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Diffusion-driven instabilities and emerging spatial patterns in patchy landscapes

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ABSTRACT

Spatial variation in population densities across a landscape is a feature of many ecological systems, from self-organised patterns on mussel beds to spatially restricted insect outbreaks. It occurs as a result of environmental variation in abiotic factors and/or biotic factors structuring the spatial distribution of populations. However the ways in which abiotic and biotic factors interact to determine the existence and nature of spatial patterns in population density remain poorly understood. Here we present a new approach to studying this question by analysing a predator–prey patch-model in a heterogeneous landscape. We use analytical and numerical methods originally developed for studying nearest-neighbour (juxtacrine) signalling in epithelia to explore whether and under which conditions patterns emerge. We find that abiotic and biotic factors interact to promote pattern formation. In fact, we find a rich and highly complex array of coexisting stable patterns, located within an enormous number of unstable patterns. Our simulation results indicate that many of the stable patterns have appreciable basins of attraction, making them significant in applications. We are able to identify mechanisms for these patterns based on the classical ideas of long-range inhibition and short-range activation, whereby landscape heterogeneity can modulate the spatial scales at which these processes operate to structure the populations.

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1. Introduction

One of the great challenges in ecology is to uncover and explain the mechanisms that lead to observed spatial patterns of species distributions. For many species, abundance varies spatially as individuals track environmental variation, such as abiotic factors or resources, across a landscape (Leroux et al., 2013; Ergon et al., 2001). Alternatively, spatial distribution patterns can arise in the absence of external forces, due to the pattern-formation mechanism of short-range activation and long-range inhibition (Zelnik et al., 2015; Rietkerk et al., 2002; Wang et al., 2010b), or due to density-dependent dispersal leading to phase separation (Liu et al., 2013). These two mechanisms typically create stationary patterns, although moving patterns occur in the presence of advection (Siero et al., 2015; Perumpanani et al., 1995; Sato and Iwasa, 1993). Temporally varying patterns may also arise from asynchronous cycling caused by invasions or obstacles (Sherratt et al., 1995,

2002; Petrovskii and Malchow, 2001). The best-studied of these processes is the Turing mechanism, and ecologists have recently identified appropriate long-range inhibition in a number of natural ecosystems and documented corresponding patterns (Rietkerk and van de Koppel, 2008; Deblauwe et al., 2008; Meron, 2012). Our work is concerned with the interplay between extrinsic and intrinsic generation of temporally constant spatial patterns. We develop a theoretical framework and illustrate it with some examples of how environmental variation and intrinsic interaction can combine to create patterns at various spatial scales.

Spatial variation in environmental conditions occurs at various (landscape) scales both naturally, e.g. altitude variation within mountainous regions, and through human intervention, e.g. networks of marine reserves, managed forests, or agricultural systems. Spatial scales of population patterns arising from species interactions (Turing scale) depend on the range of activation and inhibition, i.e. the strength of these interactions and the relative movement of individuals. On one extreme, if the landscape scale is much smaller than the Turing scale, then one can expect to observe intrinsically generated patterns that extend over large regions in space, potentially with small variations to reflect local conditions.

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Conversely if the landscape scale is large compared to the Turing scale of species interaction, one expects intrinsically generated patterns that change on the long spatial scale of environmental variation (Voroney et al., 1996).

Several authors have studied Turing pattern formation in heterogeneous landscapes. Benson et al. (1993b) investigated pattern formation with constant kinetic parameters and spatially varying diffusion coefficients, see also Benson et al. (1993a, 1998). Voroney et al. (1996) studied the interplay of Turing patterns and cyclic dynamics that result from a chemical reaction with an additional immobile but spatially heterogeneous complexing agent. Page et al. (2003) considered the generation of patterns near an interface where kinetic parameters change their values abruptly. Subsequent work included smoothly varying monotone and periodic changes in kinetic parameters (Page et al., 2005), see also Garzón-Alvarado et al. (2012) for more intensive numerical simulations in patchy, 2-dimensional domains. Recently Sheffer et al. (2013) and Yizhaq et al. (2014) investigated the interplay between environmental templates and self-organisation in the formation of patterned vegetation in semi-arid regions. Using both theoretical and empirical approaches, they showed that both mechanisms play significant roles in the pattern formation process, with their relative contributions depending on rainfall levels.

In this work, we take a landscape ecology perspective and subdivide the environment into distinct patches. A patch is defined as an environmentally homogeneous geographic region whose spatial extent is comparable to the species' dispersal scale so that a population can be assumed relatively homogeneous within a patch. Population dynamics on each patch are then coupled via migration between patches. Such multi-patch models have a long and distinguished history in spatial and community ecology (see for example Cantrell et al., 2012 for a discussion). In this framework, we study conditions for spatial patterns to evolve in the interesting range where the landscape scale is comparable to the Turing scale (see above). We implement habitat heterogeneity through patch attributes and movement bias.

