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Floristic uniformity across abrupt boundaries between *Triodia* hummock grassland and *Acacia* shrubland on an Australian desert sandplain

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ABSTRACT

The tension between pyrophytic hummock grasslands and fire-sensitive mulga shrubland is a major ecological theme in central Australia. On a sandplain on the edge of the Tanami Desert, grassland and shrubland are juxtaposed with abrupt boundaries that cut across a subtle environmental gradient. We compare woody plant diversity among vegetation types and explore correlates of the distribution of woody plant species. Alpha diversity in grassland and shrubland was almost identical, but plot-level species richness was greater in grassland. Gamma (landscape) diversity was scarcely greater than alpha diversity. Few long-lived plants, and not even the dominant hummock grass and shrub, were exclusively associated with one vegetation type, but most common species were aligned with elements – soil texture, fire frequency and the extent of physical soil crusting – that characterise the environmental gradient between vegetation types. Most species were resprouters and there was no tendency for obligate seeders or facultative resprouters to be associated with the less fire-prone shrubland. Our data are consistent with the suggestion that hummock grasslands and mulga shrubland are alternative stable states maintained by fire-soil feedback loops and possibly also by competitive exclusion of pyrophytic species by *Acacia aneura*.

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1. Introduction

Abrupt physiognomic (structural) boundaries between vegetation types such as grassland and forest need not correspond with either floristic or edaphic disjunctions. This discordance is likely to occur where the physiognomy of the dominants contrasts strongly and vegetation types represent alternative stable states (ASS). Alpine tree-lines, for instance, do not necessarily correspond with general changes in species composition (Batllori et al., 2009) or to boundaries in species richness (Camarero et al., 2006). The boundary between *Nothofagus* rainforest and mixed forest and shrubland in New Caledonia does not reflect differences in soils (Read et al., 2006). ASS arise where attritive or catastrophic disturbance triggers alternate, self-reinforcing dominance (Beckage et al., 2009; Folke et al., 2004; Scheffer et al., 2001). For example, contrasting combinations of low and high pyrophilia and pyrogenicity have been argued or demonstrated to mediate shrubland/forest states in temperate forests of the Mediterranean region (Acacio et al., 2009) and western USA (Odion et al., 2010), woodland/forest states in boreal forests (Jasinski and Payette, 2005), savanna/rainforest states in the Brazilian Amazon (Hoffmann et al., 2009) and open forest/rainforest states in northern Australia (Warman and Moles, 2009).

The abrupt ecotone between hummock grasslands dominated by spinifex (*Triodia* spp., Poaceae) and shrublands dominated by mulga (*Acacia aneura*, Mimosaceae) (Fig. 1) (hereafter *grassland* and *shrubland*) is a prominent feature of the vast semi-arid zone of central Australia (Griffin and Hodgkinson, 1986). These vegetation types each occupy c. 20% of the continent, a combined total of *c.* 3 million km^2 (DEH, 2007). The juxtaposition is repeated across a range of environmental settings from red-earth sandplains and dunes to rocky mountain ranges on a variety of substrates (Bowman et al., 1995; Murphy et al., 2010; Nano and Clarke, 2008). At times the ecotone corresponds to an abrupt edaphic disjunction with a distinct flora associated with each vegetation type (Nano and Clarke, 2008). At other times, there is little or no evidence of an edaphic disjunction, and floristic differences other than of the dominant species may not be readily apparent (Nano and Clarke, 2008; Nicholas et al., 2009).

Hummock grasslands are characterised by flammable, long-lived, hummock-forming C4 grasses of the speciose genus *Triodia*. *Triodia* are typically less than 0.5 m tall with rigid, drought-

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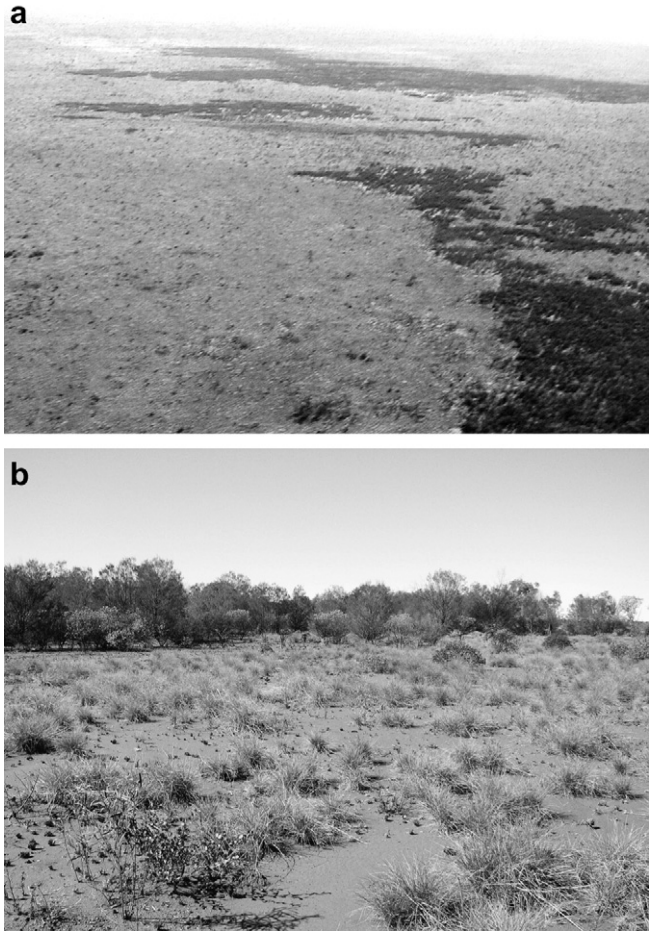

