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Spatio-temporal pattern formation in predator-prey systems with fitness taxis

Irene T. Heilmann^{a,b}, Uffe Høgsbro Thygesen^{a,b}, Mads Peter Sørensen^{*,a}

^a Department of Applied Mathematics and Computer Science, Technical University of Denmark, Denmark ^b Center for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Denmark

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ABSTRACT

We pose a spatial predator-prey model in which the movement of animals is not purely diffusive, but also contains a drift term in the direction of higher specific growth rates. We refer to this as fitness taxis. We conduct a linear stability analysis of the resulting coupled reaction-advection-diffusion equations and derive conditions under which spatial patterns form. We find that for some parameters the problem is ill posed and short waves grow with unbounded speeds. To eliminate this, we introduce spatial kernels in the model, yielding coupled integro-differential equations, and conduct a similar stability analysis for this system. Through numerical simulation, we find that a variety of patterns can emerge, including stationary spatial patterns, standing and travelling waves, and seemingly chaotic spatio-temporal patterns. We argue that fitness taxis represents a simple and generic extension of diffusive motion, is ecologically plausible, and provides an alternative mechanism for formation of patterns in spatially explicit ecosystem models, with emphasis on non-stationary spatio-temporal dynamics.

1. Introduction

Most populations in nature are not homogeneously distributed in space, but cluster together in patterns of different shapes. These patterns can arise as a response to heterogeneous environments (Cobbold et al., 2015), but they can also emerge in homogeneous environments through self–organization. For example, young mussel beds in a tidal area (van de Koppel et al., 2005) display stripe–like patterns, even if there are no prior features in the habitat within the beds that can explain why mussels exist in the stripes but not between them. The mechanism for this pattern formation is mutual protection against wave disturbance, giving positive feedback on short spatial scales, combined with competition between mussels for algal resources, giving negative feedback on longer scales (Martínez-García et al., 2015). The mechanism is therefore an example of scale-dependent feedback, a general principle behind pattern formation (Rietkerk and van de Koppel, 2008).

When patterns emerge in homogeneous environments, they can be seen as an inherent property of the system, as the example of mussel beds demonstrate. Several mechanisms, both generic and specific, have been proposed for pattern formation in homogeneous landscapes. For example, Young et al. (2001) considered the clustering that emerges in spatial birth/death processes, while Rietkerk et al. (2002) analyzed the vegetation patterns that may emerge in arid landscapes when the models may be either individual-based or population-based, and in some cases it is possible to establish the connection between the two levels (Martínez-García et al., 2015). One archetypal mechanism for self-organized patterns is the Turing diffusion-driven instability in partial differential equations of reaction-diffusion type. Turing (1952) originally conceived this as a mechanism for pattern formation in chemical systems, specifically explaining morphogenesis. The classical Turing patterns assume stable reaction dynamics in the absence of spatial effects, while the feedback between the reaction dynamics and transport gives rise to an instability which ultimately leads to stationary spatial patterns. The Turing mechanism has also been considered in trophic systems, first as a hypothesized mechanism for patchiness in plankton communities (Levin and Segel, 1976; Malchow, 1993). In such models, the Turing diffusion-driven instability may appear in conjunction with a Hopf bifurcation in the reaction dynamics (e.g., Banerjee and Petrovskii, 2011), and the combination of these two instabilities may give rise to large variety of spatio-temporal patterns, including irregular chaotic type patterns (Huang et al., 2017).

vegetation simulates the absorption of surface water in the soil. Spatiotemporal patterns may emerge when diffusion modulates unstable local

population dynamics (Petrovskii and Malchow, 1999). Pattern-forming

While the Turing mechanism has a prominent role in the literature on spatial pattern formation in ecological models, its relevance for

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^{*} Corresponding author. E-mail address: mpso@dtu.dk (M.P. Sørensen).

