Regeneration dynamics in arid subtropical thicket, South Africa

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ABSTRACT

In arid environments nurse-plants modify localised habitats and create regeneration opportunities for seedlings vulnerable to hostile conditions created by biotic and abiotic factors. Facilitation is thus recognised as an important process structuring plant communities in harsh environments. Here we use spatial patterns of species association and recruitment to infer species replacement patterns in arid subtropical thicket of South Africa. Although our study site was floristically impoverished, all major plant functional groups that characterise subtropical thicket were present. *Portulacaria afra* clumps comprised approximately 50% of the study site by area. The mean and median clump size was 16.5 and 6.9 m^2, respectively, indicating the prevalence of small individuals in the population. Approximately 90% of tree seedlings were recorded under *P. afra* clumps and 93% of *P. afra* seedlings were recorded under woody shrubs. *P. afra* seedlings were recorded more frequently than expected beneath *Rhigozum obovatum* compared with other woody shrub species. No clear recruitment patterns were recorded for *R. obovatum*. *Lycium cinereum*, a woody shrub, and the stem-succulent *Psilocaulon absimile* were distributed more frequently on nutrient rich patches than expected and both these species are replaced by grass as the nutrient rich patch ages. Mature trees were generally recorded growing to the south of the assumed founding *P. afra* stem indicating that tree establishment was more frequent on the shaded side of *P. afra* clumps. However, most trees grew towards the sunny north and east-facing aspects. Plant species replacement patterns are facilitated by nurse-plant effects in arid subtropical thicket. These recruitment patterns together with our inferred species replacement on nutrient rich patches result in a predictable sequence of species replacement that is cyclic in nature.

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1. Introduction

Facilitative or positive interactions are widespread in the natural world and have a profound influence on community structure and dynamics (Bertness and Callaway, 1994; Goldberg and Barton, 1992). By modifying local conditions benefactor species create refuges that enable beneficiaries to overcome both abiotic and biotic stress that would normally constrain their establishment (Stachowicz, 2001). Facilitation enhances species coexistence, drives succession and, by expanding the fundamental niche, extends species altitudinal and geographic ranges (Bruno et al., 2003; Verdú et al., 2009). Facilitation is recognised as an important process structuring communities in physically harsh habitats (Bertness and Callaway, 1994).

In arid environments nurse-plants modify localised habitats and create regeneration opportunities for seedlings vulnerable to hostile conditions such as temperature extremes, limited moisture and nutrient stress or herbivory (Bertness and Callaway, 1994; Bruno et al., 2003). The outcome of the post-establishment interaction influences community structure by benefitting one or both partners, or the interaction may become antagonistic (Stachowicz, 2001). For example,

an association between two shrubs in semi-arid south-eastern Spain leads to soil nutrient enrichment from which both species benefit (Pugnaire et al., 1996). More commonly, the positive interaction is transient and is replaced by direct competition from the nurse-plant which suppresses growth of the recruiting plants (e.g. Callaway and Walker, 1997; Miriti, 2006). In the Sonoran desert, woody trees facilitate establishment of cactus by ameliorating high temperatures and providing elevated nutrient levels, while shading and competition for belowground resources directly retards the performance of the young cactus (Franco and Nobel, 1989). In semi-arid grasslands, recruited shrubs benefit from shade provided by established grasses but shrub growth suffers from grass root competition (Maestre et al., 2003). Roles are reversed in the Patagonian shrub steppe with shrubs initially facilitating grass establishment by buffering aboveground conditions (Aguiar and Sala, 1994). With the death of the shrub, the shading effect is removed and root competition becomes the dominant process leading to degeneration of the grass clump (Armas et al., 2008). When the initial facilitation effect is replaced by competition, the outcome can lead to a predictable sequential replacement of species referred to as cyclical succession (Armas et al., 2008; McAuliffe, 1988; Yeaton, 1978).

Plant recruitment beneath established vegetation leads to a strongly ordered spatial organisation consisting of vegetation clumps

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embedded within a matrix of low vegetation cover (i.e. a two-phase mosaic, Aguiar and Sala, 1999). As a consequence, ecosystem processes, such as nutrient cycling, water infiltration and decomposition, are generally confined to vegetation clumps to create nutrient-enriched patches (García-Moya and McKell, 1970). Nutrient inputs to patches are further supplemented by abiotic (e.g. windborne debris) and biotic effects (Burke et al., 1998). For example, elevated moisture levels beneath vegetation patches sustain soil microbial activity (Polis, 1991) and litter attracts a suite of detrivores of which termites are the most important in arid environments (Whitford, 1996). The degeneration of vegetation clumps and associated loss of cover results in the redistribution of nutrients. Thus, there is an interactive effect between plant community dynamics and the spatial and temporal distribution of soil nutrients in semi-arid ecosystems (Burke et al., 1998; Butterfield and Briggs, 2009).

Plant community dynamics are not well documented nor adequately understood in the subtropical thicket of South Africa (Cowling, 2006; Vlok et al., 2003). The vegetation type is characterised by a dense canopy of evergreen shrubs and low trees (3–4 m tall), with a sparse understorey of herbs and occasional grasses (Cowling et al., 2005; Vlok et al., 2003). Most canopy tree species persist by means of resprouting in drier regions (Midgley and Cowling, 1993), but seedling recruitment is considered more important in mesic thicket types (Cowling et al., 1997). Vlok et al. (2003) propose that *Portulacaria afra*, an evergreen leaf- and stem-succulent arborescent shrub, may facilitate recruitment of subtropical thicket species. Overgrazing by livestock has caused extensive transformation of subtropical thicket to a savanna-like vegetation comprising remnant trees, ephemeral plants and dwarf shrubs (Lechmere-Oertel et al., 2005) associated with severe loss of ecosystem functioning (Lechmere-Oertel et al., 2008).

