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Self-organization and complex dynamics of regenerating vegetation in an arid ecosystem: 82 years of recovery after grazing

V. Lawley [a,*], L. Parrott [b], M. Lewis [a], R. Sinclair [a], B. Ostendorf [a]

[a] *Landscape Science, School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, SA 5005, Australia*
[b] *Complex Systems Laboratory, Département de géographie, Université de Montréal, C.P. 6128 succursale "centre-ville", Montréal, Québec, Canada H3C 3J7.*

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ABSTRACT

Understanding the relative contributions of internal dynamics versus external factors in the process of community assembly is important for establishing guidelines for conservation and restoration of native vegetation. The role of internal dynamics and external factors in the process of community assembly at the local scale is a poorly understood issue in ecology, especially in highly variable environments. We analyse an 82-year spatiotemporal record of vegetation recovering from a history of overgrazing within a semi-arid environment to investigate the relative contribution of internal and external factors on community assembly. Community composition and spatial structure were used as indicators of change over time in four sites within a vegetation reserve, which were subjected to the same environmental constraints, climate and grazing history. The four sites follow remarkably different, asynchronous trajectories characterized by periods of stability interrupted by episodic change. The high variability between sites suggests that initial communities are internally reinforced through random chance events, directing them on different pathways of assembly and self-organization; hence external factors may play a less significant role in long-term community assembly at the local scale than previously believed. These results have important implications for rangeland restoration and conservation in many of the world's semi-arid regions.

1. Introduction

Natural communities are temporally and spatially variable. At continental scales evolutionary history and biophysical conditions influence species assemblages (Virtanen et al., 2006), whereas at the local scale community assembly is influenced by external variables and internal dynamics (Irvine et al., 2009). External variables include precipitation, topography and other elements of habitat, whilst internal variables include population dynamics and species interactions, such as dispersal, competition and other positive and negative feedback mechanisms. These processes operate and interact at multiple levels over time producing emergent properties and patterns within ecological systems (Levin, 1998). The high complexity of these interrelationships confounds the interpretation of how ecosystems behave and respond to change. Understanding the relative influences of internal versus external factors is therefore essential for management, developing complex models, and for predicting the effects of climate change on natural systems (Brown and Lawson, 2010).

Within semi-arid environments, low erratic rainfall and soil nutrients are limiting factors and therefore are often found to be key drivers of the system (Ward et al., 2000). Rainfall drives vegetation recruitment predominantly through episodic events (Wiegand et al., 1995), but also through slow continuous processes of recruitment and mortality (Watson et al., 1997). Nutrients are also limiting, particularly in Australia (Orians and Milewski, 2007), and redistribution through runoff and wind erosion create a patchy distribution of this resource (Schlesinger et al., 1999). The concentration of both water and nutrients provides suitable sites for vegetation establishment, and this is believed to cause the heterogeneous pattern characteristic of semi-arid vegetation (Ludwig and Tongway, 1995).

Internally within semi-arid communities, species have evolved traits and feedback mechanisms to cope with a variable environment and these arguably act as strong driving forces. One of the most well known in arid environments is the positive feedback between plant density and water infiltration (HilleRisLambers et al., 2001). Another process is the "nurse plant syndrome" (Niering et al., 1963), where seedlings are more likely to establish near adult plants because of the protection from abiotic factors and herbivory, particularly in resource limited environments (Francisco

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* Corresponding author. Tel.: +61 4 03885240.
E-mail address: valerie.lawley@gmail.com (V. Lawley).

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and Francisco, 2006). Facilitation is also a known process to occur, where seedlings are more likely to establish on 'resource islands' under shrubs (Reynolds et al., 1999). Here environmental constraints are altered (Butterfield et al., 2010), as variations in rainfall are buffered against by increased water infiltration and decreased runoff. Additionally, nutrients accumulate in these areas and there is protection from frost and high evaporation rates, which further reinforces these patterns. Historical contingency thus plays a key role in shaping community assembly, structure and dynamics at the local scale.

Clearly spatial organization of vegetation affects the dynamics of recruitment and colonization within arid communities, and is also an outcome of internal processes that have occurred in the past. Such organization has been found to influence the trajectories of community assemblage and composition (Miller et al., 2010) and also increase the resilience of arid ecosystems (Koppel and Rietkerk, 2004). Site history also plays an important role in how vegetation communities develop and respond to change (Adler et al., 2004). For example, sites with a long-term history of fire or grazing are well adapted to these 'disturbances' and a regime shift can have harmful impacts on these communities (Foster et al., 2003).

