ways for a group of type j to have r_k ancestors of type S_k and x_k the overall frequency of S_k .

Diffusion approximation

The strategy frequency process $\mathbf{X}(\lfloor ND\tau \rfloor)$ *converges in law* as $D \rightarrow \infty$ to a diffusion with infinitesimal covariances

$$v_{kl}(\mathbf{x}, \mathbf{0}) = Cx_k(\delta_{kl} - x_l)$$

for some *coefficient of diffusion* C , and infinitesimal means

$$m_k(\mathbf{x}, \mathbf{0}) = \sum_l \mu_{lk}x_l - \sum_l \mu_{kl}x_k + x_k((\tilde{A}\mathbf{x})_k - \mathbf{x} \cdot \tilde{A}\mathbf{x})$$

for some *effective game matrix* \tilde{A} .

Proof: Two-time scale MC (Ethier and Nagylaki 1980)

$$E_{\mathbf{z}}(\Delta X_k) = \frac{m_k(\mathbf{x}, \mathbf{y})}{ND} + o(D^{-1})$$

$$E_{\mathbf{z}}((\Delta X_k)(\Delta X_l)) = \frac{v_{kl}(\mathbf{x}, \mathbf{y})}{ND} + o(D^{-1})$$

$$E_{\mathbf{z}}((\Delta X_k)^4) = o(D^{-1})$$

$$E_{\mathbf{z}}(\Delta Y_j) = d_j(\mathbf{x}, \mathbf{y}) + o(1),$$

$$\text{Var}_{\mathbf{z}}(\Delta Y_j) = o(1)$$

uniformly in \mathbf{z} , where $\mathbf{y} = \mathbf{z} - \hat{\mathbf{z}}$ and $d_j(\mathbf{x}, \mathbf{y}) = \sum_i z_i P_{ij}(\mathbf{z}) - z_j$

Coefficient of diffusion

$$C = 1 - f$$

$$f = \frac{(1-m)^2}{Nm(2-m) + (1-m)^2}$$

probability that 2 offspring in the same group after dispersal
are **ibd** (identical-by-descent) with an **infinite number of groups**
and therefore in the **absence of selection and mutation**

Effective game matrix

$$(1-f) \left(a_{kl} - \frac{\rho_{\bullet}}{2} a_{kl} - \frac{\rho_{\bullet}}{2} a_{lk} \right) + f(1 - \rho_{\bullet\bullet}) a_{kk}$$

$$\rho_{\bullet\bullet} = \left[\frac{N(1-m) + 2(N-1)(1-m)^3}{N^2m(3-3m+m^2) + (3N-2)(1-m)^3} \right]$$

probability that an offspring is ibd to 2 others in the same group after dispersal given that these 2 are ibd

$$\rho_{\bullet} = \frac{2f(1 - \rho_{\bullet\bullet})}{1-f}$$

probability that an offspring is ibd to either of 2 others in the same group after dispersal given that these 2 are not ibd

Approximations

$$\rho_{\bullet\bullet} \approx \rho_{\bullet} \approx \frac{2f}{1+f}$$

with equality as $N \rightarrow \infty$ and $m \rightarrow 0$ with Nm kept constant

Additive case $a_{kl} = -c_k + b_l$

Same diffusion approximation with **inclusive fitness** of type S_k

$$\tilde{w}_k = 1 + \frac{\tilde{a}_k}{ND}$$

$$\begin{aligned}\tilde{a}_k &= c_k \left(-1 + (1-f) \frac{\rho_{\bullet}}{2} + f \rho_{\bullet\bullet} \right) \\ &+ b_k \left(f - (1-f) \frac{\rho_{\bullet}}{2} - f \rho_{\bullet\bullet} \right)\end{aligned}$$

Migration after selection

- **Proportional dispersal:**

$\rho_{\bullet\bullet}$ and ρ_{\bullet} calculated in offspring before dispersal
and multiplied by $(1 - m) \leq 1$

- **Uniform dispersal:**

$\rho_{\bullet\bullet}$ and ρ_{\bullet} calculated in offspring before dispersal
and multiplied by $(1 - m)^2 \leq (1 - m)$

- Local extinction and recolonization:

like proportional dispersal

$$\text{but } C = (2 - m)(1 - f) > (1 - f)$$

- Fertility selection : complete dispersal, regulation of groups

$$w_{k,i} = 1 + \frac{(A\mathbf{x}_i)_k - \frac{a_{kk}}{N}}{ND}$$

effective game matrix $\tilde{A} = A - \frac{A+A^T}{N}$!

Concluding remarks

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- ▶ With random pairwise interactions within groups, the effect of selection on the infinitesimal means are given by the replicator equation for some *effective game matrix*.

Concluding remarks

- ▶ A *diffusion approximation* for selection, mutation and drift in group-structured populations as the number of groups increases can be ascertained by a two-time scale argument.
- ▶ With random pairwise interactions within groups, the effect of selection on the infinitesimal means are given by the replicator equation for some *effective game matrix*.
- ▶ The entries of the effective game matrix are sums of effects weighted by *coefficients of relatedness*.

- ▶ *Competition within groups* which results from population regulation is reduced by *differential contributions of groups* which result from dispersal or colonization after selection

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- ▶ An *inclusive fitness formulation* is possible in the case of interactions having additive individual effects.
- ▶ Future work will deal with other *population structures* and *migration patterns*.

Thanks