Large Fluctuations and Fixation in Evolutionary Games with Non-Vanishing Selection

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Outline

Based on the work done in collaboration with M. Assaf (Jerusalem)
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- **Intro to Evolutionary game theory**
  - Basic notions & replicator Dynamics
  - Stochastic Dynamics, Evolutionary stability & Fixation
- **Large fluctuations & WKB theory in evolutionary games**
  - WKB theory in anti-coordination games
  - General WKB treatment & Results

  - WKB calculation of the fixation probability in coordination games
  - Comparison with diffusion approximations (Fokker-Planck)
- **Outlook & Conclusion**

Need for an accurate theoretical approach to describe large-fluctuation-induced phenomena (stochastic fluctuations and nonvanishing selection), diffusion approx don't work here

What is Evolutionary Game Theory about?

- Description of complex phenomena in behavioural science and population dynamics (e.g. in ecology, genetics, economics, ...)
- Dynamical version of *classic (rational) game theory*

Some of the founders & pioneers:

- John von Neumann & Oskar Morgenstern (1944), “Theory of games and economic behavior”
- John Nash (1994 Nobel prize in Economics) → Nash equilibrium
- John Maynard Smith, “Evolution and the Theory of Games” (1972) → Evolutionary stability

Some reference books:

- J. Hofbauer & K. Sigmund, “Evolutionary Games and Population Dynamics” (1998)
- M. Nowak, “Evolutionary Dynamics” (2006)
- J. Maynard Smith, “Evolution and the Theory of Games” (1972)

Some Basics of Game Theory

Initially, "game theory" was a branch of social sciences and applied maths (von Neumann & Morgenstern, 1944). Goal: find optimal strategies ("utility function").

Evolutionary Game Theory (EGT): different approach where utility function (game's payoff) is the **reproductive fitness** $\Rightarrow$ successful strategies spread at the expenses of the others (Maynard Smith & Price, 1973).
New aspects and interpretations:

1. Strategies and their frequencies become *population species* and their *densities*
2. Dynamics is naturally implemented in EGT

The Replicator Dynamics

Traditional EGT setting: large and unstructured populations with pairwise interactions.
At *mean-field* level, the dynamics is described by the replicator equations for the density x_i of type $i = 1, ..., S$ in the population:

$$\dot{x}_i = x_i(\Pi_i - \bar{\Pi}),$$

where Π_i: average payoff (here $=$ fitness) of an individual of species i
$\bar{\Pi}$: mean payoff averaged over the entire population

Common choice, with a payoff matrix $\mathscr{P}$: $\Pi_i = (\mathscr{P}\mathbf{x})_i$ linear function of $\mathbf{x} = (x_1, ..., x_i, ..., x_S)$, $\bar{\Pi} = \mathbf{x}.\mathscr{P}\mathbf{x}$
Important case: 2×2 games with 2 species/strategies (*A* and *B*)

vs	*A*	*B*
A	a	b
B	c	d

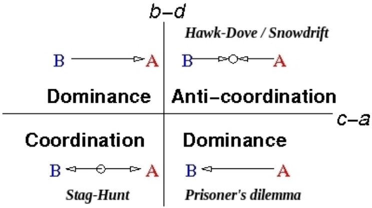
A vs *A* gets *a* and *B* vs *B* gets *d*; *A* vs *B* gets *b*, while *B* gets *c*

Replicator Dynamics for 2×2 Games

Population comprised of a density x and $1-x$ of A and B, resp.
Thus, $\Pi_A = ax + b(1-x), \Pi_B = cx + d(1-x)$ and $\bar{\Pi} = x\Pi_A + (1-x)\Pi_B$

$$\dot{x} = x(1-x)[(a-b-c+d)x + b - d] \Rightarrow$$
$$x^* = \frac{d-b}{a-b-c+d} \quad \text{(Interior fixed point)}$$

