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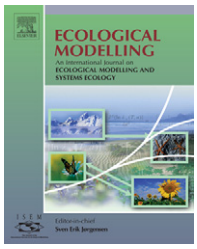

Self-organized spatial patterns of vegetation in alpine grasslands

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ABSTRACT

There is increased interest in vegetation spatial pattern as an indicator of transition shifts following catastrophes. Much, however, remains unknown about the mechanisms that underlie spatial pattern formations. In this study, we examined how the spatial heterogeneity of species distributions in the grasslands of the Central Pyrenees and Middle Atlas Mountains is associated with plant species diversity and the importance of self-organizing processes in the control of pattern formations. In the grasslands of the Central Pyrenees and Middle Atlas, the spatial heterogeneity of species distributions increased along a habitat degradation gradient defined by an increase in bare soil. In Central Pyrenees grasslands, however, the increase in heterogeneity was associated with self-organizing bare soil formations, rather than the self-organizing distribution of plant species. In Middle Atlas grasslands, the increased heterogeneity of species spatial distributions was a consequence of the self-organizing capacity of the composing species; the increase in bare soil was randomly distributed. In the more heavily grazed grasslands (Middle Atlas), but not in the more lightly grazed and better preserved ecosystem (Central Pyrenees), plant species richness and diversity declined significantly with an increase in grazing pressure because fewer species were able to colonize empty space. On the contrary, the colonization of bare soil by new species increased the diversity and spatial organization of new colonizing species in Central Pyrenees grassland.

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1. Introduction

Typically, ecosystems involve the interactions of many components, leading to multiple possible states whose representation can be altered by human activity (Scheffer and Carpenter, 2003). Furthermore, ecosystems can sometimes show little change until, suddenly, at a critical threshold, they shift to a more degraded state (Scheffer et al., 2001). Theory is based on simple models in which the ecosystem is described by a few variables and the complexity of natural ecosystems is not considered (May, 1977; Scheffer, 1998). Introduction of environmental heterogeneity (physical) into these models alters their behaviour, often leading to the amelioration of sudden transitions (van Nes and Scheffer, 2005). But, there is evidence that catastrophic shifts can be associated with self-organization of spatial patterns of vegetation (Rietkerk et al., 2004; Pascual and Guichard, 2005). Can spatial pattern, either in physical or vegetation structure be used to predict the likelihood of an abrupt transition? To answer this question we need a better understanding of the factors that determine pattern formation.

The primary objective of pattern analyses is to detect emergent properties, macroscopic phenomena that result from

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interactions among individual components. Pattern distributions and the abundance of plant species primarily result from higher-level processes such as environmental factors (e.g., climate, topography) and disturbance history (anthropogenic grazing and burning), whereas biotic factors, e.g., competition, vegetative propagation, and seed dispersal, act at local level (Frelich et al., 1998). When examining spatial patterns, it is important to know whether spatial patterns arise from external perturbations that push the system away from a homeostatic state (non-stationary change), or whether spatial patterns emerge partly within a homeostatic state, due to intrinsic dynamics of the system (stationary change). It is a challenge to distinguish fluctuations caused by intrinsic interactions from trends caused by external stimuli. Power spectrum calculations assume stationarity and cannot distinguish between stationary and non-stationary signals (Ivanov et al., 2002). Distinguishing trends from fluctuations requires the use of detrended fluctuation analysis (DFA), which removes the trends (Peng et al., 1992). DFA avoids spurious correlations caused by non-stationarities (Bunde et al., 2002), and is one of the most robust methods of fractal analysis (Taqqu et al., 1995). One of the advantages of separating spatial patterns caused by pre-existing environmental heterogeneity from self-organizing processes is that differences in the fractal-scaling exponent of self-organizing patterns can be used to detect intrinsic changes in the control mechanisms. Self-organization is distinct from the clustering or autocorrelation that can result from environmental heterogeneity.

