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Sharp changes in resource availability may induce spatial nearly periodic population abundances

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ABSTRACT

For many years, scientists have tried to understand the ubiquitous discrete nature of traits. As the emergence of nonuniform patterns in space via instability of the uniform pattern to spatial perturbations is well-understood in reaction–diffusion systems, several studies have suggested that a similar instability underlies discrete distributions of traits. In contrast, here we suggest that a different mechanism may underly species' discrete distributions of trait values. We show that a point where niche availability changes sharply along the continuous niche axis promotes the discretized distribution of trait values even far from that point. In certain cases, this mechanism may apply also to patterns of population densities over space, such as patterns that were observed in vegetation biomass, as locations where environment changes sharply may promote spatially, nearly periodic stationary patterns.

1. Introduction

A variety of dynamical systems are characterized by patterns in space and time (Cross and Hohenberg, 1993). Specifically, spatially periodic stationary patterns have been observed in thermal fluid convection (Kolodner, 1993), chemical reactions (Kærn and Menzinger, 2002; Berenstein et al., 2003; Yochelis and Sheintuch, 2009), optical systems (Staliunasa and Sánchez-Morcillob, 2000), embryonic development (Afek et al., 2011) and vegetation patterns (Valentin et al., 1999), to name but a few examples. In ecology and evolution, the emergence of stationary spatial patterns is particularly important because a continuous trait or niche axis may play the role of space (Levin and Segel, 1985). Specifically, evolution of a continuous trait may result in the selection of several trait values, a process that promotes species packing around these values (community-wide character displacement (Dayan and Simberloff, 2005)). This results in a nonuniform, multi-peaked population abundance along the trait axis (Levin and Segel, 1985).

To model resource competition over a continuous niche axis, several papers (Sasaki, 1997; Fuentes et al., 2003; Pigolotti et al., 2007; Scheffer et al., 2006) assumed that each trait fits a particular niche (resource type) and considered continuous Lotka–Volterra dynamics similar to

$$\frac{d\rho(x)}{dt} = \rho(x)\left[1 - \int_{-\infty}^{\infty} g(x-x')\rho(x')dx'\right], \tag{1}$$

where $\rho(x,\ t)$ is a density function on x for the population abundance at time t and $g(x-x')$ is a normalized kernel characterizing the magnitude of competitive interference between an individual at x and an individual at x' (e.g., $g(x) = \exp(-|x|^{\gamma})/\int \exp(-|x|^{\gamma})$). Previous studies showed that the uniform solution $\rho(x) = 1$ is stable if g is sufficiently "sharp" in its peak ($\gamma \leq 2$), but is unstable to spatial, nonuniform perturbations in $\rho(x)$ if g is sufficiently "rectangular" ($\gamma > 2$), leading to a spatially periodic stationary pattern (Fuentes et al., 2003; Pigolotti et al., 2007). In Eq. (1), x may be interpreted as a location in space, but may also be interpreted as a trait value, where each trait fits a particular niche along a corresponding continuous axis of available niches. Each peak of $\rho(x)$ corresponds to a pack of species, created where a particular trait value is selectively favored and is consequently becoming more abundant.

In this paper, we reveal a wide family of dynamics that approach stable, nearly periodic, stationary spatial patterns. We show that those dynamics do not encompass an unstable single-peaked or uniform stationary solution; rather, a positive single-peaked solution does not exist due to the presence of some "singular point" where some parameter changes steeply along the

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x-axis. We suggest that singular points play a major role in the coevolution of continuous traits and may underly species packing.

2. Competition over a nonuniform resource

We consider dynamics somewhat similar to Eq. (1), but to avoid instability to nonuniform perturbations, we consider resource explicitly as a separate variable:

$$\begin{aligned}\frac{d\rho(x)}{dt} &= \rho(x)\int_{-\infty}^{\infty} r(x')g_\sigma(x-x')dx' - m\rho(x) + \mu_\rho \rho_{xx}(x),\\ \frac{dr(x)}{dt} &= I_\Sigma(x) - r(x)\int_{-\infty}^{\infty}\rho(x')g_\sigma(x-x')dx' + \mu_r r_{xx}(x),\end{aligned} \tag{2}$$

where $\rho(x)$ is again the population abundance, $r(x)$ is the resource concentration, m is a constant mortality rate, ρ_{xx} and r_{xx} are the second partial derivatives of ρ and r with respect to x and $I_\Sigma(x)$ is the resource influx, which is changed near $x = 0$ and is given by a sigmoidal curve that monotonically increases from zero at values of x much smaller than minus Σ to one at values of x much larger than Σ (Fig. 1). According to one interpretation, $\rho(x)$ is the abundance of vegetation at a distance x from the location where the environment or the ground changes, $r(x)$ is the concentration of water, μ_ρ and μ_r are the respective diffusion coefficients and $g_\sigma(x - x')$, a normalized symmetric kernel with standard deviation σ, is the ability to absorb water at x' by the roots of a given vegetation located at x. According to another, alternative interpretation, x is a trait value along a continuous niche axis, $r(x)$ is still the resource concentration, where a resource of type x is the most suitable for an individual with a trait value x (specifically, species x consumes resources x' that are suitable to its trait according to $g_\sigma(x - x')$), and μ_ρ and μ_r are the respective mutation rates.

Without the environmental change, namely if the resource influx rate is uniform, $I_\Sigma(x) = I$, there are two uniform steady state, $\rho(x) = 0$, which is unstable, and $\rho(x) = I/m$, which is stable against uniform perturbations. Our numeric examination shows that it is also stable against spatial perturbations even when the kernel g is rectangular (in contrast to the Lotka–Volterra expectation from Eq. (1)). With the environmental change at $x = 0$, however, Eq. (2) has a solution that changes from zero at sufficiently negative values of x to $1/m$ at sufficiently large positive values of x (Fig. 2). The nontrivial question is how this change occurs over space, or how the population is distributed not very far from the singularity at $x = 0$.