- *Dominance* $(a-c)(d-b) \leq 0$*:* A dominates over B when $a \geq c$ & $b \geq d$. B dominates over A when $c \geq a$ & $d \geq b$
- *Coordination (bistability):* When $a > c$ and $d > b$, the asborbing states $x = 0$ and $x = 1$ are stable and separated by x^* (unstable)
- *Anti-coordination (coexistence):* When $c > a$ and $b > d$, x^* is stable while $x = 0$ and $x = 1$ are unstable, hence A and B coexist



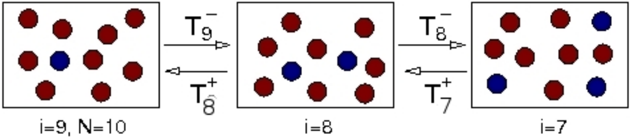
- *Neutrality:* When $a = c$ and $b = d$, there is neutral stability for all values of x

Stochastic Dynamics & Moran Process

Evolutionary dynamics involves a *finite number of discrete individuals*
$\Rightarrow$ stochastic rules given by the frequency-dependent **Moran process**

2×2 games: Markov birth-death process of i individuals of species *A* and $N - i$ of species *B* (total size N is conserved).

- At each time step, randomly pick 2 individuals
- 1 individual selected for reproduction and the other for death. The offspring replaces the deceased. N remains constant
- "Interaction" according to the payoff matrix, i.e. reproduction and death rates depend on the individuals' fitnesses f_A and f_B.
- Transition $i \to i + 1$ (birth of a *A* and death of a *B*) with rate T_i^+, while the transition $i \to i - 1$ (birth of *B* and death of a *A*) occurs with rate T_i^-. $T_i^\pm$ **are functions of** f_A **and** f_B



The probability $P_i(t)$ of having i individuals of species A at time t obeys the master equation:

$$\frac{d}{dt}P_i(t) = T^+_{i-1}P_{i-1}(t) + T^-_{i+1}P_{i+1}(t) - [T^+_i + T^-_i]P_i$$

$i = 0$ (i.e. all B's) and $i = N$ (i.e. all A's) are **absorbing states** $\Rightarrow$ $i \in [0, N]$ and $T^\pm_0 = T^\pm_N = 0$

For the frequency-dependent Moran Process (fMP):

- Fitnesses of A and B given by f_A and f_B, resp.
  2 contributions: baseline (neutral) contribution + *selection* $\Rightarrow$
  $f_A = 1 - w + w\Pi_A$ and $f_B = 1 - w + w\Pi_B$.
  Strength of selection measure by $0 \leq w \leq 1$:
  $w = 0 \rightarrow$ neutrality, $w = 1 \rightarrow$ only selection
- $T^\pm_i = \chi^\pm_i(f_A, f_B)$
- $\chi^+_i = \frac{f_A}{(i/N)f_A + (1-i/N)f_B}$ and $\chi^-_i = \frac{f_B}{(i/N)f_A + (1-i/N)f_B} \rightarrow \frac{f_B}{xf_A + (1-x)f_B}$

Markov chain with absorbing boundaries $\Rightarrow$ unavoidable **fixation**, with system ending with all A's ($i = N$) or all B's ($i = 0$)

Stochastic fluctuations alter the predictions of the replicator equations

Evolutionary Stability & Fixation

1. Fixation: possibility for a few mutants to take over the entire population
2. There is *evolutionary stability* when the population B's is proof against invasion from mutants A's

Starting with i mutants of type A, what is the probability ϕ_i^A of ending with all A's ($i = N$)? How long does it take? Dependence on w?

