ECOLOGY AND PATTERN FORMATION ON LARGE METAPOPULATION GRAPHS

Daniel Cooney

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Summary

In this presentation, we discuss reaction-diffusion models for predator-prey dynamics in patch-structured populations with between-patch dispersal takes place on a network. Using graphons (or graph limits), we derive a continuum analogue of patch reaction-diffusion models describing the role of dispersal with non-local connectivity schemes like small-world or power law networks. We show that the threshold diffusivity needed for the onset of Turing pattern formation in terms of eigenvalues of the dispersal kernel, so the metapopulation dynamics are intricately linked to the topology of the dispersal network.

Background

Spatially-explicit modeling plays an important role in understanding ecological dynamics, Reaction-diffusion models on discrete patches have a long history in the ecology literature. A continuum model with a local diffusion operator was introduced by Segel and Jackson, demonstrating Turing instability in predator-prey models with dispersal [6]. Of particular interest is the question of bistability of patterned and uniform states, which was demonstrated in a two-patch model by Segel and Levin [3, 7].

Model

Segel and Levin studied a patch model for predator-prey dynamics with diffusion along an arbitrary network with adjacency matrix W_{ij} connecting the patches.

$$\frac{dV_i(t)}{dt} = V_i(t)\left(\alpha - \beta E_i(t) - \gamma V_i(t)\right) + D_V \sum_{i=1}^{N} W_{ij}\left[V_j(t) - V_i(t)\right] \tag{1a}$$

$$\frac{dE_i(t)}{dt} = E_i(t)\left(-\delta + \eta V_i(t) - \theta E_i(t)\right) + D_E \sum_{i=1}^{N} W_{ij}\left[E_j(t) - E_i(t)\right] \tag{1b}$$

where E_i and V_i are the predator and prey density at patch i, β and θ can either be positive (self-inhibition) or negative (self-activation / Allee effect), and the other parameters are non-negative.

We now consider a continuum analogue of this reaction-diffusion system, with patches indexed by $x \in [0,1]$. Following the approach of Medvedev [4, 5], Kuehn and Throm [2] and Bellière [1], we introduce $W(x,y)$ as the adjacency function for our graphon describing connectivity between any pair of patches x and y.

$$\frac{\partial V(x,t)}{\partial t} = V(x,t)\left(\alpha - \beta E(x,t) - \gamma V(x,t)\right) + D_V \int_0^1 W(x,y)\left[V(y,t) - V(x,t)\right] dy \tag{2a}$$

$$\frac{\partial E(x,t)}{\partial t} = E(x,t)\left(-\delta + \eta V(x,t) - \theta E(x,t)\right) + D_E \int_0^1 W(x,y)\left[E(y,t) - E(x,t)\right] dy \tag{2b}$$

where $E(x,t)$ and $V(x,t)$ represent the densities of the predator and prey and we name the non-local operator $\Delta_W u(x) = \int_0^1 W(x,y)\left(u(y) - u(x)\right) dy$ the graphon Laplacian as it serves as the diffusion operator for dispersal along the graphon.

If the adjacency function depends only on the difference in location $W(x,y) = J(y-x)$, then the eigenvalues of the graphon Laplacian can be written as

$$\lambda_W^k = \hat{J}_k - \hat{J}_0 \tag{3}$$

where $\hat{f}$ is the Fourier transform of f for wavenumber k.

Small-World Graphons

We consider the Small-World graphon considered in recent coupled oscillator models [5, 4, 2]. This model assumes a radius r of near neighbors and a rewiring parameter p, resulting in an adjacency function of

$$W(x,y) = \begin{cases} 1-p & : d(|x-y|) \le r \\ p & : d(|x-y|) > r \end{cases}$$

The small-world graphon Laplacian has negative eigenvalues given by the formula

$$\lambda_W^k = \left(\frac{1-2p}{\pi k}\right) \sin\left(2\pi k r\right) - 2r - p + 4rp$$

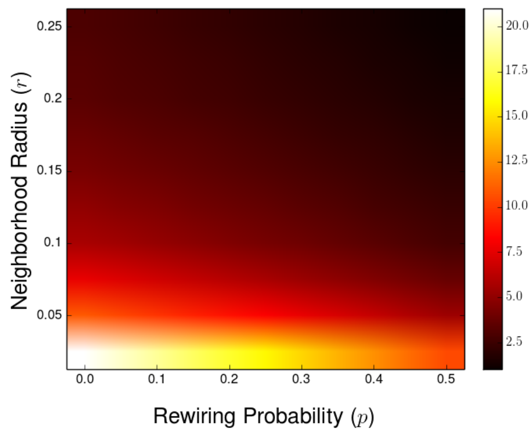

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Figure 1: Largest magnitude eigenvalue of small-world graphon Laplacian for various r and p.

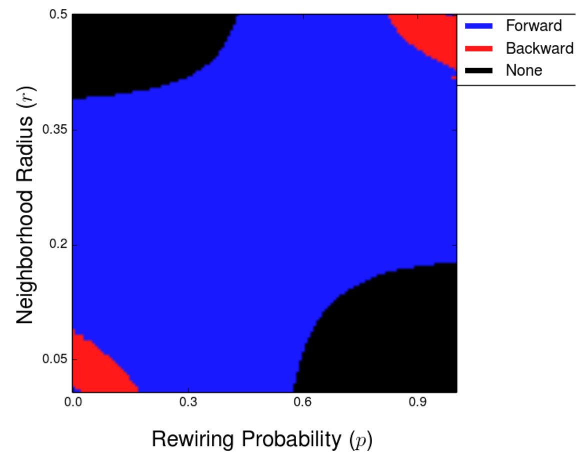

Figure 2: Type of pattern forming bifurcation predicted by Equation 4 for given r and p: forward (blue), backward (red), or none (black).

Spatially-Uniform Steady State

To understand the spatial dynamics of the predator-prey system, we first consider the spatially-uniform steady state solution correspond to steady state solutions of the reaction terms

$$V(x,t) \equiv \overline{V} = \frac{\alpha\theta + \delta\gamma}{\beta\theta + \eta\gamma} \;\;,\;\; E(x,t) \equiv \overline{E} = \frac{\alpha\eta - \beta\delta}{\beta\theta + \eta\gamma}$$

If $\beta, \theta > 0$, we use a Lyapunov functional to show that uniform steady state is globally stable, so pattern formation is impossible in the absence of an Allee effect.

Turing Instability

If there is an Allee effect in one species but not the other, we can use a linearized stability analysis to show instability of the uniform steady state when

$$\left(D_V \lambda_W^k - \beta\overline{V}\right)\left(D_E \lambda_W^k - \theta\overline{E}\right) + \eta\gamma\overline{EV} < 0$$

If $\beta < 0$ and $D_V = 0$, this condition becomes

$$D_E > \frac{(\beta\theta + \eta\gamma)\,\overline{E}}{\beta \min_k\{\lambda_W^k\}}$$

We have learned that we need sufficient dispersal rate of predators to cause pattern formation, and that this threshold depends on the graphon connectivity through the eigenvalues of $W(x,y)$.

Weakly Nonlinear Stability Analysis

To consider the stability of patterns near the Turing instability threshold, we can use a perturbation expansion to derive a Stuart-Landau equation for the amplitude $A(T)$ of the pattern-forming solution

$$\frac{dA(T)}{dT} = \mathcal{B}A(T) + \mathcal{C}A(T)^3 \tag{4}$$

For the Small-World graphon, we use this to classify whether the Turing instability arises as a forward (supercritical) or backward (subcritical) pitchfork bifurcation for different values of r and p.

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