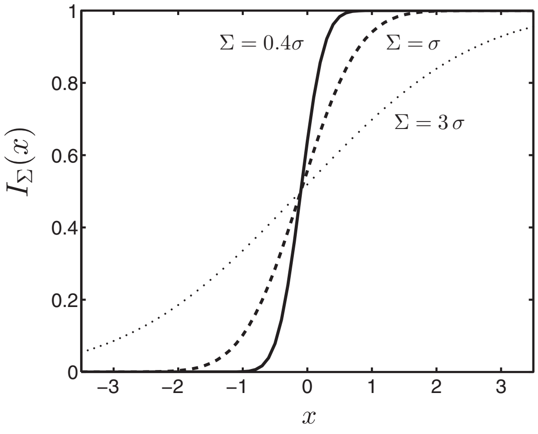

Fig. 1. Environment may change gradually or sharply over space or niche axis. The sigmoidal function $I_\Sigma(x) = \frac{1}{2} + \frac{1}{2}\mathrm{erf}(x/\Sigma)$ is demonstrated for various values of Σ. A large Σ characterizes a gradual change in the environment or in the resource influx, while a small Σ characterizes a sharp change. Where $\Sigma \to 0$, I_Σ becomes a step function: resource is uniformly supplied where $x > 0$, and is not supplied where $x < 0$.

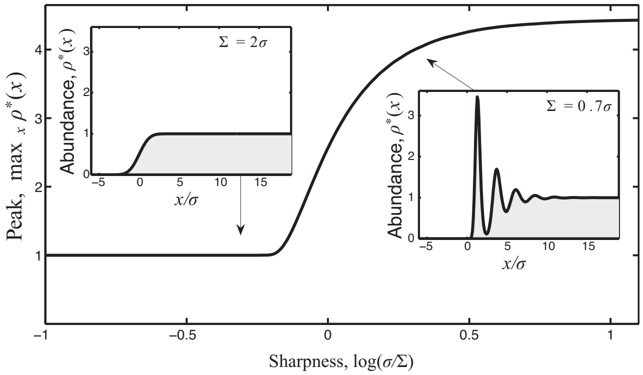

Fig. 2. Points where environmental gradient is sharp promote lumpy stationary spatial patterns. For gradual environmental gradients, where $\Sigma \gg \sigma$, steady state species abundance is monotone (left inset), whereas sharp environmental gradients, $\Sigma \sim \sigma$, lead to a lumpy steady state abundance (right inset). We emphasize that the monotone steady state does not lose stability, but rather, it no longer exists when environmental gradients become sufficiently sharp. We emphasize that this figure does not show a bifurcation as the unimodal solution does not lose stability; rather, it gradually becomes more lumpy, as indicated from the smooth shape of the graph. Parameters: $m = 1$, $\mu_\rho = 2\times10^4$, $\mu_r = 0.1$ and $g(x) = (\sqrt{2\pi\sigma})^{-1}\exp(x^2/2\sigma^2)$ (Gaussian).

Numerical solutions of Eq. (2) show that if the environment changes gradually, over much larger spatial scales than the interaction kernel ($\Sigma \gg \sigma$), then the steady state population abundance changes almost monotonically from zero to $1/m$ (Fig. 2, left inset). However, if the environment changes sharply, over the same spatial scale of the interaction kernel ($\Sigma \sim \sigma$), Eq. (2) still has a stable steady state solution, but this solution is now multi-peaked and comprises spatial oscillations near the singularity at $x = 0$ (Fig. 2, right inset). These oscillations are gradually diminished along space as x increases, until the uniform solution, $\rho(x) = 1/m$, is approached far from the singularity, at large values of x. The case where the environment changes sharply, on the same spatial scale of the interaction kernel can be realized at a hilltop, on a cliff, or at any other location where a change in the soil leads to a sharp change in water infiltration. Alternatively, according to the niche interpretation, sharp changes in $I_\Sigma(x)$ are typical when some resource types or niches are absent from a given environment, for example, if there are no resources smaller than or larger than a given size.

3. Singular points induce lumpy patterns

We prove mathematically (*Supplementary Material* (SM)) that the emergence of multi-peaked pattern for a sufficiently sharp environmental change applies to any smooth symmetric kernel g that satisfies $g'(|x|) \le 0$ (Fig. 3A and B). For a non-smooth kernel (e.g., where $g'(0)$ is undefined) this theorem does not apply (Fig. 3C; (Barabás et al., 2013)). The underlying idea is that, for extreme environmental change ($\Sigma \to 0$) and without diffusion or migration ($\mu_\rho = 0$), the steady state solution of Eq. (2) satisfies

$$\rho(x) = 0 \quad \text{or} \quad \int_0^\infty r(x')g_\sigma(x-x')dx' = m \tag{3}$$

for all x. The solution $\rho(x) = 0$ for all x is unstable where x is positive because $I_\Sigma(x) = 1$ where $x < 0$, and then $r(x)$ is sufficiently large to support the growth of small populations. At the same time, however, the solution of the integral comprises both positive and negative parts, whereas $r(x)$ is positively defined (SM). We show that near the singularity, any steady state solution of Eq. (2) comprises intervals where $\rho(x) = 0$ and a discrete set, x_i, where $\rho(x)$ has zero-width peaks (delta functions). As the diffusion coefficients increase, the widths of the peaks also increase, and the length over which the pattern approaches the uniform solution decreases.