In the neutral case ($w = 0$), $\phi_i^A = i/N \Rightarrow$
State with all B's evolutionary stable if *selection* opposes replacement by A mutants A, i.e. if $\phi_i^A < i/N$

2×2 evolutionary games are formulated as 1D single-step birth-death processes and thus (formally) solvable:

- $\phi_i^A = \frac{1+\sum_{k=1}^{i-1}\prod_{l=1}^{k}\gamma_l}{1+\sum_{k=1}^{N-1}\prod_{l=1}^{k}\gamma_l}$, with $\gamma_i = T_i^-/T_i^+ = \chi_i^-/\chi_i^+$
- Unconditional fixation time:
  $\tau_i = -\tau_1 \sum_{k=i}^{N-1}\prod_{m=1}^{k}\gamma_m + \sum_{k=i}^{N-1}\sum_{l=1}^{k}\frac{1}{T_l^+}\prod_{m=l+1}^{k}\gamma_m$,
  with $\tau_1 = \phi_1^A \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{1}{T_l^+}\prod_{m=l+1}^{k}\gamma_m$

Large Fluctuations & WKB-based Theory

1. Exact expressions: difficult to generalise and analyse
2. Common approach: Fokker-Planck approximation (FPA) $\longrightarrow$ good only for weak selection (diffusive dynamics: tractable)
3. Evolutionary dynamics: generally combination of random fluctuations and non-vanishing selection $\longrightarrow$ Other approach is needed

When there is *metastability* fixation is reached following an "optimal path" obtained by a WKB theory

- ACG: WKB analysis $\Rightarrow$ quasi-stationary distribution (QSD), probability and mean times of fixation (MFTs)
- CG: WKB calculation of the fixation probability

Anti-coordination Games & WKB Theory (I)

In ACGs ($c > a, b > d$), after relaxation time t_r, the system converges to the **metastable state** $n_* = Nx^*$. The latter has a very long mean time of decay, τ, that coincides with the (unconditional) MFT

WKB treatment requires: (1) $\tau \gg t_r$, (2) N and $Nx^* \gg 1$, (3) transition rates of order $\mathscr{O}(1)$ away from the absorbing boundaries

Idea: At time $t \gg t_r$, $P_i(t) \simeq \pi_i e^{-t/\tau}$ for $1 \leq i \leq N-1$ and $P_0(t) \simeq \phi(1 - e^{-t/\tau})$, $P_N(t) \simeq (1-\phi)(1 - e^{-t/\tau})$

From fluxes of probability into the absorbing states:

- Unconditional MFT: $\tau = [T_1^- \pi_1 + T_{N-1}^+ \pi_{N-1}]^{-1}$
- Conditional MFTs: $\tau^A = [T_{N-1}^+ \pi_{N-1}]^{-1}$ and $\tau^B = [T_1^+ \pi_1]^{-1}$
- Fixation probability: $\phi^B = 1 - \phi^A = \phi = T_1^- \pi_1 \tau$

This requires the full QSD π_i. Assuming π_i/τ negligible, the *quasi-stationary master equation* (QSME)

$$0 = T_{i-1}^+ \pi_{i-1} + T_{i+1}^- \pi_{i+1} - [T_i^+ + T_i^-]\pi_i$$

is solved using the **WKB approach**

Anti-coordination Games & WKB Theory (II)

To solve the QSME $T_{i-1}^{+}\pi_{i-1} + T_{i+1}^{-}\pi_{i+1} - [T_i^{+} + T_i^{-}]\pi_i = 0$ away from the boundaries, one uses the WKB Ansatz ($x = i/N$):

$$\pi(x) = \mathscr{A}\, e^{-NS(x) - S_1(x)}$$

$S(x)$ is the "action" and $S_1(x)$ is the amplitude, while $\mathscr{A}$ is a constant. With this ansatz and $\mathscr{T}_{\pm}(x) \equiv T_i^{\pm}$, one obtains to order $\mathscr{O}(N^{-1})$

$$\begin{aligned}
&\pi(x)\left\{\mathscr{T}_{+}(x)\left[e^{S'}\left(1-\frac{1}{2N}S''+\frac{1}{N}S_1'\right)-1\right]\right.\\
&+\mathscr{T}_{-}(x)\left[e^{-S'}\left(1-\frac{1}{2N}S''-\frac{1}{N}S_1'\right)-1\right]\\
&\left.+\frac{1}{N}\left[e^{-S'}\mathscr{T}_{-}'(x)-e^{S'}\mathscr{T}_{+}'(x)\right]\right\}=0.
\end{aligned}$$

