Non-local Models for Eco-Evolutionary Processes

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Eco-Evolutionary Processes

Multiscale Modeling

Eco-evolutionary problems necessary bridge multiple scales. Evolution acts on the scale of the population and Ecological processes are closer to the individual scale.

1. Without spatial structure: **Mean Field Approximation**
   The individual scale and the population scale are unified
2. With spatial structure: **PDE Approximation**
   The population scale is unattainable from the individual scale

Non-local models and the intermediate scale

Non-local models offer an "intermediate scale" when the scale of individual interactions are comparable to but separate from the population.

General non-local model

Consider a game theoretic process where every individual $x \in \Omega$ interacts with other individuals in the environment according to an integrable kernel $K(x, y) \in C_0^b(L^1; \Omega)$.

- if the population **State** is given as $u(x)$
- and the individual **Objective** is given as $w[u](x) = \int_\Omega K(x, u) f(u(x), u(y)) dy$
- then a population **Evolution** can be constructed

$$\frac{\partial}{\partial t} u(x, t) = \int_\Omega K(x, y) \partial_1 f(u(x, t), u(y, t))$$

Non-local models and the intermediate scale

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Non-local example

Consider a coordination game. Each player is trying to minimize the distance between their strategy and the strategies of the players in their vicinity.

- the population **State** is the strategy profile $u(x)$
- the individual **Objective** is the payoff function $w[u](x) = \frac{-1}{2} \int_\Omega K(x,y)(u(x) - u(y))^2 dy$
- so the population **Evolution** equation under MBR is

$$\frac{\partial}{\partial t} u(x,t) = \int_\Omega K(x,y)(u(y,t) - u(x,t))dy = \Delta_K u$$

Limiting behavior of Non-local models

These non-local models bridge the gap between the unstructured and structured continuous models

Unstructured Limit

If $K(x, y) \to \chi_\Omega(y)$ we are practically using the **Mean Field approximation**

$$\frac{\partial}{\partial t} u(x, t) = C(u(x) - \bar{u})$$

Every individual is reacting to the population mean

Zero Horizon Limit

If $K(x, y) \to \delta_x(y)$ We recover a **PDE approximation**

$$\frac{\partial}{\partial t} u(x, t) = \Delta u$$

Every individual is reacting to a vanishingly small neighborhood

Why does this matter?

When models are naturally formulated in the intermediate scale, these limits give us access to many helpful results.

Discrete Strategy Coordination Example

Consider players $x \in \mathbb{R}^n$ choosing a strategy from the set $\{A, B\}$.

1. The population **State** is given as $u : \mathbb{R}^n \to \{A, B\}$
2. The individual **Objective** is to maximize

$$w[u](x) = \int_{\mathbb{R}^n} K(x, y)\langle u(x), u(y)\rangle dy$$

   where $\langle a, b\rangle$ is 1 if $a = b$ and 0 otherwise
3. So we can construct the population **Evolution** in discrete time.

$$u_{t+1}(x) = \text{argmax}_{c\in\{A,B\}} \int_{\mathbb{R}^n} K(x, y)\langle c, u_t(y)\rangle dy \qquad (1)$$

Myopic-Best-Response and the Mean Curvature Flow

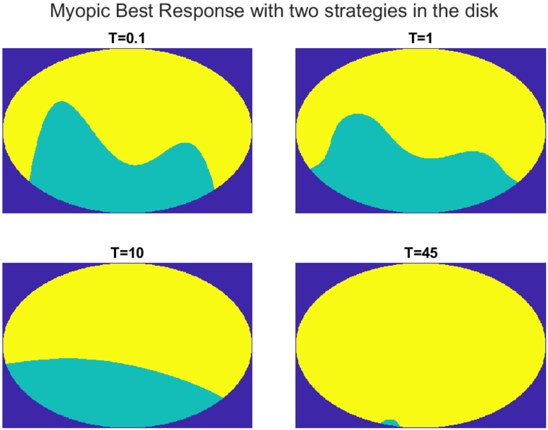
The zero horizon limit relates this problem which is naturally formulated in the intermediate scale to a well understood problem from differential geometry.

MBR Recapitulates MCF (M., Mengesha 2026)

Consider an initial strategy profile $u_0 : \mathbb{R}^n \to C$ is given as $U_0^2 = (U_0^1)^c$ so that $\partial U_0^1 = \partial U_0^2$. Let payoffs be given as in (1) with the kernel $K_\epsilon(x, y) = (4\pi\epsilon)^{\frac{-n}{2}} e^{\frac{-|x-y|^2}{4\epsilon}}$. Under the Myopic Best Response process with time step $\Delta t = \epsilon^2$, the strategic boundary ∂U^1 will move according to mean curvature flow in the limit as $\epsilon \to 0$.

Myopic Best Response and the free boundary Mean Curvature Flow

Now we seek to show that, in a bounded domain, MBR recapitulates the mean curvature flow with free boundary



Why else does this matter?

These models are still helpful even when the Zero-Horizon limit is inappropriate.

Non-local Structured Replicator Equation

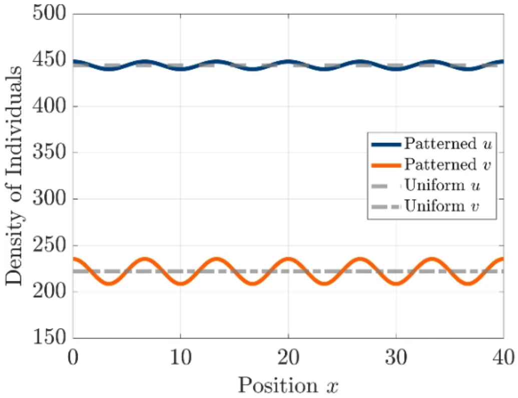
Consider a normal form game with a payoff matrix $A \in \mathbb{R}^{m \times m}$ and with players in Ω.

