Mathematical Biosciences 271 (2016) 1–18

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Pattern formation – A missing link in the study of ecosystem response to environmental changes

Ehud Meron[*]

[a] *Department of Solar Energy and Environmental Physics, Swiss Institute for Dryland Environmental and Energy Research, BIDR, Ben-Gurion University of the Negev, Sede Boqer Campus 8499000, Israel*
[b] *Department of Physics, Ben-Gurion University of the Negev, Beer Sheva, 8410501, Israel*

ARTICLE INFO

Article history:
Received 28 May 2015
Revised 17 October 2015
Accepted 23 October 2015
Available online 31 October 2015

MSC:
35K55
35K57
45K05
92B05

PACS:
05.65.+b
87.23.Cc
89.75.−k

Keywords:
Vegetation pattern formation
Functional diversity
Desertification
Ecosystem engineers
Homoclinic snaking
Spatial resonances

ABSTRACT

Environmental changes can affect the functioning of an ecosystem directly, through the response of individual life forms, or indirectly, through interspecific interactions and community dynamics. The feasibility of a community-level response has motivated numerous studies aimed at understanding the mutual relationships between three elements of ecosystem dynamics: the abiotic environment, biodiversity and ecosystem function. Since ecosystems are inherently nonlinear and spatially extended, environmental changes can also induce pattern-forming instabilities that result in spatial self-organization of life forms and resources. This, in turn, can affect the relationships between these three elements, and make the response of ecosystems to environmental changes far more complex. Responses of this kind can be expected in dryland ecosystems, which show a variety of self-organizing vegetation patterns along the rainfall gradient. This paper describes the progress that has been made in understanding vegetation patterning in dryland ecosystems, and the roles it plays in ecosystem response to environmental variability. The progress has been achieved by modeling pattern-forming feedbacks at small spatial scales and up-scaling their effects to large scales through model studies. This approach sets the basis for integrating pattern formation theory into the study of ecosystem dynamics and addressing ecologically significant questions such as the dynamics of desertification, restoration of degraded landscapes, biodiversity changes along environmental gradients, and shrubland–grassland transitions.

1. Introduction

Much effort is devoted in ecology to the understanding of ecosystem response to environmental variability and to the impact of this response on ecosystem function [1–3]. A challenging question in this research effort is how do organism-level traits and small-scale spatial processes scale up to higher levels of organization and larger spatial scales, and determine ecosystem functions, such as bio-productivity and resilience in varying environments.

Species often develop organism-level mechanisms to cope with environmental stresses. These mechanisms generally involve phenotype changes [4], and are particularly relevant to immobile organisms, such as plants, which cannot migrate to less stressful environments. Plant species, for example, can maintain their water uptake under conditions of water stress by increasing the root-to-shoot ratio, or increase their specific leaf area in order to increase the interception of light in the shade. At higher organization levels and larger spatial scales additional mechanisms appear. Communities can respond to environmental stresses by changing their structure, and by self-organizing in spatial patterns.

A community-structure change is generally a combined result of environmental filtering and species interactions. Environmental filtering [5] is an organism-level process by which an initial community is selected out of a species pool in response to specific environmental conditions. The community is selected according to the distribution of response traits that determine the abilities of organisms to cope with environmental stresses. Interspecific interactions within the selected community induce community dynamics that further shape the community structure and determine the distribution of

---

[*] Correspondence address: Department of Physics, Ben-Gurion University of the Negev, Beer Sheva, 84105, Israel. Tel.: +972 8 6477556.
E-mail address: ehud@bgu.ac.il
URL: http://www.bgu.ac.il/~ehud

http://dx.doi.org/10.1016/j.mbs.2015.10.015
0025-5564/

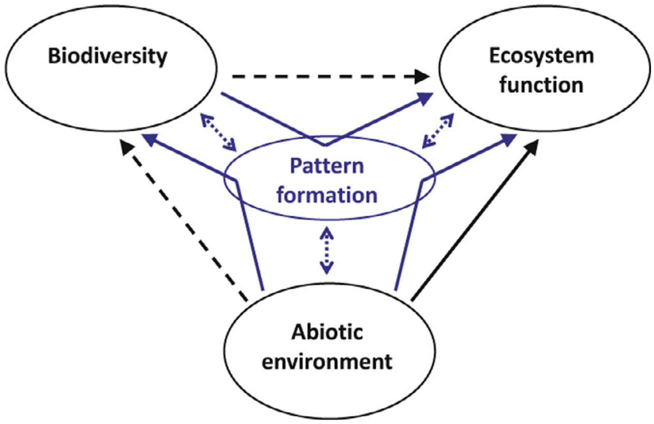

Fig. 1. The impact of environmental changes on ecosystem function. The abiotic environment can affect ecosystem function by its direct effect on any individual organism (solid black line), or indirectly by inducing a shift in community structure that changes the biodiversity of the system (two dashed black lines). Indirect relationships (broken solid blue arrows) can also be induced by pattern formation, which is linked to all three elements, the abiotic environment, biodiversity and ecosystem function (dotted blue arrows) (see the text for examples). Adapted from [12]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

effect traits – the traits that affect ecosystem function [6]. Scaling up organism-level attributes to community-level properties that determine ecosystem function involves then the identification of response and effect traits and the analysis of the complex nonlinear dynamics of large communities.