To order $\mathscr{O}(1)$, with the "momentum" $p(x) = dS/dx$:
Hamilton-Jacobi equation, $H[x, S'(x)] = 0$, where the Hamiltonian is $H(x,p) = \mathscr{T}_{+}(x)(e^{p} - 1) + \mathscr{T}_{-}(x)(e^{-p} - 1)$

Anti-coordination Games & WKB Theory (III)

To solve the QSME $T_{i-1}^{+}\pi_{i-1} + T_{i+1}^{-}\pi_{i+1} - [T_i^{+} + T_i^{-}]\pi_i = 0$ away from the boundaries, one uses the WKB Ansatz ($x = i/N$):
$$\pi(x) = \mathscr{A}\, e^{-NS(x) - S_1(x)}$$

To order $\mathscr{O}(1)$: zero-energy trajectories of Hamiltonian $H[x, S'(x)]$ yields $p_a(x) = -\ln[\mathscr{T}_+(x)/\mathscr{T}_-(x)] \Rightarrow$ "optimal path" to fixation is $S(x) = -\int^x \ln[\mathscr{T}_+(\xi)/\mathscr{T}_-(\xi)]\, d\xi$

To order $\mathscr{O}(N^{-1})$: $S_1(x)$ by solving a differential equation

Constant $\mathscr{A}$: by Gaussian normalization of the QSD $\pi(x)$ about x^*

- To order $\mathscr{O}(1)$: $S(x) = -\int^x \ln[\mathscr{T}_+(\xi)/\mathscr{T}_-(\xi)]\, d\xi$
- To order $\mathscr{O}(N^{-1})$: $S_1(x) = \frac{1}{2}\ln[\mathscr{T}_+(x)\mathscr{T}_-(x)]$

Near the boundary $x = 0$, expand $\mathscr{T}_\pm(x) \simeq x\mathscr{T}_\pm'(0)$ in the QSME
$\Rightarrow \mathscr{T}_+'(0)(i-1)\pi_{i-1} + \mathscr{T}_-'(0)(i+1)\pi_{i+1} - i[\mathscr{T}_+'(0) + \mathscr{T}_-'(0)]\pi_i = 0$,
yielding $\pi_i = \frac{(R_0^i - 1)\pi_1}{(R_0 - 1)i}$ with $R_0 \equiv \mathscr{T}_+'(0)/\mathscr{T}_-'(0)$.
Similarly with the boundary $x = 1$

Anti-coordination Games & WKB Theory (IV)

WKB solution for the QSD in the bulk (for $N^{-1/2} \ll x \ll 1-N^{-1/2}$):

$$\pi(x) \quad = \quad \mathcal{T}_+(x^*)\sqrt{\frac{S''(x^*)}{2\pi N\,\mathcal{T}_+(x)\mathcal{T}_-(x)}}\,e^{-N[S(x)-S(x^*)]},$$

Near the boundaries, matching the recursive and WKB solutions yields (with $R_1 \equiv \mathcal{T}'_-(1)/\mathcal{T}'_+(1)$):

$$\pi_1 \quad = \quad \sqrt{\frac{NS''(x^*)}{2\pi}}\,\frac{\mathcal{T}_+(x^*)\,(R_0-1)}{\sqrt{\mathcal{T}'_+(0)\mathcal{T}'_-(0)}}\,e^{-N[S(0)-S(x^*)]}$$

$$\pi_{N-1} \quad = \quad \sqrt{\frac{NS''(x^*)}{2\pi}}\,\frac{\mathcal{T}_+(x^*)\,(R_1-1)}{\sqrt{\mathcal{T}'_+(1)\mathcal{T}'_-(1)}}\,e^{-N[S(1)-S(x^*)]}$$

Thus, $\tau = N\left[\mathcal{T}'_-(0)\pi_1 + |\mathcal{T}'_+(1)|\pi_{N-1}\right]^{-1}$ and $\phi = N\mathcal{T}'_-(0)\pi_1\,\tau$

