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Modelling the critical transition from Chilean evergreen forest to savanna: Early warning signals and livestock management

Andres Baeza

Global Institute of Sustainability, Arizona State University, Tempe, AZ, United States

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ABSTRACT

Semi-desert areas are sensitive to changes in rainfall and agricultural pressure, prone to abrupt changes and to the collapse of ecological functions. The sclerophyllous evergreen forest of central Chile, known as *matorral*, has been extensively overgrazed by domestic livestock. As a consequence, the native and endemic species of this forest community have been replaced by a savanna-type environment dominated by the species *Acacia caven*, known as *espinales*. It has been hypothesized that the collapse of matorral forest can be abrupt, and the two ecosystems represent two alternative stable states. To understand the ecological dynamics that occur during this transition, their signature in space, and the consequences of livestock management, a cellular automata model that considers the local interaction among forest vegetation, Acacia, and livestock management was developed. By simulating and analyzing the process of fragmentation in space and time, in a gradient of livestock pressure and aridity, the results show that the system exhibits properties of "robust criticality", with a shift of patch-size distributions from models matching power-laws to models matching truncated power-laws as livestock pressure increases nearby the point of collapse. Simulation results in scenarios with rotation of livestock at the tipping point reveal the interaction between resting frequency and forest conservation. These results provide information to design better management strategies in human-modified landscapes in the remaining Chilean matorral.

1. Introduction

Semi-desert areas cover more than 41% of the surface of the planet and sustain 2 billion people via agriculture and livestock. These are ecological systems highly vulnerable to climate- and human-induced changes. As a consequence, these environments have been largely degraded (Millennium Ecosystem Assessment, 2005). Grazing and browsing pressure from livestock, along with extensive droughts and heavy rains, are the major drivers of degradation in semi-desert areas. More than 70% of the total pastoral terrain and rangeland in semi-desert areas has been somehow degraded (Millennium Ecosystem Assessment, 2005). Obtaining early-warning indicators that can provide timely information about the condition of the ecological functions in semi-desert ecosystems is critical for developing a new generation of preventive rangeland management strategies (Reynolds et al., 2007).

Early-warning indicators of transitions are clues provided by the spatial and temporal structure of systems. In ecological systems, these clues inform us of the possibility that the ecological functions of the system are close to a point of transition or collapse (Scheffer, 2010; Scheffer et al., 2012). In recent years, several studies have formalized the type of information that needs to be obtained from ecological systems to understand and predict these critical transitions, and new, rigorous statistical tools have been developed to detect early signals (Kéfi et al., 2014). Yet, there is still an important gap in the literature in terms of how to incorporate this information into management strategies that can improve conservation and restoration in landscapes shared by human activities and natural ecosystems (Kéfi et al., 2011).

In semi-desert environments, clues about the spatial structure of vegetation are associated with the formation of patches of different sizes (Kéfi et al., 2007). The lack of water in semi-desert environments generates harsh conditions for plants to germinate in bare soil far from the shade of adult vegetation. Some trees and bushes are more likely to germinate close to other plants, which facilitates the growth of juveniles. From a spatial scale larger than individual plants, it is possible to observe patches of vegetation of different sizes. While the complexity of the ecological interactions make generalization of early-warning signals challenging (Moreno-de las Heras et al., 2011), theoretical studies at local scales with test-plots in areas of Mediterranean semi-deserts have shown that the patch-size distributions (relationship between the patch sizes of a system and their frequencies) change from closely resembling power law-like patterns (i.e., there are many small patches and only few that are very large) to truncated power laws (similar to power laws, but lacking the largest patch sizes) when the system approaches a point of imminent collapse (Kéfi et al., 2007). Studies at regional scales have

E-mail address: abaezaca@asu.edu.

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confirmed the melting of the power law-like patterns in ecosystems associated with the loss of function and processes of desertification (Berdugo et al., 2017).

In the semi-arid region of central Chile, the landscape has been dominated by a dense evergreen forest known as *matorral*. The matorral is composed primarily of perennial sclerophyllous trees such as *Peumus boldus* (boldo), *Cryptocarya alba* (peumo), and *Quillaja saponaria* (quillay), as well as woody sclerophyllous scrubs (small trees) such as *Cassia coquimbensis, Schinus polygamous*, and *Litrea caustica* (Gajardo, 1994). Over the last 100 years, this forest has been extensively reduced. More than 80% of the native and highly-endemic vegetation has been depleted (Fuentes and Simonetti, 1981; Fuentes et al., 1986; Holmgren, 2002). The fall of the forest gave rise to a savanna-like type of environment dominated by the species *Acacia caven*, known as *espinales* (Fuentes et al., 1989; Ovalle et al., 1996). Between 1975 and 2009, more than 45% of the land covered by forest has transitioned to espinales (Van de Wouw et al., 2011). Today, Acacia trees are the most common species in central Chile (Ovalle et al., 1990).

