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Self-organization of mobile populations in cyclic competition

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ABSTRACT

The formation of out-of-equilibrium patterns is a characteristic feature of spatially extended, biodiverse, ecological systems. Intriguing examples are provided by cyclic competition of species, as metaphorically described by the 'rock-paper-scissors' game. Both experimentally and theoretically, such non-transitive interactions have been found to induce self-organization of static individuals into noisy, irregular clusters. However, a profound understanding and characterization of such patterns is still lacking. Here, we theoretically investigate the influence of individuals' mobility on the spatial structures emerging in rock-paper-scissors games. We devise a quantitative approach to analyze the spatial patterns self-forming in the course of the stochastic time evolution. For a paradigmatic model originally introduced by May and Leonard, within an interacting particle approach, we demonstrate that the system's behavior—in the proper continuum limit—is aptly captured by a set of stochastic partial differential equations. The system's stochastic dynamics is shown to lead to the emergence of entangled rotating spiral waves. While the spirals' wavelength and spreading velocity is demonstrated to be accurately predicted by a (deterministic) complex Ginzburg–Landau equation, their entanglement results from the inherent stochastic nature of the system. These findings and our methods have important applications for understanding the formation of noisy patterns, e.g. in ecological and evolutionary contexts, and are also of relevance for the kinetics of (bio)-chemical reactions.

1. Introduction

Spatial distribution of individuals, as well as their mobility, are common features of real ecosystems that often come paired (May, 1974). On all scales of living organisms, from bacteria residing in soil or on Petri dishes, to the largest animals living in savannas—like elephants—or in forests, populations' habitats are spatially extended and individuals interact locally within their neighborhood. Field studies as well as experimental and theoretical investigations have shown that the locality of the interactions leads to the self-formation of complex spatial patterns (May, 1974; Murray, 2002; Turing, 1952; Nowak and May, 1992; Hassell et al., 1991, 1994; Blasius et al., 1999; Kerr et al., 2002; King and Hastings, 2003; Hauert and Doebeli, 2004; Scanlon et al., 2007; Kefi et al., 2007; Szabó and Fath, 2007; Perc et al., 2007; Nowak, 2006). Another important property of most individuals is mobility. For example, bacteria swim and tumble, and animals migrate. As motile individuals are capable of enlarging their district of residence, mobility may be viewed as a mixing, or stirring mechanism which 'counteracts' the locality of spatial interactions.

The combined influence of these effects, i.e. the competition between mobility and spatial separation, on the spatio-temporal development of populations is one of the most interesting and complex problems in theoretical ecology (May, 1974; Murray, 2002; Turing, 1952; Hassell et al., 1994; King and Hastings, 2003; Janssen, 2001; Reichenbach et al., 2007a). If mobility is low, locally interacting populations can exhibit involved spatio-temporal patterns, like traveling waves (Igoshin et al., 2004), and for example lead to the self-organization of individuals into spirals in myxobacteria aggregation (Igoshin et al., 2004) and insect host–parasitoid populations (Hassell et al., 1991), or more fractal-like structures in competing strains of *E. coli* (Kerr et al., 2002). On the other hand, high mobility results in well-mixed systems where the spatial distribution of the populations is irrelevant (Maynard Smith, 1982; Hofbauer and Sigmund, 1998). In this situation, spatial patterns do no longer form: The system adopts a spatially uniform state, which therefore drastically differs from the low-mobility scenario.

An intriguing motif of the complex competitions in a population, promoting species diversity, is constituted by three

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subpopulations exhibiting cyclic dominance. This basic motif is metaphorically described by the rock-paper-scissors game, where rock crushes scissors, scissors cut paper, and paper wraps rock. Such non-hierarchical, cyclic competitions, where each species outperforms another, but is also itself outperformed by a remaining one, have been identified in different ecosystems like coral reef invertebrates (Jackson and Buss, 1975), rodents in the high-Arctic tundra in Greenland (Gilg et al., 2001), lizards in the inner Coast Range of California (Sinervo and Lively, 1996) and microbial populations of colicinogenic *E. coli* (Kerr et al., 2002; Kirkup and Riley, 2004). In the latter situation, it has been shown that spatial arrangement of quasi-immobile bacteria (because of 'hard' nutrient or substrate) on a Petri-dish leads to the stable coexistence of all three competing bacterial strains, with the formation of irregular patterns. In stark contrast, when the system is well-mixed, there is spatial homogeneity resulting in the take over of one subpopulation and the extinction of the others after a short transient.

It is worth noting that the emergence of noisy patterns, as those studied here, is a feature shared across disciplines by many complex systems characterized by their out-of-equilibrium nature and nonlinear interactions. Examples range from the celebrated Belousov–Zhabotinsky reaction (Zaikin and Zhabotinsky, 1970) (spiraling patterns) and many other chemical reactions (Kapral and Showalter, 1995), to epidemic outbreaks (traveling waves) (Grenfell et al., 2001; Cummings et al., 2004), excitable media (Muratov and Vanden-Eijnden, 2007; Kapral and Showalter, 1995), and calcium signaling within single cells (Lechleiter et al., 1991; Falcke, 2004; Bootmann et al., 2006). Moreover, cyclic dynamics as described by the rock-paper-scissors game occur not only in population dynamics but have, e.g. been observed in social dilemmas relevant in behavioral sciences (Sigmund et al., 2001; Hauert et al., 2002). Therefore, we would like to emphasize that the methods presented in this work are not limited to theoretical ecology and biology, but have a broad range of multidisciplinary applications and notably include the above fields.