A series of papers explores pattern formation in epithelia where cell–cell interaction is dominated by nearest-neighbour (juxtacrine) signalling (Owen and Sherratt, 1998; Owen et al., 2000; Webb and Owen, 2004a; O'Dea and King, 2011, 2013; Wearing et al., 2000; Wearing and Sherratt, 2001). In these works, all cells have equal properties (i.e. there is no spatial variation), and interaction between neighbouring cells is non-linear. We will adapt some of the analytical methods used there for our model. A closely related model for a linear inhomogeneous array of coupled chemical reactors was studied in Horsthemke and Moore (2004) as a discretised version of the work in Voroney et al. (1996).

We begin by deriving the predator–prey patch model that forms the basis of our study. We explore emergent patterns with a numerical bifurcation analysis when the number of patches is small. We find a large number of patterns, often stably coexisting, and complex bifurcation diagrams. In the second part, we perform a linear stability analysis when the number of patches is large. For reference and comparison, we identify the stability conditions for the spatially homogeneous model. We compare and contrast these results and discuss the ecological implications of our findings.

2. The model

In a linear landscape of patches of two types (type 1 and type 2), arranged to be periodically alternating, we denote by $u_{1,2}, v_{1,2}$ the respective densities of two interacting species. In our explicit calculations, we focus on predator–prey interaction where a type-1 patch is suitable for the prey and a type-2 patch is not. Viewing landscapes as mosaics of patches of different quality is common in

landscape ecology and also arises in managed ecosystems, for example, a series of marine reserves along a coastline (Botsford et al., 2001; Gouhier et al., 2010) or intercropping in agriculture (Jones and Sieving, 2006).

On a patch of type i , the dynamics of these species evolve according to the equations:

$$\dot{u}_i = f_i(u_i, v_i), \quad \dot{v}_i = g_i(u_i, v_i). \quad (1)$$

Throughout, we assume that functions f_i, g_i are sufficiently smooth and that the system preserves non-negativity of solutions.

We denote by L_i the length of patch type i , and by $L = L_1 + L_2$ and $l = L_1/L_2$ the landscape period and patch size ratio, respectively. We say that a *tile* consists of a patch of type 1 and its adjacent patch of type 2 on the right. Hence, a tile represents one period of the landscape (see Fig. 1(a)). We denote species' densities on tile j by $u_{1,2}^j, v_{1,2}^j$. We note here that “tile” is introduced only as a convenient way to describe the system, not as an ecological unit.

We model movement by a discrete diffusion process, so that moving from one good patch to the next requires moving through a bad patch. Individuals of species u (v) leave a patch of type 1 with migration rate μ_u (μ_v) and move to one of the adjacent patches of type 2 with equal probability. The leaving rate for patch type 2 is multiplied by κ_u (κ_v) to account for patch-dependent dispersal behaviour. If $\kappa_{u,v} > 1$ ($\kappa_{u,v} < 1$) then the average time spent in a patch of type 2 is shorter (longer), so that overall movement is biased towards patch type 1 (type 2). The spatially coupled model system reads

$$\begin{aligned} \dot{u}_1^j(t) &= \mu_u \left[\kappa_u \frac{u_2^j + u_2^{j-1}}{2} - u_1^j \right] + f_1(u_1^j, v_1^j), \\ \dot{u}_2^j(t) &= \mu_u l \left[\frac{u_1^j + u_1^{j+1}}{2} - \kappa_u u_2^j \right] + f_2(u_2^j, v_2^j), \\ \dot{v}_1^j(t) &= \mu_v \left[\kappa_v \frac{v_2^j + v_2^{j-1}}{2} - v_1^j \right] + g_1(u_1^j, v_1^j), \\ \dot{v}_2^j(t) &= \mu_v l \left[\frac{v_1^j + v_1^{j+1}}{2} - \kappa_v v_2^j \right] + g_2(u_2^j, v_2^j), \end{aligned} \quad (2)$$

where the multiplication of μ_u, μ_v by l in the equations on type-2-patches is the scaling factor that accounts for conservation of individuals. In the case of a finite number of tiles (N) we close the system by assuming periodic boundary conditions such that $u_1^1 = u_1^N$ and $v_1^1 = v_1^N$. Periodic boundary conditions allow for easy comparison to dynamics on an infinite domain, moreover they are equivalent to Neumann boundary conditions on a domain of length $N/2$.

2.1. Dynamics on a patch

On patches of type 1 ('good') we choose the non-dimensional Leslie or May model (May, 1974; Strohm and Tyson, 2009; Mukhopadhyay and Bhattacharyya, 2006) for predator species v and prey species u , given by

$$f_1(u, v) = u(1-u) - \frac{uv}{b+u}, \quad g_1(u, v) = sv \left(1 - \frac{v}{qu} \right). \quad (3)$$

In this scaling, b denotes the half-saturation constant of the Holling type II functional response. The predator grows logistically with intrinsic rate s and carrying capacity qu . This formulation arises from the assumption of variable predator-territory size (Turchin, 2001).

Patches of type 2 ('bad') are unsuitable for the prey so that we replace the logistic growth term by a linear death term. Predator

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