- The population **State** is $u : \Omega \to \Delta^{m-1}$
- The individual **objective** is $w[u](x) = \int_\Omega K(x,y) u(x)^\intercal A u(y) dy$
- Then the population **Evolution** equation is given through the replicator equation

$$\frac{d}{dt} u_i(x,t) = u_i(\hat{e}_i - u)^\intercal \left(\int_\Omega K(x,y) A u(y) dy \right) \quad (2)$$

Hawk-Dove pattern Formation

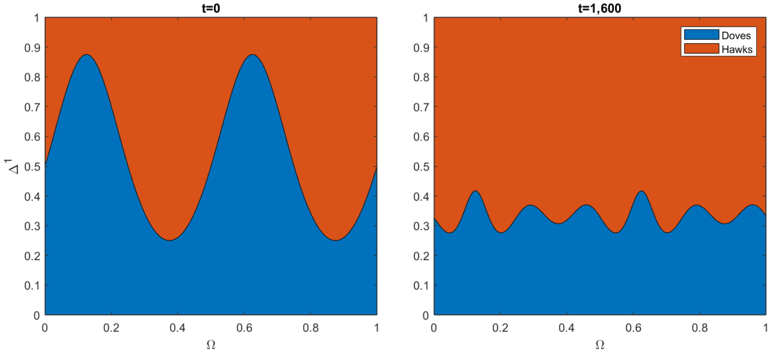
Hawk-Dove PDE Pattern Formation (Yao, Xu, and Cooney 2026)



Yao, T., Xu, C. & Cooney, D.B. Pattern Formation in Agent-Based and PDE Models for Evolutionary Games with Payoff-Driven Motion. Bull Math Biol (2026).

Hawk-Dove pattern Formation

Hawk-Dove Non-local Pattern Formation

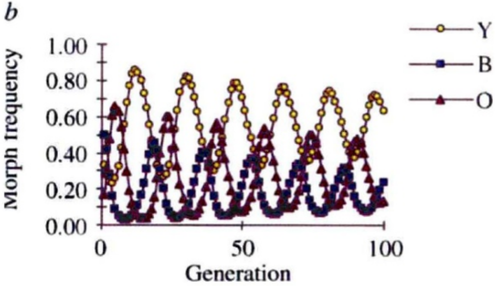


The non-local model captures the same pattern formation behavior

Cyclic dominance

Rock Paper Scissors Mean Field Model (Sinervo and Lively 1996)

Consider side blotched lizards[a]. Males have phenotypes Y,B, and O. Females prefer O over B, Y over O, and B over Y.

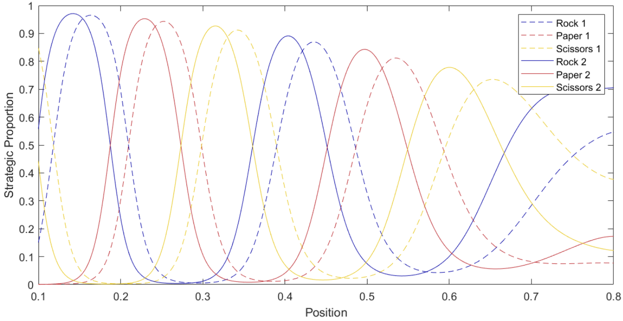


Sinervo, B., Lively, C. The rock–paper–scissors game and the evolution of alternative male strategies. Nature (1996)

Cyclic dominance

Rock Paper Scissors Non-local Model

The temporal pattern is present in the non-local model with the addition of a spatial component



Optimization and Stability

Optimization and Stability analysis can be done after a spatial Fourier Transform.

Coordination Stability (Fefferman, M., Mengesha 2026)

For a coordination game, $A = I$, $u^\star = [\frac{1}{m}, \frac{1}{m}, ..., \frac{1}{m}]$ is a Nash equilibrium but not an ESS because it is *spectrally unstable*. We can see this with the standard linearization about $u^\star$ through the Gâteaux derivative

$$DF\phi = \frac{1}{m}K * \phi$$

This means that we can examine spectral stability easily in the Fourier space

$$\mathcal{F}[DF\phi] = \mathcal{F}[\frac{1}{3}K * \phi] = \frac{1}{3}\hat{K} \cdot \hat{\phi} = \lambda\hat{\phi} = \lambda\mathcal{F}[\phi]$$

$\lambda \in Im(\hat{K})$ and so if K is a Gaussian kernel then $\lambda > 0$ and $u^\star$ is spectrally unstable.

Why does this matter?

Eco-evolutionary processes

Spatially explicit Eco-evolutionary models demand thoughtful consideration of the scale of the individual and the population

Some Eco-evolutionary processes are more naturally defined in the non-local setting than the PDE limit.

- Coordination in arbitrarily large domains

For some Eco-evolutionary processes the PDE limit is inappropriate, especially when individuals are interacting or competing at a distance.

- Hawk-dove pattern formation
- Circular dominance in space
- Coordination in small domains

Thank you

Questions?

For publications and code, visit my website

jmcalis.github.io