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Self-Organized Vegetation Patterns: Early Warning Signals for Prediction of Ecosystem Transitions

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Extended Abstract

Introduction

The significance of spatial heterogeneity in understanding ecological processes has been recognized long ago. One of the earliest expressions of this recognition is the habitat heterogeneity hypothesis that links spatial heterogeneity to niche vegetation patterns formation and species coexistence. Yet, an important if not crucial aspect of landscape heterogeneity has escaped deep consideration, that is, the possible occurrence of spatial instabilities leading to self-organized heterogeneity. Self-organized heterogeneity or pattern formation is ubiquitous in the nature. In theory, spatial patterns may provide more powerful leading indicators, as they contain more information than a single data point in a time-series. For systems that have self-organized patterns formation, there are specific signals. However, these signals tend to be specific to the particular mechanism involved and cannot be generalized to other systems. The interaction between vegetation and hydrologic processes is particularly tight in water-limited environments where a positive feedback links water redistribution and vegetation. The vegetation of these systems is commonly patterned, that is, arranged in a two phase mosaic composed of patches with high biomass cover interspersed within a low-cover or bare soil component. These patterns are strongly linked to the redistribution of runoff and resources from source areas (bare patches) to sink areas (vegetation patches) and play an important role in controlling erosion (runoff-run-on mechanism). Disturbances of such overgrazing or aridity, can alter the structure of vegetation patterns and reduce its density and size which leads to a "leaky" system. A leaky system is less efficient at trapping runoff and sediments and loses of valuable water and nutrient resources. This induces a positive-feedback loop that reinforces the degradation process. The most common vegetation pattern found in arid and semi-arid ecosystems is usually referred to as spotted or stippled and consists of dense vegetation clusters that are irregular in shape and surrounded by bare soil. Another common pattern is banded vegetation, also known as "tiger bush", in which the dense biomass patches form bands, stripes or arcs. Banded vegetation is usually aligned along contour lines and is effective in limiting hillslope erosion. Banded patterns commonly act as closed hydrological systems, with little net outflow and sediment coming out of the system. The effect of spotted vegetation on erosion is more complex and depends greatly on the connectivity of the bare soil areas. Depending on the spatial mechanisms dominated in arid ecosystems, particular changes in spatial patterns may signal whether vegetation is close to collapse into bare ground. During the past few decades, mathematical countinume models have been employed for evaluation tend of vegetation pattern as, an early warning signal for prediction of desertification transitions in the arid ecosystems. In the present paper, we describe interaction between vegetations nonlinear dynamics, environmental disturbances and different vegetation patterns according to countinume model of GILAD. Analysis of vegetation patterns can be helpful in understanding desertification.

Materials and Methods

Vegetation dynamic Models

There is a variety of models for the simulation of vegetation dynamics in water-limited ecosystems. The recent models that capture the interaction between spatial water redistribution and vegetation patterns can be divided into two main groups: the first models are discrete or individual-based models and the second are continuum models or partial-differential-equations (PDEs) models. Discrete models are numerical algorithms that go down to the level of individual plants and often describe them in great details. Continuum models are consisted of

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spatially continuous variables satisfying sets of coupled PDEs. These models are capable of describing continuous processes such as overland water flow, soil-water dynamics, erosion-deposition processes, and etc. PDE models are reaction – diffusion equations, that is, systems of PDE that combine linear diffusion with nonlinear interactions. From the implementation point of view, discrete models are formulated in terms of algorithms that are executed by numerical computations, whereas continuum PDEs models are amenable to mathematical analysis besides numerical computations. The continuum PDEs models are powerful tools for investigation of pattern formation theory.