Fig. 1. Abrupt boundaries between Mulga shrubland and Spinifex hummock grassland on a semi-desert sandplain: a. from the air (shrubland is dark); b. on the ground.

resistant stems and spiny foliage that are little-grazed by stock. The hummock growth form is unusual amongst grasses and functionally that of a shrub; correspondingly, the roots of *Triodia* can reach depths of more than 10 m (Reid et al., 2008). Fire intervals in these grasslands are from "less than 3 years to more than 30 years" (Allan and Southgate, 2002), the hummocks variously and vigorously recovering by basal resprouting or seeding (Rice and Westoby, 1999). In contrast, the shrubland dominant *A. aneura* is a relatively slow-growing, woody species 2–10 m tall that is readily killed by fires of moderate to high intensity (Hodgkinson, 2002; Hodgkinson and Griffin, 1982), though with some capacity for saplings to resprout basally (Nicholas et al., 2009; Wright and Clarke, 2007). *A. aneura* is able to influence soil characteristics (Ludwig et al., 1997) by improving moisture infiltration (Dunkerley, 2002) and fixing nitrogen (Schortemeyer et al., 2002). Low grass cover in shrubland acts to slow the spread of fires (Griffin and Friedel, 1984), suggesting asymmetric competition in which *A. aneura* suppresses *Triodia*. However and intriguingly, Nano and Clarke (2010) found the converse in a sanddune system – that *Triodia basedowii* hummocks suppressed seedlings of *A. aneura* whereas mature *A. aneura* did not suppress *Triodia* seedlings. Both *Triodia pungens* and *A. aneura* retain foliage throughout the year and under all moisture conditions, but the foliage of both partially dessicates during prolonged dry periods.

Start et al. (1991) provided anecdotal evidence of fire-driven transitions from mulga shrubland to *Triodia* grassland. On a red-earth sandplain on the fringe of the Tanami Desert – our study area – where the occurrence of shrubland and grassland is antagonistic (Fig. 1; also Murphy et al., 2010), changes to these boundaries over 52 years were correlated with fire history (Bowman et al., 2008). Notwithstanding, the broad distribution of shrubland and grassland on the sandplain has been essentially stable for millennia (Bowman et al., 2007). The sub-surface and surface soils of shrubland and grassland differ only subtly and non-discretely (Bowman et al., 2007; Nicholas et al., 2009). However, the implications of the disjunction for plant biomass and vegetation structure are profound (Fig. 1b). The sandplain grassland and shrubland appear, therefore, to be disturbance- (fire-) mediated alternative stable states, with a possible role for competitive exclusion in stabilising the system (Nano and Clarke, 2008, 2010).

Here, we examine patterns of occurrence of long-lived plant species in the hummock grassland – shrubland mosaic of the semi-desert red-earth sandplain on the fringe of the Tanami Desert. We have previously demonstrated that floristic patterning at this site is almost entirely due to the contribution of the dominants, *A. aneura* and *T. pungens*, and that the vegetation dichotomy is related non-exclusively to a subtle gradient combining soil texture, fire frequency and physical soil crusting (Nicholas et al., 2009). This suggests the hypothesis that the distribution of species other than the dominants is related to factors other than those contributing to the underlying gradient, an hypothesis we test by examining the correlates of the distribution of 19 common species. We examine whether plant reproductive strategy (resprouter/seeder) is related to vegetation preference, with the hypothesis that seeders will be most strongly associated with the less fire-prone shrubland. With a view to seeking correlative evidence of competitive exclusion or facilitation of species by *A. aneura*, we also compare the plot-level species richness and alpha diversity of long-lived plants in hummock grassland, shrubland and mixed vegetation, and the relationship of these to gamma (landscape) diversity.

2. Methods

2.1. Study site

The 512 km^2 study site (21°54'S, 132°07'E) was in the northern, little-used portion of the Mt Denison cattle station, 50 km north-east of Yuendumu on the southern fringe of the Tanami Desert in central Australia. The sandplain lies 600 m above sea level and lacks topographic features. Soils are infertile sandy red-earths with little profile development – Arenic Rudosols intergrading to Red-Orthic Tenosols (McKenzie et al., 2004). Monthly and annual rainfall totals are extremely variable, with a mean annual rainfall of 373 mm (Yuendumu) and the chance of substantial rainfall markedly greater in the summer months. Summers are hot (mean daily maximum 40 °C) and winters mild with cool to cold (occasionally sub-zero) nights.

We recognise three vegetation types on structural grounds: shrubland, grassland and mixed vegetation (Nicholas et al., 2009). Shrubland patches are embedded in the grassland matrix and vary in area from 0.2 ha to 25 km^2 (Fig. 1). Mixed vegetation occupies less than 1% of the landscape. Shrubland has 25–55% cover of *A. aneura* and contains occasional *T. pungens* with <1% cover. The grassland is dominated by *T. pungens* (10–30% cover) with scattered trees and shrubs including occasional *A. aneura* with <1% cover. Mixed vegetation commonly comprises >> 1% cover of both *A. aneura* and *T. pungens*. At this site (though not everywhere; Rice and Westoby, 1999), *T. pungens* resprouts freely after fire.

2.2. Field survey

One hundred and five plots, each 80 × 20 m, were selected on a stratified random basis to represent the range of vegetation types

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