Non-random spatial patchiness of vegetation can result from positive feedback mechanisms associated with plant facilitation (Bertness and Callaway, 1994; Pugnaire et al., 1996; HilleRisLambers et al., 2001) or from self-organizing patches of bare soil, which increase run-off and soil erosion when vegetative cover is reduced (Elwell and Stocking, 1976). On the other hand, negative feedback processes caused by competition, while stemming runaway trends due to positive feedback, can decrease self-organization and increase randomness (Calé et al., 1989; Solé et al., 2002). The effects of positive and negative feedback loops acting simultaneously, even in strictly homogeneous and isotropic environments, can generate spatial patterns of vegetation (Lefever and Lejeune, 1997; Lejeune et al., 2002).

In this study, we analyzed the underlying mechanisms that influenced the spatial patterns of vegetation along degradation gradients in alpine grassland ecosystems in the Central Pyrenees (Spain) and the Middle Atlas Mountains (Morocco). In doing so, we addressed the following questions:

(1) Is the spatial heterogeneity of plant distributions associated with ecosystem conservation in subalpine grasslands?
(2) How does the relationship between spatial heterogeneity and ecosystem conservation vary with differences in the intensity of grazing pressure and soil loss?
(3) How do positive and negative feedback processes, such as spatial self-organization and plant competition, influence spatial patterns along a gradient of grazing disturbance?

2. Methods

2.1. Study areas

The Middle Atlas site (13,429 ha, 1900 m asl) is in the Ait Beni Yacoub (Morocco) fraction rangeland area (33°14′N, 5°04′W) where the average annual rainfall is 800 mm and the mean annual temperature is 22 °C. The vegetation is subalpine grassland dominated by *Carex* spp. and *Poa* spp., with some remnant species from the degraded *Cedrus* forest, such as *Genista pseudopilosa* Casson and *Thymus* spp. In 2000, at 29 locations within the Middle Atlas site, we identified the settled sheep producers and grazing areas, and recorded flock size and the amount of time sheep spent in the grazing areas. The locations were georeferenced using geographical position system (GPS) and, to create digital maps, the data were entered into a Geographical Information System (GIS). The average stocking rates of small ruminants ranged from 1.00 to 5.44 animals per ha per year.

In the Spanish Pyrenees, we studied two areas that are 48 km apart, Aísa (42°42′N, 0°34′W) and Ordesa (42°36′N, 0°00′), which are representative of the calcareous summer pastures of the Central Pyrenees. At Ordesa National Park (15,608 ha) and Aísa (8154 ha), mean annual temperatures and mean annual rainfall are 4.9 °C and 1721 mm, and 6.2 °C and 1249 mm, respectively. The vegetation of the areas is typical of the alpine and subalpine belts of the calcareous Pyrenees (Braun-Blanquet, 1948; Vigo and Ninot, 1987). Data were collected in the dense pastures of *Bromion erecti* and *Nardion strictae* that are between 1800 and 2000 m asl (García-González et al., 1991; Aldezabal, 2001). Between July and September (2002), the Aísa pastures (1241 ha) were used by 150 cattle and 2000 sheep. The Ordesa site has two pastoral areas, Góriz and Sesa. Góriz (5700 ha) held 6500 ewes and 200 cows. Sesa (1600 ha) held 2800 ewes, 550 cows, and 91 horses (Fillat, personal communication). In Góritz, Aísa, and Sesa, the average stocking rates were 0.338, 0.584, and 1.038 small ruminants per ha per year, respectively. To determine the equivalents of large livestock and small ruminants, body weights (W) were transformed into metabolic weights ($W^{0.75}$). As such, six sheep are equivalent to one cow (Heitschmidt and Taylor, 1991).

2.2. Data collection and analysis

In 2000 and 2001 at the Middle Atlas site, and in 2004 in the Pyrenees, vegetation surveys were conducted during the peak of vegetation growth (June–July). At each site, we randomly selected 27 transects (250 m long) parallel to the slope line. To estimate plant abundance and richness in each transect, we used the point-intercept method (every 20 cm) (Goodall, 1952).

The proportional diversity H' index, which is equivalent to Shannon entropy, integrates richness and evenness using the Shannon information index (Shannon, 1948). Evenness is the ratio between the non-equilibrium entropy and the corresponding equilibrium entropy (H/H_{max}), and it reflects the disorder-based complexity (Landsberg and Shiner, 1998).

The proportion of intercepts attributed to plant species i (p_i) depends on the length of the transect segment (window size = ε) over which presence or absence is recorded. Thus, $H'_{(\varepsilon)}$

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