Ecological Informatics 32 (2016) 156–166

Contents lists available at ScienceDirect

Ecological Informatics

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

The response of shrubland patterns' properties to rainfall changes and to the catastrophic removal of plants in semi-arid regions predicted by Reaction–Diffusion simulations

Elena Roitberg *, Maxim Shoshany, Yehuda Agnon

Faculty of Civil and Environmental Engineering, Technion–Israel Institute of Technology, Haifa 32000, Israel

A R T I C L E I N F O

Article history:
Received 9 February 2015
Received in revised form 1 February 2016
Accepted 3 February 2016
Available online 11 February 2016

Keywords:
Shrubland
Pattern dynamics
Reaction-diffusion equations
Climate change
Landscape metrics
Vegetation regeneration

A B S T R A C T

Extended areas of the Mediterranean and semi-arid ecosystems are predicted to face decreased water availability, alongside increased human disturbances owing to an increase in population during this century. The use of geosimulations is instrumental for studying the expected ecosystem's response to predicted changes in habitat conditions due to the lack of field data at appropriate spatial and temporal resolutions over wide regional extents throughout sufficient time spans. Computational simulations, based on reaction-diffusion equations (RDE), were performed in order to quantitatively assess the form of shrubland pattern changes in response to decreasing and increasing rainfall regimes and during recovery following catastrophic removal of plants, which would result from fires or droughts. Patch pattern properties were analyzed using the Shannon–Wiener fragmentation (SW) metric ($=\Sigma$ Si Ln Si, where Si is the area fraction of patch i of n patches) and the edge ratio (ER) metric ($=$sum of edge area/sum of patches' area). The SW fragmentation change during pattern formation is characterized by 3 phases, where in the first phase there is decreased fragmentation, and the third phase represents the evolution of equilibrium. The second phase is the most interesting one, where we have observed pattern regularization obtained by rearranging the shrubs' patches while increasing the fragmentation of the shrub patches. Such regularization phases seem to be a primary characteristic of self-organized behavior in these ecosystems. The general form of pattern properties change with decreasing or increasing rainfall according to SW fragmentation levels reached at equilibrium, which revealed a non-linear configuration with three divergence points. At these divergence points, the pattern evolution trajectories diverge according to the rainfall change rates. The most important divergence point occurs when rainfall drops below the critical desertification level. Whereas a slow reduction in rainfall would allow the shrub patches to be maintained below this critical rainfall level, rapid changes would cause immediate desertification. Edge ratios are closely linked to rainfall levels, and thus, they may provide early warnings and allow changes in the habitat conditions to be monitored due to climate changes.

1. Introduction

Desertification and land degradation, stemming from increasing anthropogenic pressures and global warming, are threatening to cause severe losses and damages to natural and semi-natural ecosystems, especially in hot water-limited ecosystems (IPCC, 2007). Although there is early evidence concerning such damages (Diffenbaugh and Field, 2013; Tilman et al., 2001; WMO, 2005), their rates of processes and relationships with their driving forces are not well understood. The lack of field data at appropriate spatial and temporal resolutions and at wide regional extents, throughout sufficient time spans, has greatly hampered studying these processes (e.g., Dagbovie and Sherratt, 2014). Furthermore, the field information available regarding environmental changes cannot be explicitly attributed to a single driving force (anthropogenic or natural), nor to a single disturbance–recovery cycle.

