Original Research Article

Beyond Turing: The response of patterned ecosystems to environmental change

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ABSTRACT

Spatially periodic patterns can be observed in a variety of ecosystems. Model studies revealed that patterned ecosystems may respond in a nonlinear way to environmental change, meaning that gradual changes result in rapid degradation. We analyze this response through stability analysis of patterned states of an arid ecosystem model. This analysis goes one step further than the frequently applied Turing analysis, which only considers stability of uniform states. We found that patterned arid ecosystems systematically respond in two ways to changes in rainfall: (1) by changing vegetation patch biomass or (2) by adapting pattern wavelength. Minor adaptations of pattern wavelength are constrained to conditions of slow change within a high rainfall regime, and high levels of stochastic variation in biomass (noise). Major changes in pattern wavelength occur under conditions of either low rainfall, rapid change or low levels of noise. Such conditions facilitate strong interactions between vegetation patches, which can trigger a sudden loss of half the patches or a transition to a degraded bare state. These results highlight that ecosystem responses may critically depend on rates, rather than magnitudes, of environmental change. Our study shows how models can increase our understanding of these dynamics, provided that analyses go beyond the conventional Turing analysis.

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1. Introduction

Spatially periodic patterning of sessile biota can be observed in a variety of ecosystems including arid ecosystems (Macfadyen, 1950), mussel beds (van de Koppel et al., 2005), boreal peatlands (Malmström, 1923) and tropical peatlands (Baldwin and Hawker, 1915). Such spatially periodic patterns can typically not be explained by underlying heterogeneity in the environment, which suggests that they are self-organized. Self-organization into periodic patterns is the result of positive feedbacks that act locally (short range activation) in combination with distal negative feedbacks (long range inhibition; Gierer and Meinhardt, 1972). This combination of feedbacks is also referred to as scale-dependent feedbacks (Rietkerk and van de Koppel, 2008). In arid ecosystems, the combination of locally reduced evaporation through shading and water uptake by laterally extended roots is known to induce such scale-dependent feedbacks (Gilad et al., 2004; Meron, 2012). Scale-dependent feedbacks can also result from the fact that in arid ecosystems plants tend to improve soil structure which allows more water to infiltrate during rain events (Rietkerk et al., 2000; Thompson et al., 2010). This results in increased water availability and increased plant growth, meaning that locally a positive feedback loop is active. However, water availability farther away is negatively affected by this facilitative effect: surface water accumulates on bare soils during intense rain events and moves towards vegetated areas due to a gentle slope or due to infiltration differences on flat terrain (Klausmeier, 1999; Rietkerk et al., 2002). In arid ecosystems, local positive feedbacks are therefore linked to a flux of resource that results in long range inhibition and consequently in pattern formation. This type of scale-dependent feedback is referred to as the resource-concentration mechanism (Rietkerk et al., 2004). The positive feedbacks that are often involved in pattern formation (Rietkerk and van de Koppel, 2008) are associated with nonlinear

ecosystem response to environmental change (DeAngelis et al., 1980; Rietkerk et al., 2004). This means that gradual changes in environmental conditions may result in sudden significant losses in productivity and in degradation of patterned ecosystems.

Reaction–(advection–)diffusion models have been developed to understand the mechanisms responsible for pattern formation, to study the conditions under which scale-dependent feedbacks are strong enough for patterning to occur and to get more insight in the possible nonlinear behavior of patterned ecosystems (e.g. Klausmeier, 1999; Von Hardenberg et al., 2001; Rietkerk et al., 2002; Gilad et al., 2004). In these models, patterns typically arise from a uniform system state that becomes unstable to heterogeneous perturbations. This type of instability is referred to as Turing instability (after A.M. Turing, 1912–1954; Turing, 1953) and is thought to be involved in for example the formation of patterns on animal coats (Meinhardt, 1982), on sea shells (Meinhardt, 1995) and in chemical systems (Gray and Scott, 1984; Pearson, 1993). Using linear stability analysis, it is possible to find the parameter ranges for which a uniform system state is Turing unstable.