Pioneering work on the role of mobility in ecosystems was performed by Levin (1974), where the dynamics of a population residing in two coupled patches was investigated: Within a deterministic description, Levin identified a critical value for the individuals' mobility between the patches. Below the critical threshold, all subpopulations coexisted, while only one remained above that value. Later, more realistic models of many patches, partly spatially arranged, were also studied, see Hassell et al. (1991, 1994); Blasius et al. (1999); Alonso and McKane (2002) as well as references therein. These works shed light on the formation of patterns, in particular traveling waves and spirals. However, patch models have been criticized for treating the space in an "implicit" manner (i.e. in the form of coupled habitats without internal structure) (Durrett and Levin, 1998). In addition, the above investigations were often restricted to deterministic dynamics and thus did not address the spatio-temporal influence of noise. To overcome these limitations, Durrett and Levin (1997) proposed to consider interacting particle systems, i.e. stochastic spatial models with populations of discrete individuals distributed on lattices. In this realm, studies have mainly focused on numerical simulations and on (often heuristic) deterministic reaction–diffusion equations, or coupled maps (Durrett and Levin, 1994, 1997, 1998; King and Hastings, 2003; Czárán et al., 2002; Liebermann et al., 2005; Mobilia et al., 2006, 2007; Szabó and Fath, 2007).

Here, we demonstrate how a—spatially explicit—stochastic model of cyclically interacting subpopulations exhibits self-formation of spatial structures which, in the presence of individuals' mobility, turn into surprisingly regular, geometric spiral waves. The latter become visible on the scale of a large number of interacting individuals, see Fig. 1 (right). In contrast, stochastic effects solely dominate on the scale of a few individuals, see Fig. 1 (left), which interact locally with their nearest neighbors. Spatial separation of subpopulations starts to form on an intermediate scale, Fig. 1 (middle), where mobility leads to fuzzy domain boundaries, with major contributions of noise. On a larger scale, Fig. 1 (right), these fuzzy patterns adopt regular geometric shapes. As shown below, the latter are jointly determined by the deterministic dynamics and intrinsic stochastic effects. In the following, we elucidate this subtle interplay by mapping—in the continuum limit—the stochastic spatial dynamics onto a set of stochastic partial differential equations (SPDEs) and, using tools of dynamical systems (such as normal forms and invariant manifolds), by recasting the underlying deterministic kinetics in the form of a complex Ginzburg–Landau equation (CGLE). The CGLE allows us to make analytical predictions for the spreading velocity and wavelength of the emerging spirals waves. Below, we provide a detailed description of these methods and convey a thorough discussion of the spatio-temporal properties of the system with an emphasis on the role of spatial degrees of freedom, mobility and internal noise.

In our first article on this subject (Reichenbach et al., 2007a) we have described how a mobility threshold separates a biodiverse regime (arising for low mobilities) from a high-mobility regime where diversity is rapidly lost. In Reichenbach et al. (2007b) we have further analyzed the traveling spiral waves that arise for low mobilities and computed correlation functions as well as the spirals' wavelength and spreading velocity. In this article, we provide a comprehensive discussion of the quantitative analysis of the system's properties. This includes the detailed derivation of all mathematical equations, an accurate description of the numerical simulations (via the implementation of an efficient algorithm for the lattice simulations taking exchange processes into account) as well as the analytical treatment of the

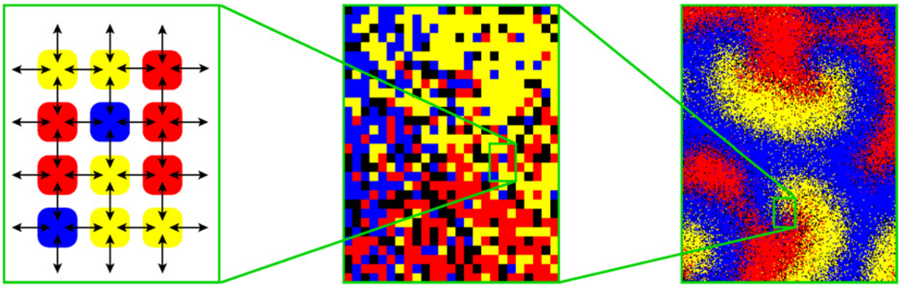

Fig. 1. The stochastic spatial system at different scales. Here, each of the colors yellow, red, and blue (level of gray) represents one species, and black dots identify empty spots. *Left*: Individuals are arranged on a spatial lattice and randomly interact with their nearest neighbors. *Middle*: At the scale of about 1000 individuals, stochastic effects dominate the system's appearance, although domains dominated by different subpopulations can already be detected. *Right*: About 50,000 mobile interacting individuals self-organize into surprisingly regular spiral waves.