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predator-prey systems can be questioned from an evolutionary perspective. In Turing models, the diffusion term, which corresponds to random unbiased movements of individuals, always leads to a net migration of individuals from regions with higher densities to regions with lower densities, and this transport is crucial for maintaining the stationary spatial patterns. When stationary Turing patterns have formed, the regions with high densities also have positive surplus production. This surplus production is then transported by diffusion to regions with low densities, where the surplus production is negative. This state cannot be evolutionary stable: mutants with lower diffusivity would be able to invade: an observation that was made in a single-species context by Hastings (1983). While dispersal may have other advantages such as avoidance of inbreeding (Gandon, 1999), it appears implausible that animals should accept diffusion to move them from regions with positive production to regions with negative production. A fair generalizing statement is that the more data becomes available on the movements of a particular organism, the less plausible is the hypothesis of pure diffusion (Turchin, 1998), and even organisms as primitive as bacteria and algae are capable of directing their motion towards more attractive regions (Brown and Berg, 1974; Eggersdorfer and Häder, 1991; Kay et al., 2008). For predators searching for heterogeneously distributed prey, simple postulates about the microscale behavior may lead to a directed motion on the macroscale towards higher prey densities (Kareiva and Odell, 1987). From the point of view of pattern formation, this raises the question if patterns can emerge in models where such directed motion is included. One approach to this question involves cross-diffusion terms, modeling pursuit-evasion movements in predator-prey models (Biktashev et al., 2004; Tsyganov et al., 2004), which may lead to a quasi-soliton type of wave that is not seen in reaction-diffusion systems. Regarding the possibility of pattern formation in such predator-prey models, a taxis of predators towards higher prey concentrations has been shown not to destabilize the uniform steady state (Ainseba et al., 2008; Lee et al., 2009; Wang et al., 2015).

The assumption behind the present paper is that the movements of predators and prey are neither completely random nor a response to just the other species, as in pursuit and evasion, but also a response to the densities of conspecifics. We propose the notion of fitness taxis as a conceptually simple and reasonably generic movement model. Here, we take fitness taxis to mean motion in the direction of the spatial gradient of the specific growth rate, modeled by including an advective term in the flux of organisms. While this model is not intended to accurately describe actual movements of specific organisms, it appears to be a useful first generalization of pure diffusion models. Our model thus continues in the direction set out by Cosner (2005), who considered the evolutionary stability of dispersal strategies and in particular taxis terms that relate to the specific growth rate. A similar reasoning let Armsworth and Roughgarden (2005) to consider a corresponding twopatch model. Later Cantrell et al. (2008) used a similar advective term in a model of a single species and investigated the effect of heterogeneous environment, and (Cantrell et al... 2013: Jonathan T. Rowell, 2010) extended to two competing populations. The overarching question initiating our work is if and how spatial and spatiotemporal patterns may form in predator-prey models, when each species performs fitness taxis. A similar question was addressed by Abrams (2007) in the context of a two-patch system with three trophic levels; there, spatiotemporal patterns were found.

Our predator-prey model consists of two coupled reaction-advection-diffusion equations and the initial model is local, corresponding to predators only consuming prey which are at the same location as the predator. It turns out that for some parameter combinations, this system is not well posed; the growth rate of spatial disturbances diverges as the wave number diverges. We circumvent this problem by allowing the predator to consume prey within a specified spatial range, introducing a spatial kernel which describes the rate with which predators at one location encounter prey at a different location. Thus, the growth rate of predators depend on an integral over space of the prey densities, and the mortality of prey depend on a similar integral of predator densities. Similar non-local models have been studied previously (Banerjee and Volpert, 2016a; 2016b; Grindrod, 1988; Malchow et al., 2008). The integral operator effectively smooths out small-scale fluctuations in densities and thus renders the system wellposed, as has been shown for a single-species model (Cantrell et al., 2008; Cosner and Winkler, 2014).

The outline of the manuscript is as follows: First, we pose a local predator–prey model with fitness taxis, and conduct a stability analysis of the spatially uniform equilibrium solution. Next, we pose the nonlocal model based on a spatial kernel and conduct a similar stability analysis. Further, we perform numerical simulations of patterns in one spatial dimension. Finally, we offer some conclusions.