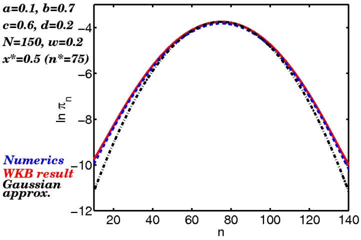
For the fMP:

$$e^{-NS(x)} = [Ax+B(1-x)]^{Nx-N\left(\frac{B}{B-A}\right)}\,[Cx+D(1-x)]^{-Nx-N\left(\frac{D}{C-D}\right)},$$

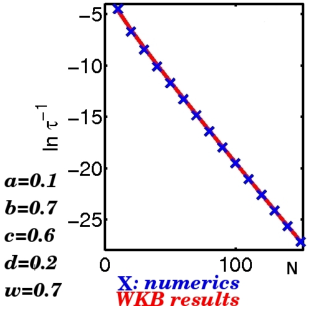
with $A = 1-w+wa$, $B = 1-w+wb$, $C = 1-w+wc$, and $D = 1-w+wd$.

Anti-coordination Games & WKB Theory: Results (I)

- *QSD:* bell-shaped function peaked at x^*. Systematic non-Gaussian effects near the tails, well accounted by the WKB approach



- *MFTs:* exponential dependence on the population size ($Nw \gg 1$), $\tau \propto N^{1/2} e^{N(\Sigma - S(x^*))}$, where $\Sigma \equiv \min(S(0), S(1))$
For "small" selection intensity, the MFTs grow exponentially as $\tau^A \sim N^{1/2} e^{Nw(a-c)^2/[2(c-a+b-d)]}$, $\tau^B \sim N^{1/2} e^{Nw(b-d)^2/[2(c-a+b-d)]}$, and $\tau = \tau^A \tau^B / (\tau^A + \tau^B)$

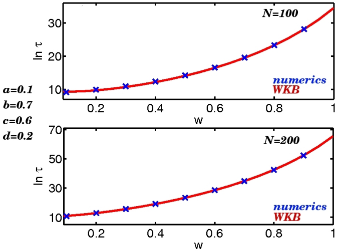


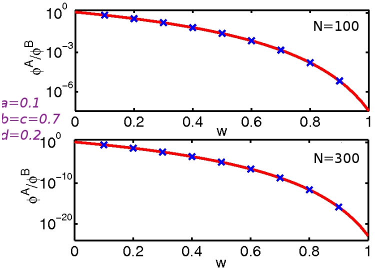
Anti-coordination Games & WKB Theory: Results (II)

- For $Nw \gg 1$, the MFTS increase monotonically with w, faster than exponentially
- *Fixation probability:* When $w = 0$, $\phi^A/\phi^B = x/(1-x)$ depends on initial fraction of mutants. No longer the case when $w > 0$ (selection):

$$\frac{\phi^A}{\phi^B} \to \sqrt{\frac{BD}{AC}} \left(\frac{C-A}{B-D} \right) \times \frac{B^{N\left(\frac{B}{B-A}\right)} D^{N\left(\frac{D}{C-D}\right)}}{A^{N\left(\frac{A}{B-A}\right)} C^{N\left(\frac{C}{C-D}\right)}}.$$

$\Rightarrow$ Exponential dependence: ϕ_A/ϕ_B is exponentially large/small when $N \gg 1$, except for $w \ll 1$





Coordination Games & WKB Theory (I)

In CGs, $i=0$ and $i=N$ are attractors and x^* is unstable.
Starting with i A individuals, what is the probability ϕ_i^A that species A fixates the system?