Here we examine plant regeneration processes in dry subtropical thicket (referred to as Arid Thicket, Vlok et al., 2003). We test whether regeneration by constituent plant species of Arid Thicket is random. The vegetation at our study site is relatively depauperate of species but all major plant functional groups that characterise subtropical thicket (e.g. *P. afra*, low trees, woody shrubs, grasses) are present. The aim of this study was to develop general principles for plant community dynamics in arid subtropical thicket. By selecting a floristically simple environment we detect regeneration patterns that may otherwise be concealed in more diverse communities.

2. Material and methods

2.1. Study site

The study site is on Hillside farm (33°06′S, 24°31′E), 25 km south-west of Jansenville in the Eastern Cape, South Africa. The site is characterised by stands of *P. afra* that form distinct and discrete oval shaped clumps that may increase to >200 m² in area. Pioneer grasses (mostly *Aristida* spp.), interspersed by bare patches, form the matrix between the *P. afra* clumps. Three woody shrub species (*Rhigozum obovatum*, *Lycium cinereum*, *Pentzia incana*) are common in these grassy areas. A suite of tree species (e.g. *Pappea capensis*, *Diospyros lycioides*, *Gymnosporia polyacantha*) is distributed throughout the rangeland as single individuals or in mixed-species clumps and is located either within *P. afra* clumps or in the open matrix. Less common in the *P. afra* rangeland is slightly raised, oval-shaped mounds of variable size but within a range of 14 m² to 90 m² in area. These mounds, referred to as nutrient rich patches (hereafter NRPs), show evidence of extensive mammal digging activity. *Psilocaulon absimile*, a dwarf stem-succulent shrub, is restricted to NRPs. The *P. afra* rangeland site was located on a slight (±1°) north-facing slope. At the time of the study (1996–1997) Hillside farm was managed as an Angora goat (*Capra aegagrus hircus*) stud.

Mean annual rainfall (106 years, Jansenville) is 271 mm and falls throughout the year although almost 60% of the yearly mean falls from November to March. The mean maximum temperature at Jansenville (63 years) exceeds 30 °C from December to February while the hottest temperatures for the same period exceed 40 °C. The mean minimum temperatures for June and July are below 5 °C and the coldest temperatures for the same months fall below freezing point (Anon, 1986).

2.2. Rangeland structure and tree establishment

We recorded all trees, woody shrubs, *P. afra* clumps and NRPs in ten 20 m × 20 m quadrats. *P. afra* clumps were disregarded if more than half their area fell outside the quadrat. The longest axis (L) and the maximum width at right angles to the long axis (W) of all *P. afra* clumps and NRPs were measured and cover calculated as πLW / 4 (Cody, 1986). The position of tree seedlings was recorded as within *P. afra* clumps, beneath woody shrubs or in the open. Differences in establishment environment were tested with the Chi-square goodness-of-fit test (Siegel and Castellan, 1988). Open areas were defined as bare ground or ground with a grass covering. Tree seedlings were individuals less than 50 cm in height without the excessive stem thickening characteristic of older, overgrazed trees. We disregarded seedlings in clumps if conspecific mature individuals were present to avoid recording resprouts.

2.3. P. afra establishment

The establishment position of at least 50 *P. afra* seedlings was recorded from five transects (100 m × 4 m). *P. afra* seedlings were defined as individuals less than 30 cm in height. Individuals were examined to confirm they were not resprouting from adult individuals. We used the Chi-square goodness-of-fit test to determine whether the frequency of woody shrub nurse plants occurred in the same proportion as woody shrubs in the rangeland. Woody shrub frequency was determined by recording the identity of the nearest shrub (n = 150) encountered at 15 m intervals along straight line transects.

P. afra seedlings were recorded most frequently beneath *R. obovatum*. To determine whether *P. afra* displaced this inferred nurse plant, we regressed the area of *P. afra* clumps against the canopy area of the original *R. obovatum* nurse plant, assumed to be that individual closest to the thickest *P. afra* stem. We assumed that a negative relationship indicated that *R. obovatum* was displaced as the *P. afra* clump increased in size. Canopy areas were determined by measuring the longest axis (L) of each canopy and the greatest width at right angles to the long axis (W). Cover was calculated by πLW / 4 (Cody, 1986).

2.4. R. obovatum establishment

We searched four microhabitats (bare ground, grass, under *P. incana*, under *P. afra*) for *R. obovatum* seedlings. *R. obovatum* seeds are winged and likely to accumulate in a patchy distribution. Consequently, we located the four microhabitats within one 5 m × 5 m quadrat (n = 30) and all seedlings within a 1 m diameter circle placed in each of the four microhabitats were recorded. The Chi-square test for r × 2 tables tested for microhabitat differences in *R. obovatum* establishment with column headings the number of quadrats with or without *R. obovatum* seedlings and row headings the four microhabitats.

2.5. Vegetation patterns on nutrient rich patches (NRPs)

The frequency of woody shrubs and the presence of *P. absimile* were recorded on randomly selected NRPs (n = 20) in the *P. afra* rangeland. An area equal to the focal NRP was marked in the grass-dominated matrix adjacent to the NRP and all shrubs recorded. This control area never included *P. afra* clumps and, to avoid nutrient contamination, was never down-slope of the NRP. We used the Sign test (Siegel and Castellan, 1988) to determine whether *L. cinereum*