2. Fitness taxis in a generic predator-prey model

We study a predator-prey system where animals move both randomly and towards higher values of their individual fitness, quantified through their specific growth rate. The model is

$$\frac{\partial u}{\partial t} = f(u, v)u - \nabla \cdot (u \gamma_u \nabla f(u, v)) + D_u \nabla^2 u, \qquad (1a)$$

$$\frac{\partial v}{\partial t} = g(u, v)v - \nabla \cdot (v \gamma_v \nabla g(u, v)) + D_v \nabla^2 v$$
(1b)

for the prey density u(x, t) and the predator density v(x, t) in space $x \in \Omega$ for time t > 0. Here, the functions f and g are the specific growth rate of prey and predators, respectively, while D_{uv} , $D_v \ge 0$ are the diffusion coefficients. The second term in each equation is what we term fitness taxis: The animals move up the gradients of f and g, respectively, with the taxis coefficients γ_{uv} , $\gamma_v \ge 0$ expressing the magnitude of the effect. Since the fitness f(u, v) of the prey (say) depends on the local density of both prey u and predators v, the directed movement of the prey will be affected by gradients in both the prey and predator population. For the analysis of the model, we consider the one-dimensional space domain $x \in \Omega = \mathbb{R}$.

3. Linear stability analysis

Pattern formation in the system (1) may be investigated with a standard linear stability analysis (Cross and Hohenberg, 1993; Segel and Jackson, 1972) of a non-trivial equilibrium solution $u(x, t) = u^*$, $v(x, t) = v^*$, where $u^* > 0$, $v^* > 0$, and $f(u^*, v^*) = g(u^*, v^*) = 0$.

Linearization of the system (1) gives

$$\frac{\partial u}{\partial t} = u^* (f_u^* \tilde{u} + f_v^* \tilde{v}) - \gamma_u u^* (f_u^* \nabla^2 \tilde{u} + f_v^* \nabla^2 \tilde{v}) + D_u \nabla^2 \tilde{u} , \qquad (2a)$$

$$\frac{\partial \tilde{v}}{\partial t} = v^* (g_u^* \tilde{u} + g_v^* \tilde{v}) - \gamma_v v^* (g_u^* \nabla^2 \tilde{u} + g_v^* \nabla^2 \tilde{v}) + D_v \nabla^2 \tilde{v} .$$
(2b)

where $\tilde{u}(x, t)$, $\tilde{v}(x, t)$ are small perturbations from the equilibrium (u^*, v^*) , and $f_u^* := \frac{\partial f}{\partial u}(u^*, v^*)$, etc. For a harmonic perturbation with wave number k, the dynamics are governed by a stability matrix $\boldsymbol{M}(k)$ given by

$$\boldsymbol{M}(k) = \boldsymbol{A} + k^2 \boldsymbol{T} - k^2 \boldsymbol{D} \quad . \tag{3}$$

Here the matrices A, T and D describe population dynamics, fitness taxis and diffusion, respectively. Note that both taxis and diffusion scale with the wave number k squared. The matrices are given by

$$\boldsymbol{A} = \begin{pmatrix} u^{*}f_{u}^{*} & u^{*}f_{v}^{*} \\ v^{*}g_{u}^{*} & v^{*}g_{v}^{*} \end{pmatrix}, \quad \boldsymbol{T} = \begin{pmatrix} \gamma_{u}u^{*}f_{u}^{*} & \gamma_{u}u^{*}f_{v}^{*} \\ \gamma_{v}v^{*}g_{u}^{*} & \gamma_{v}v^{*}g_{v}^{*} \end{pmatrix}, \quad \boldsymbol{D} = \begin{pmatrix} D_{u} & 0 \\ 0 & D_{v} \end{pmatrix}.$$
(4)

Notice the relation $T = \text{diag}(\gamma_u, \gamma_v)A$ between the matrices describing population dynamics and fitness taxis. We are interested in pattern formation induced by movement, i.e. the existence of a wave number $k \ge 0$ such that M(k) is unstable, while the population dynamics given

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