According to the literature and fieldwork, herbivory and pastoralism activities have played a key role in this transition, and the transformation from forest to savanna has been mostly human-induced due to overgrazing and browsing by large livestock mammals (goats and cows), the introduction of invasive species (rabbits), and land clearing for agriculture and mining (Fuentes et al., 1989, 1986, 1983; Pickett et al., 1987). First, the presence of livestock influences vegetation dynamics by increasing mortality, changing species composition, and decreasing biodiversity. Livestock grazing induces soil compaction, which subsequently can increase rainfall runoff, soil erosion and, finally, the depletion of nutrients in the soil (Silva et al., 1978). Second, the presence of domestic livestock has an indirect benefit on the colonization of *Acacia caven*. Specifically, Acacia trees provide succulent pods that are eaten by livestock, and in return germination is facilitated, the distance of seed dispersal increases, and Acacia intraspecific competition is reduced. This ecological mechanism thus creates an advantage for Acacia over the native vegetation in livestock-dominated landscapes (Holmgren, 2002; Armesto and Pickett, 1985).

Significant distinctions exist between these two ecosystems. As mentioned above, forest coverage is highly dense. Acacia-dominated environments, on the other hand, are characterized by large open areas, with sparse vegetation coverage and low biodiversity (Ovalle et al., 1996; Fuentes et al., 1989; Bahre, 1979). An important ecological characteristic of the matorral forest is the role of local positive interactions between species. The colonization success of seeds inside the forest is facilitated by the presence of nearby sclerophyllous vegetation, which helps reduce water loss in a water-limited environment (Fuentes et al., 1984). Dry summers and short rainfall seasons characterize the climate of this region. The long and dry summers, combined with long-lasting droughts, generate adverse conditions for seedlings from sclerophyllous species. Adult plants near seedlings can create favorable microclimatic conditions that help the soil retain moisture and reduce its temperature in summers (Cares et al., 2013). These local conditions provide a "nursing effect" (Fuentes et al., 1984) that facilitates the successful establishment of young trees and shrubs (Cuevas et al., 2013; Jiménez and Armesto, 1992; Fuentes et al., 1984).

The interaction of the biotic effect of local facilitation and the abiotic effect of rainfall plays an important role in the persistence of seedlings. Low rainfall availability, especially at sites with high exposure to sunlight, generates more arid conditions. Recurrent and prolonged droughts reduce seedling recruitment of many species (Holmgren et al., 2001). Intense rainfall, on the other hand, causes soil erosion and nutrient runoff that negatively affect soil fertility.

The two ecosystems in the desert region of Chile, sclerophyllous and Acacia-dominated communities, are considered to be two alternative stable states with hysteresis (Holmgren, 2002). This implies that if the forest crosses a threshold of degradation, it can collapse to a savanna environment without the possibility of a fast recovery. In this region, therefore, a system for the development of early indicators of the transition is an important management tool needed to support the conservation and restoration of the remaining matorral ecosystems (Holmgren et al., 2006). While previous studies have provided a framework to consider the interaction among forest, Acacia, and management (Holmgren, 2002; Armesto and Pickett, 1985), so far, there has not been an attempt to simulate the dynamics of the transition and the ecological interactions within the same analytical framework.

The purpose of this work is therefore to explore the mechanisms of disturbance that may play a role in promoting the transition of the Chilean matorral to savanna, and to investigate the interaction between the signals of degradation and the management of the system. The forest community of central Chile has a type of semi-desert vegetation that is prone to forming patchy landscapes composed of woody vegetation, and several studies have confirmed the fragility of the system when faced with human perturbation. Furthermore, recent studies have investigated the local interaction within the system and the possibility of detecting these changes based on spatially-explicit information associated with the patchiness of the vegetation (Fuentes-Castillo et al., 2012). Therefore, this work proposes an important model for investigating the interaction between the signals of degradation, and their association with conservation and management efforts.

A type of environmental management that could benefit from incorporating this information is the use of rotational and resting strategies. Rotational and resting schemes, or multi-paddock grazing strategies, involve rotating livestock to distribute the grazing pressure over large areas. The use of multi-paddock rotation systems (Hart et al., 1988) is a widely-used strategy by pastoral communities around the world (Briske et al., 2008), and it involves the movement of animals from one paddock to another for the sake of providing resting time for vegetation biomass to regenerate. Two important properties of multi-paddock rotation management are 1) the number of animals to be moved and 2) the time required to do so (Hart et al., 1988).

Three specific questions guide this research:

1) Under what conditions of aridity and livestock pressure are the two alternative stable states more likely to be observed?
2) What kind of spatial patterns and early indicators of transition emerge as the system transitions to savanna?
3) How do rotational management strategies influence the likelihood of this transition?

To provide insight into these questions, a cellular automata model was developed to simulate the birth-death process of sclerophyllous vegetation and Acacia in the Chilean matorral. The model was then simulated in a gradient of aridity and livestock pressure, and under different strategies of rotation, to investigate the trajectories of the forest under different pulses of livestock pressure.

2. Methods: the model

A cellular automata is a type of spatially-explicit model that allows for the incorporation of local ecological interactions into models of population and community dynamics, using a discrete set of sites and discrete time steps (Balzter et al., 1998; Durrett and Levin, 1994; Hogeweg, 1988). Here, the cellular automata approach is used to simulate the dynamics of a landscape composed of four land types: a bare soil type, D; annual grasses, G; Acacia, A; and forest, F (Fig. 1).

In each time step, t, the probability that a site will change from one state to another is determined by the state of the nearest neighbors, which are defined as the sites in radius 1 within a Moore neighborhood structure. The possible land type transitions are depicted in Fig. 1. The model includes the influence of livestock pressure, represented by symbol $\mathscr{L}$, and the effect of aridity or lack of rainfall, ϕ. Livestock pressure influences the mortality rates, and aridity influences colonization rates. Livestock pressure, additionally, influences the rate of