ϕ_i^A is a cumulative distribution function obeying

$$T_i^+ \phi_{i+1}^A + T_i^- \phi_{i-1}^A - [T_i^+ + T_i^-]\phi_i^A = 0, \quad \text{with} \quad \phi_0^A = 0, \phi_N^A = 1$$

Convenient to work with $\mathscr{P}_i = \phi_{i+1}^A - \phi_i^A$ such that $\phi_i^A = \sum_{m=0}^{i-1} \mathscr{P}_i$.
When $N \gg 1$, $\mathscr{P}_i = \mathscr{P}(x)$ and the latter obeys

$$\mathscr{T}_+(x)\mathscr{P}(x) - \mathscr{T}_-(x)\mathscr{P}(x - N^{-1}) = 0\,.$$

Eq. solved by the WKB ansatz

$$\mathscr{P}(x) = \mathscr{A}_{\mathrm{CG}}\, e^{-N\mathscr{S}(x) - \mathscr{S}_1(x)}$$

As for ACGs, this leads to $\mathscr{S}(x) = -S(x) = \int^x \ln[\mathscr{T}_+(\xi)/\mathscr{T}_-(\xi)]d\xi$
and $\mathscr{S}_1(x) = -\frac{1}{2}\ln[\mathscr{T}_-(x)/\mathscr{T}_+(x)]$

Coordination Games & WKB Theory (II)

One therefore obtains:

$$\mathscr{P}(x) = \sqrt{\frac{|S''(x^*)|}{2\pi N} \frac{\mathscr{T}_-(x)}{\mathscr{T}_+(x)}} e^{N[S(x)-S(x^*)]}$$

To leading order when $N^{-1} \ll w \ll 1$:

$$\phi^A(x) \simeq \sqrt{\frac{N|S''(x^*)|}{2\pi}} \int_0^x dy\; e^{N[S(y)-S(x^*)]}$$

Criterion of evolutionary stability (of “wild species” B): $\phi^A(x) < x$, for $x \ll 1 \Rightarrow$ *relevant to consider the limit* $x \ll x^*$ *with finite* w

Approximation for $N^{-1} \ll x \ll 1$ (where $S'(x) > 0$) and $Nw \gg 1$:

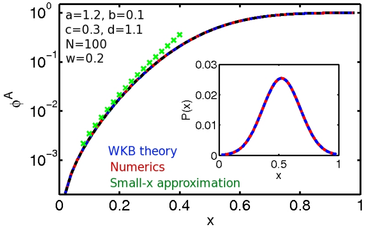
$$\phi^A(x) \simeq \frac{\mathscr{P}(x)}{e^{S'(x)} - 1}$$

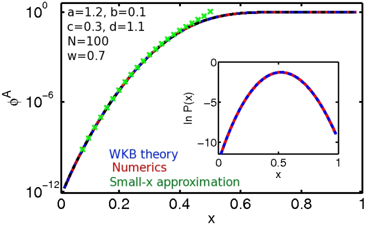
As $\phi^A(x)$ is exponentially small, $\phi^A(x) < x$ and the *selection opposes replacement of B's by A's $\Rightarrow$ the state with all B's is always evolutionary stable when w is finite*

Coordination Games & WKB Theory: Results (I)

- *Fixation probability:* $\phi^A(x) \to 1$ when $x \to 1$, with $\phi^A(x^*) = 1/2$, and is exponentially small $\phi^A \to 0$ when $x \to 0$. "Jump" from finite to exponentially small value of ϕ^A becomes steeper when w increases

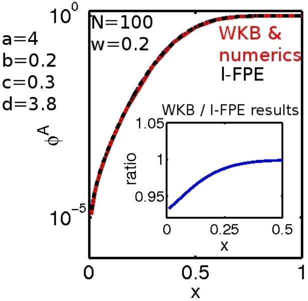
- *Behaviour for $x \ll 1$:* When w is finite, $N \gg 1$ and $x \ll 1$, the exponentially small value of $\phi^A(x)$ is approximated by $\phi^A(x) \simeq \frac{\mathscr{P}(x)}{e^{S'(x)}-1}$

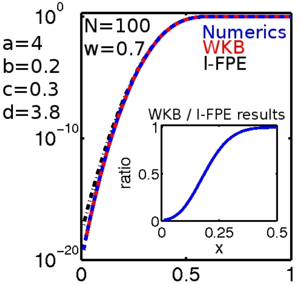




Coordination Games & WKB Theory: Results (II)