The use of geosimulations for studying the expected ecosystem's response to predicted changes in habitat conditions is almost the only way to coherently assess the scenarios of change. Diverse types of geosimulations have been implemented for this purpose: physical, kernel based, and stochastic (Borgogno et al., 2009). However, in the absence of adequate field data, none of these methods has been validated (Borgogno et al., 2009; Dagbovie and Sherratt, 2014). Since the pioneering work of Turing (1952), reaction–diffusion equations (RDE) have been implemented in most diverse fields of pattern-forming mechanisms. Furthermore, since the early work of Lefever and Lejeune (1997), RDE have been used extensively for assessing vegetation pattern evolution in water-limited ecosystems. Among the numerous existing works that have gained ecological recognition (e.g., Cantrell and Cosner, 2003;

---

* Corresponding author. Tel.: +972 48292361; fax: +97248234757.
E-mail address: elenaroitberg@gmail.com (E. Roitberg).

http://dx.doi.org/10.1016/j.ecoinf.2016.02.001
1574-9541/© 2016 Elsevier B.V. All rights reserved.

Klausmeier, 1999), there are almost no works that have utilized RDE for explicitly assessing the response of pattern properties (beyond simple cover and density measures) to rainfall changes.

Landscape metrics are frequently used for assessing land degradation and desertification in patterns observed in nature. There are works that have examined the area-frequency relationships, suggesting that truncated power-law distributions serve as an indicator of disturbances and desertification (Kefi et al., 2007a; Lin et al., 2010). However, among the few existing studies, almost no work has followed the changes in these indicators throughout processes explicitly representing rainfall change (see Kefi et al., 2010; Sherratt, 2015). Such investigations rely on the recorded (see Appendix **B**, Fig. B1) and simulated variations in precipitation that took place in the last century and on multi-model forecast simulations, which predict even greater precipitation alterations in the Mediterranean water cycle characteristics in the 21 century (Mariotti et al., 2008). From 2070 to 2099, the average of the models predicts a 20% decrease in land surface water availability and a 24% increase in the loss of fresh water around the Mediterranean Basin owing to reduced precipitation and warming-enhanced evaporation, with a remarkably high consensus among the analyzed models (see Appendix B, Fig. B2).

The present study utilizes RDE for simulating scenarios of the response of vegetation patch patterns to changes in rainfall and to the catastrophic and complete removal of shrub cover. Vegetation and soil patterns reaching equilibrium at a certain rainfall level are used in the first scenario as input for the following simulations by implementing a decrease or increase in precipitation. The latter scenario is attained by decreasing shrub cover from previous simulations to zero, while keeping their heterogeneous soil conditions as input for the following simulations. These later scenarios represent the effects from fires (Naveh, 1994; Pausas, 2004) and extreme and long draughts that occur at certain frequencies in the Mediterranean and in desert fringe ecosystems (e.g., Hoerling et al., 2012).

Calculating the changes in the patch pattern properties using these simulated processes would (1) allow us to attain a better understanding of the patch patterns that are supposed to evolve under the predicted scenarios of climate change and (2) may facilitate early detection of degradation and desertification processes.

1.1. Implementation of Reaction-Diffusion equations

In the last 20 years, there has been a growing use of RDE for studying pattern changes within the context of desertification and climate change (e.g., Barbier et al., 2006). There are numerous studies that have modeled the formation of various patterns (spotted, labyrinths, rings, and banded stripes) in desert fringe ecosystems (e.g., Aguiar and Sala, 1999; Bromley et al., 1997; D'Odorico et al., 2006; Klausmeier, 1999; Leprun, 1999; Meron et al., 2004; Rietkerk et al., 2002; Von Hardenberg et al., 2001; and Zelnik et al., 2013). Positive feedback between plant density and water infiltration is often included in hypotheses concerning possible causes for vegetation pattern formation (Gilad et al., 2007; Hille Ris Lambers et al., 2001). This positive feedback is due to the fact that at higher plant densities more water infiltrates into the soil than at lower plant densities. In vegetation-patterned areas, rain falling on bare soil will hardly infiltrate and some of it will be lost through runoff and evaporation (e.g., Reynolds et al., 1999), whereas a certain amount may subsequently accumulate in the vegetated patches, where water infiltration is easier (Hille Ris Lambers et al., 2001). Reaction-diffusing simulations were developed for representing this type of water redistribution and productivity in water-limited ecosystems (Gilad et al., 2007; Hille Ris Lambers et al., 2001; Klausmeier, 1999; Leprun, 1999; and Scheffer et al., 2001). However, there has been relatively limited use of these models in explicitly simulating the effects of decreased or increased rainfall conditions on these patterns' properties.