Long-term studies are necessary for analysing these complex dynamics. This is particularly true for semi-arid environments, where growth of perennial vegetation is notoriously slow, and the lag effects following disturbance may mask changes for decades (Guo, 2004; Valone et al., 2002). Several studies have investigated the relative roles of external and internal factors as drivers of community assembly (Butterfield et al., 2010; Guo, 2004; Houlahan et al., 2007; Reynolds et al., 1999; Schlesinger et al., 1999), however there is no common consensus. Houlahan et al. (2007) found from analysing 41 different animal and plant datasets that the primary drivers of community assembly are external environmental factors rather than competition; however these datasets were relatively short and implied that competition may be relatively more important at smaller spatial scales than at larger ones. Butterfield et al. (2010) used a 65 year dataset of decadal data (eight contiguous 100 m^2 plots, in which each plot was sampled 7 times with all locations of perennial plant canopies and their stem bases mapped) and using modelling found that internal processes of facilitation and competition are significant in driving community assembly. Hubbell (2005) used evidence from the past 30 years to argue that dispersal and recruitment limitation, by delaying competitive exclusion, can explain long-term assemblages of plant communities. Our study, using a dataset which is significantly longer and collected much more frequently, adds support to the argument that internal factors are significantly more important drivers of community assembly in semi-arid environments. Obtaining a better understanding of the underlying vegetation dynamics in semi-arid regions is essential for developing better restoration and management plans for the world's rangelands (Call and Roundy, 1991).

Here, we use an 82-year record of perennial vegetation change within four permanent quadrats which are in close proximity and have been subjected to the same climate and history of overgrazing; this allows assessment of the relative roles of external and internal factors in community assembly. We hypothesize that if the dynamics of species composition and spatial pattern are dissimilar between recovering sites despite major biophysical factors being equal (we explore rainfall, micro-topography and soils), then internal dynamic processes (such as historical contingency and interspecific interactions) are relatively more important for community assembly as compared to external environmental variables. Note, the term 'community' is used throughout to describe the species assemblages within and between quadrats at a given time, and not different vegetation types.

2. Methods

2.1. Study site

TGB (Theodore George Bentley) Osborn Vegetation Reserve (previously Koonamore Vegetation Reserve), and hereafter referred to as the reserve, lies within the semi-arid rangelands of South Australia (32°S, 139°E, Fig. 1). It is a 390 ha fenced exclosure, located approximately in the centre of Koonamore Station. It was named after Theodore George Bentley, the professor at the University of Adelaide who set up the site in 1925.

The substrate consists of low lying sand dunes with hard loamy soils on the intervening flats (Osborn et al., 1931). The three dominant soil types found on the reserve are sand and sandy loam, silt flats, and hard loamy soils with calcrete. These are representative of the main soil types of the arid plains of South Australia (Osborn et al., 1931).

Rainfall is low and highly variable with an annual average of 218 mm (StDev ± 125 mm), typically occurring in a few large isolated events during summer and early autumn. The region is essentially flat and does not exhibit differences in solar radiation, air temperature or orographic rainfall; hence, microclimatic conditions may be assumed to be equal across the reserve.

Vegetation is predominantly low open-woodland, with an upper storey dominated by *Acacia aneura, Eremophila* species, *Myoporum platycarpum* and *Alectryon oleifolius*. The understory is dominated by the shrubs *Atriplex vesicaria, Atriplex stipitata*, *Maireana sedifolia*, other shorter-lived chenopod shrubs and *Senna artemesioides* subspecies.

2.2. Grazing by sheep

The Koonamore pastoral lease was taken up in 1862 to graze livestock. The 95 km^2 paddock, in which the reserve lies, was fenced early in the 20th century. There are no existing records of stocking rates prior to the establishment of the reserve; however it is believed that the site of the reserve was grazed continuously from 1870 at a minimum of 15 sheep/km^2 (Crisp, 1975). The reserve was fenced in 1925 to exclude sheep and rabbits. At the time it was the most degraded section of the paddock (through over-grazing by sheep), with only mature trees remaining (Osborn, 1926). Paddocks

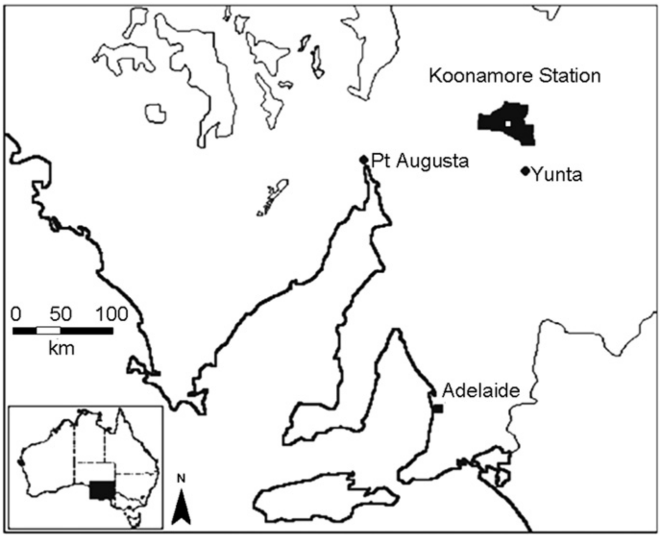

Fig. 1. Study area. Location map of Koonamore Station. TGB Osborn Vegetation Reserve lies approximately in the centre of the station.