Vegetation Pattern formation based on the GILAD model

Vegetation pattern formation based on the GILAD model is a result of positive feedbacks operating at local scale. We focus here on two important feedbacks. The first is a positive feedback between above-ground and below-ground biomass (hereafter the root-augmentation feedback) and is related to the root-to-shoot ratio, a characteristic trait of plant species (Fig. 1a). As a plant grows, its root zone extends to new soil regions where water can be taken up from. As a result, the amount of water available to the plant increases and the plant grows even further. The second feedback is a positive feedback between biomass and water (hereafter the infiltration feedback) (Fig. 2b). Bare soils in arid regions are often covered by biological soil crusts reducing the infiltration rate of surface water into the soil relative to the infiltration rate in vegetation patches. As a consequence, vegetation patches act as sinks for runoff water generated by their crusted neighborhoods. This accelerates their growth, sharpens the infiltration contrast and increase even further the soil moisture in the patch areas. Soil erosion in bare areas and deposition in vegetation patches is another mechanism that can induce or enhance infiltration contrast.



Fig. 1. Schematic illustrations of the root-augmentation feedback (a) and the infiltration feedback (b).

Results and Discussion

The model discussed in this article shows that the resource concentration mechanism predicts global bistability associated with catastrophic shifts at large spatial scales and self-organized patterns. A variety of mechanisms in ecosystems lead to resource concentration through consumer-resource feedback. The consumers, harvest resources from their surroundings and harvest are facilitated by mass flow of resources toward consumers, triggered by the consumers themselves. Furthermore, consumers spread relatively slowly as compared to flow of resources. A general pattern emerging from these interactions is that consumers are positively associated with resource abundance at short spatial range, but negatively at long spatial range. Thus, a common principle applies to these locally reinforced consumers, in that there is a positive feedback effect that is short-ranged and a negative feedback effect that is long-ranged. This is a necessary condition for self-organized patterns to form. Such scale-dependent feedback can explain a diversity of patterns in ecosystems. The differences in structure and scale of patterns are the result of varying strengths and scales of feedback influence, illustrating the general nature of the underlying scale-dependent mechanisms explaining self-organized patterns in ecosystems. The notion of scale-dependent feedback controlled by the resource concentration mechanism is crucial for a predictive theory of catastrophic shifts in ecosystems. This suggests that catastrophic shifts can be predicted by self-organized patterns. Therefore, the concepts of catastrophic shifts and self-organized patterns are tightly linked, whereby a scale-dependent feedback is triggered by resource concentration. This mechanism predicts global bistability and catastrophic shifts between spotted and uniform states. Vegetation pattern formation theory and appearance of spatially mixed and intermediate patterns in bistability systems of uniform and spatially periodic states (multitude of intermediate states in the bistability range of bare soil and a periodic spot pattern) according to GILAD model, suggests that desertification may not necessarily be abrupt, but rather a gradual process.

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Conclutions

Geomorphic systems are typically nonlinear, owing largely to their threshold-dominated nature. Nonlinear geomorphic systems may exhibit complex behaviors not possible in linear systems, including dynamical instability and deterministic chaos. Linking self-organized patterns with catastrophic shifts by the resource concentration mechanism may help bridge the present gaps among theory, observation, and management. The self-organized patterns may indicate imminent shifts if resource input is decreased in time. For instance, the spotted state may be developed only when resource input is decreased, not when it is increased. This means that a snapshot in time of a spotted state would already indicate imminent catastrophic shift. Applications of the pattern formation approach to water-limited landscapes predict the possible emergence of spatial heterogeneity as a self-organization phenomenon. The predicted spatial patterns can be periodic (spots, stripes and gaps), irregular with a characteristic length scale, or scale free. The pattern formation approach provides clear criteria for the realizations of these different pattern types in terms of environmental conditions, such as precipitation rate, infiltration rate, water-ground friction force, topography and disturbances, and in terms of species traits, such as biomass growth rate, uptake rate and root-to-shoot ratio. Three values of the pattern formation modeling approach have been emphasized: 1. It reveals universal elements such as instabilities, bistability ranges, and resonant responses, for which a great deal of knowledge is already available; 2. It captures processes across different length scales and organization levels and adaptive response to environmental changes; 3. It provides an integrative framework for studying problems in spatial ecology, coupling aspects of landscape, population, community and restoration ecology.

Keywords: bistability, continume models, desert transition, early warning signals, vegetation patterns.