

# Diffusion approximations for matrix games in group-structured populations

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THE  
GENETICAL THEORY OF  
NATURAL SELECTION

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OXFORD  
AT THE CLARENDON PRESS  
1930

Université de Montréal  
Bibliothèque

## 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  $A = (a_{kl})$ , and conversely if  $A$  symmetric.

## Evolutionary stability for finite populations

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

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

*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)*

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

# 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:** uniform dispersal of a fraction  $m$  of offspring

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

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

**Mutation:** from  $S_k$  to  $S_l$  with probability

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

**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

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

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  $\tilde{A} = (\tilde{a}_{kl})$ .

*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

$$C = \phi_{I/J} = 1 - \phi_{IJ}$$

$$\phi_{IJ} = P(I \equiv J) = \frac{(1-m)^2}{Nm(2-m) + (1-m)^2}$$

probability for  $I$  and  $J$  in the same group after dispersal to be **ibd** (identical-by-descent) with an **infinite number of groups** and therefore in the **absence of selection and mutation**, then

## Effective population size

$$ND(1 - \phi_{IJ}) \leq ND$$

## Effective game matrix

$$\tilde{a}_{kl} = \phi_{IJ}a_{kk} + \phi_{I/J}a_{kl} - \phi_{I_cIJ}a_{kk} - \phi_{I_cI/J}a_{kl} - \phi_{I_cJ/I}a_{lk}$$

$$\phi_{I_cIJ} = P(I_c \equiv I \equiv J) = \frac{(N(1-m) + 2(N-1)(1-m)^3)\phi_{IJ}}{N^2m(3-3m+m^2) + (3N-2)(1-m)^3}$$

$$\phi_{I_cI/J} = P(I_c \equiv I \not\equiv J) = \phi_{I_cI} - \phi_{I_cIJ}$$

$I, J$  in interaction and  $I, I_c$  in competition

in the same group after dispersal



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

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

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

$$\tilde{a}_k = c_k (-1 + \phi_{II_c}) + b_k (\phi_{IJ} - \phi_{IJ_c})$$

$I, I_c$  in competition and  $J, J_c$  in competition  
in the same group after dispersal

## Migration after selection

- **Proportional dispersal:**

ibd measures in  $\tilde{a}_{kl}$  for offspring before dispersal

and competition terms multiplied by  $(1 - m) \leq 1$

- **Uniform dispersal:**

ibd measures in  $\tilde{a}_{kl}$  for offspring before dispersal and

competition terms multiplied by  $(1 - m)^2 \leq (1 - m)$

- Local extinction and recolonization:

like proportional dispersal

$$C = (2 - m)(1 - \phi_{IJ}) > (1 - \phi_{IJ})$$

$$\text{with } \phi_{IJ} = \frac{1-m}{Nm+1-m}$$

- **Fertility selection** : complete dispersal, regulation of groups

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

$$\tilde{A} = A - \frac{A+A^T}{N}$$

effect of competition

between an individual and itself!

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

Thanks!