At present, Turing analysis is used as a relatively simple way to study the environmental conditions under which one would expect periodic patterns to be observed (e.g. Klausmeier, 1999; HilleRisLambers et al., 2001; Meron et al., 2004; Gilad et al., 2004; Kefi et al., 2008; Eppinga et al., 2009). However, since Turing analysis only considers the stability of uniform system states, it provides very little information about the behavior of ecosystems that are in a patterned state. Therefore, previous studies have been exploring this behavior using numerical approaches. These studies revealed a number of interesting properties of patterned ecosystems. Various model studies suggest that patterns can be expected under conditions where uniform system states are still stable and under conditions too harsh for uniform cover to be sustained (e.g. Von Hardenberg et al., 2001; Rietkerk et al., 2002). These findings imply that stable uniform and stable patterned states can coexist for a range of environmental conditions (Rietkerk et al., 2004). The coexistence of alternative stable ecosystem states can result in so-called critical transitions (Scheffer, 2009) if environmental conditions change, which are associated with sudden losses of productivity and ecosystem degradation (Scheffer et al., 2001). Numerical studies that looked in more detail to the dynamics of patterned ecosystem states suggest that multiple stable patterned states, with different wavelength or spatial configurations, can coexist and that this can result in hysteresis and more gradual ecosystem adaptation if environmental conditions change (Sherratt and Lord, 2007; Bel et al., 2012).

Although studies with numerical approaches uncovered some interesting characteristics of patterned ecosystems, recent studies have been exploring whether the use of analytically based methods provides more detailed insights (Van der Stelt et al., 2013; Sherratt, 2013a). These approaches go one step further than Turing analysis as they consider the stability of patterned rather than uniform ecosystem states. By combining stability analysis on patterned states with model runs, Sherratt (2013a) demonstrated that hysteresis can be explained by the coexistence of multiple stable states. His study also suggests that the rate at which environmental conditions change may affect system response. This is of particular importance as current human activities induce anomalous rates of environmental change (e.g. Joos and Spahni, 2008). Although these results suggest that information about the stability of patterned states is essential in understanding ecosystem response to changing environmental conditions, the application of stability analysis on patterned states in the field of ecology has been limited so far and various ecologically relevant questions remain to be answered (Van der Stelt, 2012, pp. 95–100).

One of the processes that are not well understood is the process of pattern wavelength adaptation. Patterned ecosystems can respond to environmental change by adapting pattern wavelength and the study by Sherratt (2013a) showed that this process is affected by the rate of environmental change. It is, however, unknown why and how patterned ecosystems adapt and why this depends on the rate of change. In this study we therefore aim to provide a mechanistic understanding of how patterned ecosystems respond to environmental change, considering both the magnitude of change as well as the rate of change. By applying stability analysis on patterned system states, we first show that the use of Turing analysis can yield false negatives and false positives with regard to predicting the existence of observable (i.e. stable) patterns. Based on the mechanisms that are involved in pattern destabilization, we then discuss possible types of pattern adaptation. Using model runs, we demonstrate that knowledge about the stability of patterned states is crucial in understanding the response of ecosystems subject to environmental change and show how the rate of change in environmental conditions and the level of imposed spatio-temporal noise affect system response. Finally, we propose that competition for resources between patches of vegetation provides a possible ecological explanation for the obtained results. In this study we use an extended version of an arid ecosystem model by Klausmeier (1999) as introduced by Van der Stelt et al. (2013), which we will discuss in the next section.

2. Model description and analyses

2.1. Model description

The extended version of the Klausmeier model is a reaction–advection–diffusion model in which the formation of spatial vegetation patterns is the result of competition for surface water. The model has two state variables that are functions of both time t and space x ($x \in \mathbb{R}$): plant biomass n and surface water w. Notice that we will consider only one spatial dimension (x), following Van der Stelt et al. (2013) and Sherratt (2013a). The model is given by Eqs. (1) and (2). We use a non-dimensional version the model in order to reduce the number of parameters. For a dimensional version of the model and the physical meaning of the parameters, see Appendix A.

$$\frac{\partial w}{\partial t} = a - w - wn^2 + v\frac{\partial w}{\partial x} + e\frac{\partial^2 w^{\gamma}}{\partial x^2} \tag{1}$$

$$\frac{\partial n}{\partial t} = wn^2 - mn + \frac{\partial^2 n}{\partial x^2} \tag{2}$$

The change in surface water w (Eq. (1)) is controlled by rainfall a, surface water losses (second term) and uptake by plants through infiltration and transpiration (third term). As in the original model by Klausmeier (1999), the movement of surface water due to gradients in the terrain is captured with an advection term (fourth term). We extended the model by adding diffusion of surface water (fifth term). We did this for three reasons. First, the diffusion term has a physical basis as it can be derived from the shallow water equations (Gilad et al., 2004). Second, it allows us to capture the movement of surface water induced by spatial differences in infiltration rate (Rietkerk et al., 2002). Third, it enables us to demonstrate that the type stability analysis we use to study the system's response to change can be applied to both reaction–advection–diffusion and reaction–diffusion model ($v \neq 0$ and $v = 0$ respectively).

The dynamics in plant biomass n (Eq. (2)) are determined by plant growth which is linearly related to water uptake (first term) and by plant mortality (second term). As in the original model, plant dispersion is modeled with a diffusion term (third term).