

Original Research Article

Geodiversity increases ecosystem durability to prolonged droughts

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ABSTRACT

Interactions between biotic and abiotic factors dictate the response of ecosystems to varying conditions and disturbances. The importance of the relationship between these factors is demonstrated in the extensively studied interactions between water-limited vegetation and its ecosystem's physical components. Landscape geodiversity is often neglected in studies of vegetation dynamics and response to drought. Here, we combine field studies and mathematical modeling to elucidate the effects of geodiversity on shrub mortality following drought. In Israel's semi-arid northwestern Negev Desert, we found that homogeneous hillslopes, with little or no stoniness, experienced considerable shrub mortality following droughts, while neighboring slopes with higher stoniness showed little or no mortality. A mathematical model describing the dynamics of water-limited vegetation and accounting for landscape geodiversity predicted similar responses. The measurements and the model suggest that geodiversity increases the amount of water available for the shrubs, thereby increasing their durability. Future climate predictions of reduced precipitation and increased drought frequency in many regions make studies of ecosystem responses to water deficiency timely. Our findings suggest that future studies should account for landscape geodiversity in order to explain local differences in vegetation mortality and to better assess the possible impacts of climate fluctuations on ecosystem dynamics. In particular, geodiversity has a great effect on regime shifts and their nature.

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1. Introduction

An ecosystem's responses to extreme climate events are dependent on the interactions between its abiotic and biotic components. The spatial and temporal distribution of the abiotic conditions (e.g., geology, topography, soil type and climate) dictates the present biotic organization and the future reorganization (Ackerly et al., 2010; Anderson and Ferree, 2010; Beier and Brost, 2010). The relationships between abiotic diversity or nature's stage, extreme climatic conditions and biotic reorganization, on both the population and community levels, are unclear due to the complex interactions between these three variables (Lawler et al., 2015).

Geology, soil, and topography, as components of geodiversity, all affect the availability of resources for vegetation, modifying

biotic organization and reorganization. Geology is an important determinant of the formation (pedogenesis) and diversity of soils (pedodiversity), through its influence on the chemical and physical properties of soil and water flow. These physical properties affect the organization of plants and microbes that regulate ecosystem primary production and decomposition (Kruckeberg, 2002). Therefore, pedodiversity is a substantial component of studies related to geodiversity-biodiversity relationships (Ibáñez et al., 2012; Mcbratney, 1992; Phillips 1999; Petersen et al., 2010).

Drought is a primary driver that shifts these relationships. For instance, droughts are known to decrease primary productivity (Ciais et al., 2005), drive the reorganization of communities and ecosystem function (Engelbrecht et al., 2007), affect water and nitrate dioxide fluxes and reduce plants' water-use efficiency (Reichstein et al., 2002). Studies have shown that droughts have both episodic and continuous effects on woody vegetation mortality rates that induce ecosystem state change (Bowers, 2005). In addition to plant mortality, vegetation responses to drought-induced water deficiency, on the landscape level, include modification of plant spatial patterns (Tongway et al., 2001; Rietkerk et al., 2008; Borgogno et al., 2009).

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Many mathematical models have been developed to explain the relationships between water flow and vegetation pattern formation (Klausmeier 1999; Lejeune et al., 2002; Rietkerk et al., 2002; Gilad et al., 2004). These models are based on short range facilitation of vegetation and longer range competition for water, which is the main growth limiting factor. The different models capture different facilitation mechanisms. These mechanisms include the infiltration contrast—the higher infiltration rate of surface water in vegetated spots due to the effect of vegetation on the soil crust (Rietkerk et al., 2002; Gilad et al., 2004; Getzin et al., 2016); the water uptake feedback—denser vegetation's higher water uptake rate due to more developed root systems and higher water extraction efficiency (Klausmeier 1999; Zelnik et al., 2013; Kinast et al., 2014; Sherratt 2015); and the root augmentation feedback—the higher growth rate of denser vegetation due to its spatially extended root system, which allows it to extract water from larger soil volumes (Gilad et al., 2004).

All the models mentioned above describe the dynamics over spatial scales that allow continuous description of the vegetation in terms of biomass density (usually on the scale of tens of centimeters to tens of meters) and temporal scales that are larger than the typical time scales for vegetation growth (usually months to years). The models predict five basic vegetation pattern states along the rainfall gradient (from wet to dry): uniform vegetation cover, a gap pattern (Zelnik et al., 2015; Getzin et al., 2016), a labyrinthine pattern, a spotted pattern, and bare soil. These models assume a homogeneous landscape and the spatial heterogeneity of vegetation results from its interaction with water. However, most ecosystems are not homogeneous, and heterogeneity exists due to soil texture, stoniness, micro-topography, nutrient distribution and other factors. Our specific objective was to integrate field and modeling studies in order to elucidate the effects of abiotic diversity on the biotic responses to drought.