Comparison with Fokker-Planck:
Fixation probability often approximated using the Fokker-Planck Equation (FPE).
This diffusion approx. yields
$\phi^A_{\mathrm{FPE}}(x) = \frac{\Psi(x)}{\Psi(1)}$ with
$\Psi(x) = \int_0^x e^{-\int_0^y \Theta_{\mathrm{FPE}}(z)dz} dy$ and
$\Theta_{\mathrm{FPE}}(x) = 2N \left(\frac{\mathcal{T}_+(x) - \mathcal{T}_-(x)}{\mathcal{T}_+(x) + \mathcal{T}_-(x)} \right)$
Often used within linear noise approx., where $\phi^A_{\ell\mathrm{FPE}}(x) = \frac{\Psi(x)}{\Psi(1)}$ with
$\Theta_{\ell\mathrm{FPE}}(x) = 2N(x - x^*) \left(\frac{\mathcal{T}'_+(x^*) - \mathcal{T}'_-(x^*)}{\mathcal{T}_+(x^*) + \mathcal{T}_-(x^*)} \right)$ instead of $\Theta_{\mathrm{FPE}}(x)$
To leading order, WKB result can be rewritten as $\phi^A(x) \simeq \frac{\Psi(x)}{\Psi(1)}$, with
$\Theta(x) = N \ln[\mathcal{T}_+(x)/\mathcal{T}_-(x)]$ instead of $\Theta_{\mathrm{FPE}}(x)$

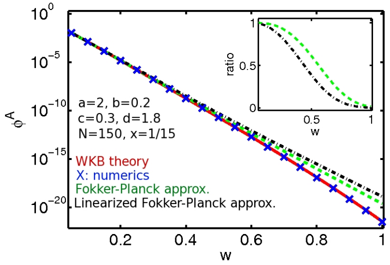


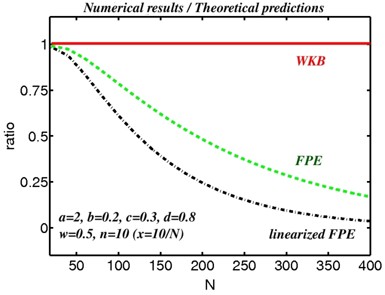


Coordination Games & WKB Theory: Results (III)

- Excellent agreement between numerics and WKB results for any x and $w > 0$
- FPE in good agreement with WKB and numerics when w is small (and/or $x \simeq x^*$).
- However, exponentially large deviations when w and N are raised and x deviates from x^*

As $\Theta(x) - \Theta_{\rm FPE}(x) \sim N(w\Delta x)^3$ and $\Theta(x) - \Theta_{\ell{\rm FPE}}(x) \sim N(w\Delta x)^2$ ($\Delta x = x - x^*$) $\Rightarrow$ Exponentially large errors in $\phi^A_{\rm FPE}(x)$ and $\phi^A_{\ell{\rm FPE}}(x)$ when $w \gtrsim N^{-1/3}$ and $w \gtrsim N^{-1/2}$, resp.





Outlook & Conclusion

Presentation of a WKB-based approach allowing to compute large-fluctuation-induced phenomena in evolutionary processes

- Account naturally for large fluctuations and non-Gaussian behaviour
- Application to a class of evolutionary games modelling:*combined effect of stochasticity and non-linearity (selection)?*
- Metastability in Anti-Coordination Games: calculation of the QSD, ϕ and MFTs $\Rightarrow$ when $w > 0$ and $N \gg 1$, non-Gaussian QSD and MFTs grow exponentially with N
- ϕ^A in Coordination Games: asymptotically exact results for $\phi^A \Rightarrow$ exponentially small when $w > 0$ and $N \gg 1$
- Comparison with Fokker-Planck: FPE is only accurate around x^* and for vanishingly small selection strength w
- Generalization to other rules/interactions
- Method can be adapted to study non-exactly solvable problems (e.g. 3×3 games)