Spatial self-organization is induced by positive feedbacks that operate at small scales and lead to symmetry-breaking instabilities and pattern formation at large scales. An important context that shows such a response to environmental changes is water-limited vegetation [7–10]. Positive feedbacks in this context depend on organismic traits, such as biomass growth rate, water-uptake rate and root architecture, and on small-scale abiotic processes, such as overland water flow, surface-water infiltration and soil-water diffusion. Vegetation pattern formation is then a population-level response that increases water availability by the formation of vegetation patches and the transport of water toward the patch locations, a response that affects ecosystem functions such as resilience and bio-productivity. The spatial coupling and the resulting self-organized patchiness add another dimension to the complexity of the up-scaling problem.

The mediating role that community-level processes play in the response of ecosystems to environmental changes can be illustrated schematically by a diagram that relates three elements of ecosystem dynamics, as Fig. 1 shows [11]: the *abiotic environment*, representing rainfall, temperature, soil fertility, disturbances, etc., *biodiversity*, representing interspecific interactions, species richness, community composition, etc., and *ecosystem function*, which stands for biomass production, nutrient cycling, resilience, and other functions. The abiotic environment affects ecosystem function not only directly by the response of any organism as if other organisms were absent (solid black arrow), but also indirectly, through interspecific interactions that change community structure and the distribution of effect traits (dashed black arrows).

The main thesis we pursue here is that studies of ecosystem response to environmental changes should also scale up small-scale pattern-forming feedbacks, whenever they exist, and analyze the mediating effects of pattern formation. As Fig. 1 illustrates, pattern formation is directly linked to any of the three elements of ecosystem dynamics (small dotted blue arrows). It is linked to the abiotic environment because environmental stresses often induce spatially patterned states or transitions between different patterned states. It is linked to biodiversity because pattern formation generally involves resource redistribution, which affects interspecific interactions. It is also linked to ecosystem function since pattern formation involves changes in biomass production, resource-use efficiency, and ecosystem resilience. Understanding these and other links is essential for gaining a deeper insight into the processes that drive ecosystem dynamics and affect ecosystem function in varying environments.

We study these links using mathematical models of water-limited landscapes, employing the methods of pattern formation theory. Such landscapes provide a good case study in that they show a wide variety of vegetation patterns that are in good agreement with model predictions. The study of water-limited landscapes is significant also because it relates to two outstanding current problems in environmental research, desertification and biodiversity loss, and bears on the implications for ecosystem function.

We begin with a detailed description of the general mathematical model to be used and two simplified versions thereof that are motivated by specific ecological contexts (Section 2). We then briefly describe a few model studies of processes that link pattern formation to the abiotic environment, to biodiversity and to ecosystem function (Section 3), and discuss manners by which these processes can mediate the relationships between these three elements (Section 4). We conclude with a few remarks on the significance of pattern formation processes to other types of terrestrial ecosystems and to marine ecosystems, and on the reciprocal benefits of studying complex ecosystems to pattern formation theory (Section 5).

2. Modeling water-limited landscapes

Two main modeling approaches are in use in studies of plant population dynamics, agent-based models (also called individual-based models) [13], and partial differential equations (PDEs). The former are computational algorithms that go down to the level of individual plants and often describe them in great detail. The latter do not address individual plants but rather processes at small spatial scales, and characterize the population by a continuous biomass areal density. We use here the PDEs approach since it lends itself to the powerful methods of pattern formation theory [12,14,15].

2.1. Continuum modeling of discrete plant populations

The biomass of a plant population in a water limited system can often be regarded as a continuous deterministic variable for two main reasons [12]. The first is related to the modular design that dryland plants typically have. Rather than having a single stem that acts as an integrated hydraulic system, and is vulnerable to hydraulic failures caused by droughts, dryland plants often develop hydraulically independent multiple stems. The redundancy of independent conduits increases the plant's resistance to drought, as a failure of a single or a group of conduits can lead to partial plant mortality but still leaves the plant viable [16]. As a consequence, the response of a plant individual to water stress often involves a gradual biomass decrease rather than a sharp mortality event. The second reason is related to the availability of long-lived seeds and their non-vanishing probability to germinate whenever the biotic and abiotic conditions allow, which reduce strong population fluctuations and prevent the extinction of small populations. These considerations suggest the description of a plant population in terms of a deterministic continuous biomass variable, representing the above-ground biomass per unit area, irrespective of the number or identity of the plant individuals contributing to it.

Another question is how detailed continuum models should be [12]. Obviously, in order to account for vegetation pattern formation the models should capture pattern-forming feedbacks, i.e. feedbacks that can induce nonuniform instabilities of uniform vegetation. This has already been achieved with a single-variable model for the population biomass that does not take into account the associated