Reaction-Diffusion (RD) models were developed for representing bistable ecosystems evolving through positive feedback between plant density and water infiltration. The version of the model utilized here was adopted in numerous studies in this field (e.g., Dagbovie and Sherratt, 2014; Kefi et al., 2010; and Yizhaq et al., 2014). The RD model is formulated (Hille Ris Lambers et al., 2001) as a system of three partial differential equations describing the dynamics of three state variables: plant density $P[\frac{g}{[m^2]}]$, soil water W [mm], and surface water O [mm]. RDE have been shown to allow realistic simulation of patch pattern dynamics (PPD) (Rietkerk et al., 2002).

The full model reads as follows:

$$\begin{aligned}\frac{\partial P\left(\vec{x},t\right)}{\partial t} &= \left[\text{plant growth at } \vec{x} \text{ at t}\right] \\ &\quad - \left[\text{plant loss at } \vec{x} \text{ at t}\right] \pm [\text{plant dispersal}]\end{aligned} \tag{1a}$$

$$\begin{aligned}\frac{\partial W\left(\vec{x},t\right)}{\partial t} &= \left[\text{infiltration rate at } \vec{x} \text{ at t}\right] - \left[\text{plant water uptake at } \vec{x} \text{ at t}\right] \\ &\quad - \left[\text{evaporation and drainage at } \vec{x} \text{ at t}\right] \pm [\text{water movement}]\end{aligned} \tag{1b}$$

$$\begin{aligned}\frac{\partial O\left(\vec{x},t\right)}{\partial t} &= \left[\text{rainfall rate at } \vec{x} \text{ at t}\right] \\ &\quad - \left[\text{infiltration rate at } \vec{x} \text{ at t}\right] \pm [\text{overland flow}]\end{aligned} \tag{1c}$$

The parameters for this model are listed in Appendix A.

In this model, patterns emerge through the balance among water infiltration, evaporation, plant uptake, and surface runoff, with positive feedback mechanisms between biomass and water, and where plant growth is promoted by the increase in infiltration under and near the colonizing plants.

1.2. Parameterization of the Patch Dynamics

Assessment of the patch pattern properties in response to changes in habitat conditions has attracted wide attention in ecology. Most diverse types of landscape metrics have been implemented for this purpose (Lustig et al., 2015). However, almost no works have explicitly linked the changes in climate to the patch pattern properties (Uuemaa et al., 2013). However, measures of ecosystem disturbances, such as the increase in pattern fragmentation, may serve as indicators of an ecosystem's response to climate change. The breakdown of patches can be detected by examining the parameters of patch size distributions, such as Shannon–Wiener fragmentation (utilizing Shannon and Wiener, 1949, information index), dominance (Shoshany, 2002), the power law (Kéfi et al., 2007b), and the simple average patch size and standard deviation (D'Odorico et al., 2006). Within this perspective, an increase in the number of small patches is regarded as a sign of desertification (e.g., Kéfi et al., 2007b; Lin et al., 2010). In studies concerning the formation of tiger stripes as indicators of desertification, Valentin et al. (1999) and Sherratt (2015), for example, investigated the link between the stripes' wavelength and rainfall. With convoluted and connected patterns, parameters describing the shape of patches, such as edge ratios (Shoshany, 2012) may be instrumental for detecting morphological changes linked to desertification. In this study, we used both types of metrics, those representing parameterization of patch size distribution and those representing edge ratios (Table 1) owing to differences in their information content throughout the pattern evolution process.

2. Methodology

The methodology consists of three stages: (1) developing experiments representing four different scenarios of habitat changes,