The field study was carried out in a Long Term Ecological Research (LTER) site where, presumably, severe droughts (during 2008–2009) caused a state change over the last decades (Sher et al., 2012; Paz-Kagan et al., 2014; Hoffman et al., 2016). Most notably, the cover by mature shrubs dropped substantially due to high mortality rates of the dominant shrub species, *Noaea mucronata*. The shrub mortality in the study region (Fig. 1S and Fig. 2S of the Supplementary materials) has been clearly observed as white patches caused by the accumulation of snail shells on the ground. Before the sequence of drought years, the snails fed on and lived in the shrubs. The mortality of the dominant shrub species was estimated as 90% (Sher et al., 2012) of the total population. Increased shrub

mortality in additional sites across the region supports the hypothesis of a climate-driven event (DeMalach et al., 2014; Shoshany and Karnibad 2015).

The abovementioned studies neglected spatial heterogeneity and referred to the mortality across the entire site. However, a careful inspection of the hillslopes in the site reveals that the mass shrub mortality has not been spatially uniform and, in fact, strongly depends on the hillslopes' geodiversity. Two different types of hillslopes (with regard to the surface cover) were identified; one with no stones or rock fragments (homogeneous hillslopes) and the second with rock fragment cover (heterogeneous hillslopes) ranging from ~10 to 30%. In the homogeneous hillslopes, the shrub mortality was massive (>90%), whereas in the heterogeneous hillslopes, it was quite small (~7%).

Recently, theoretical studies have suggested that landscape heterogeneity can increase vegetation survivability and make regime shifts more gradual (Yizhaq et al., 2014; Yizhaq and Bel 2016). However, these theoretical studies have not suggested the mechanism by which the heterogeneity influences vegetation dynamics. Here, we attempt to identify this mechanism affecting regime shifts in vegetation ecosystems. To achieve this goal, we combined field measurements and theoretical studies of a well-explored mathematical model.

2. Methods

2.1. Description of the study site

The field study was implemented in the LTER station of the Sayeret Shaked Park, in Israel's semi-arid northwestern Negev Desert (31°27' N, 34°65' E, 190 m a.s.l., shown in Figs. 1S and 2S of the Supplementary materials). The LTER site is located in the transition zone between the semi-arid Negev region and the dry sub-humid Mediterranean region of central Israel. The climate conditions in the region are typical semi-arid Mediterranean, with cool wet winters and hot dry summers (>six month dry period). Across the region, a rainfall gradient exists from west to east and from north to south, but inter-annual variability can drive the aridity isohyet farther north in extremely dry years. The LTER station spans an area of ~20 ha, which has been surrounded by a fence since the late 1990s to prevent livestock access. The region's lithology comprised of chalk of the Eocene and Plio-Pleistocene eolianite. The landform is dominated by rolling hills, with hillslope inclines ranging between 3° and 6°. The soil in the LTER site is classified as loessial Calcic Xerosol, with a sandy loam to loamy sand texture (Singer, 2007).

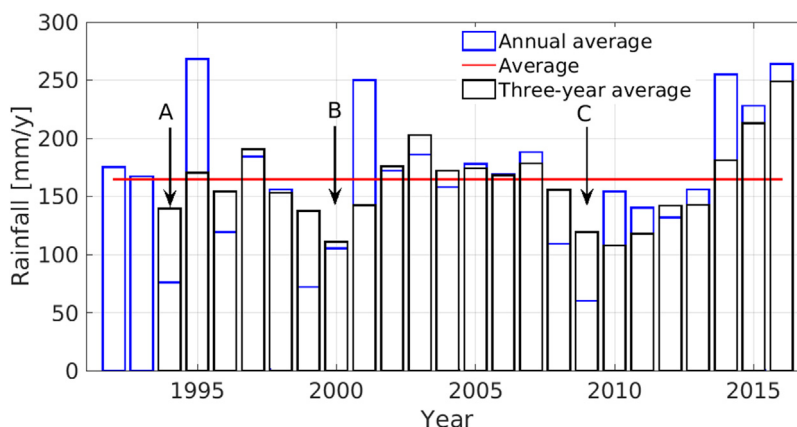


Fig. 1. Average annual precipitation in the Sayeret Shaked Park LTER. The blue bars show the measured annual accumulated precipitation and the black bars show the annual average of the previous three years. The average annual precipitation is 164.8 mm/year and is marked by the horizontal black line. The letters A, B and C denote years with significantly low precipitation rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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