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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*.

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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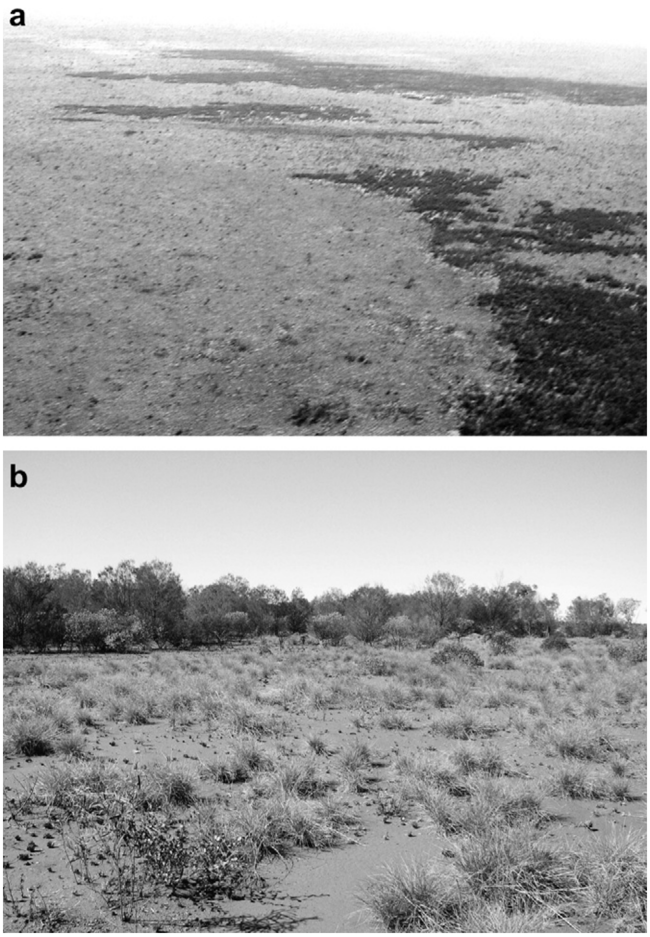

Fig. 1. Abrupt boundaries between Mulga shrubland and Spinifex hummock grassland on a semi-desert sandplain: a. from the air (shrubland is dark); b. on the ground.

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 and fire histories present. Forty-two plots were in shrubland, 24 in mixed vegetation, and 39 in hummock grassland.

Plots were surveyed for floristics and surface soil characters in May–September 2005. Although the cover of each woody and other long-lived perennial species was estimated, in this paper we employ presence/absence data for models for individual species and present cover data only for all long-lived species (excluding *A. aneura* and *T. pungens*) combined. Forbs and other grasses were not recorded because in this environment their cover responds rapidly to rain and fire and they may be undetectable (other than in the seed bank) for lengthy periods (Friedel et al., 1990).

Surface soil variables evaluated were texture, bulk density, pH and the surface cover of sand, gravel, physical soil crust and biological soil crust. These are pragmatic selections designed to capture plausible physiochemical differences informed by prior studies. For example, where mulga shrubland and *Triodia* hummock grassland occurred adjacent, Bowman et al. (1995) found that mulga shrubland grew on soils that were more acidic and gravelly and Nano and Clarke (2008) that mulga shrubland grew on soils that were more acidic and more clayey. In the field, soil texture was determined using the squeeze test described by Handreck and Black (1999) and graded as: sandy, loamy sand, clayey sand, sandy loam, fine sandy loam or sandy clay loam. Two 7.5 cm soil cores of standard volume (117.1 cm^3) were collected from each plot. The unvegetated ground in each plot was described at 100 points placed at 1-m intervals along a transect across the plot. Each point was scored as one of sand, gravel, physical soil crust or biological crust rated against standard photographs.

2.3. Soil analysis

Soil samples were dried overnight in an oven at 100 °C. The mass of each sample was measured with an electronic balance to the nearest milligram and converted to bulk density. The pH of each sample was determined using a Hanna pHep3 pH meter to one decimal place.

2.4. Fire history

In this landscape, fire scars remain detectable on LANDSAT images for several years. Examination of a sequence of images for the period 1980–2004 was used to identify fourteen images that displayed evidence of fires during the previous two months. Plot locations were projected onto these images using the GIS computer program ArcView 9.0 and the number of fires summed for each plot.

2.5. Data analysis

Rarefaction curves for each vegetation type were calculated using 500 random sub-samples for each estimation in PC-Ord 4.01 (McCune and Mefford, 1999).

For each species present in >5 shrubland or hummock grassland plots, a Grassland Association Index (GAI) was calculated as $GAI = p_S/(p_G + p_S)$, where p is the proportion of plots in which the species occurred, G = hummock grassland plots and S = the shrubland plots. Mixed plots have been excluded from this analysis. It follows that the Shrubland Association Index is 1 − GAI.

The response of the more abundant species to fire was obtained from a plant database “CurrentEcologicalAttributes” maintained by Northern Territory government researchers (Kym Brennan, Personal communication) and current at May 2010. In this database, the field “Fire_response_adult” contains the options: 1. Seeder (when subject to 100% leaf scorch >70% mortality); 2. Resprouter (when subject to 100% leaf scorch <30% mortality); and 3. Facultative resprouter (response variable depending on conditions e.g. moisture and fire intensity), and species may receive one or any combination of these classifiers. The database also contains estimates of time from germination to first seed set in the field.

In order to identify edaphic and fire-history variables that contribute to the floristic structure of the sandplain vegetation, we developed empirical binomial models with a probit link function relating presence/absence of each of 19 species present in 25 or more plots to soil texture, pH, bulk density, % gravel, % physical soil crusting and the number of fires. The 19 species include *A. aneura* and *T. pungens* on the basis that each is present in mixed vegetation and, at low frequency, in the vegetation type in which they are not dominant: grassland (*A. aneura* − 6 plots) and shrubland (*T. pungens* − 18 plots). All explanatory variables were treated as continuous. %gravel and %physical soil crusting were $\ln(x + 1)$-transformed whilst pH was square root-transformed. Soil texture was rated from 1 (sandy) to 6 (sandy clay loam). Explanatory variables were screened for collinearity with a correlation matrix. Data analysis was conducted in the Generalised Linear/Non-Linear Models module of Statistica (StatSoft Inc., 1984–2006). We considered all possible sub-sets of explanatory variables but without interactions, and assessed statistical support for each with Akaike’s Information Criterion corrected for small sample size and the percentage of null model deviance explained (Burnham and Anderson, 2002). For each well-supported model (see below), we ranked the strength of contribution of variables to the model by deleting one variable at a time; variables which, when deleted, resulted in models with greater remaining deviance are greater contributors to the model being assessed.

We acknowledged several caveats with our approach. First, by treating all variables as linear, we acknowledge the possibility that peak occurrence at intermediate levels of a variable will not be detected. Limited edaphic variability within the study area (see *Results*) is likely to minimise this risk. Furthermore, as our aim is to identify the main variables and the direction of their effect across a range of species, and not to quantify their effect on any one species, this approach is reasonable. Second, by considering all possible sub-sets of variables for each species, there is a high probability that many models will be supported. There was no clear *a priori* basis for considering only a limited sub-set of possible models. To avoid a proliferation of uninterpretable models and identify a parsimonious set of key variables that describe the distribution of species within the study area, we adopted the following set of procedures for each species: a. we considered only models that were well-supported ($\Delta_{AICC} < 2.0$; Burnham and Anderson, 2002); b. we ranked well-supported models by Δ_{AICC} (a score of zero indicates the model with the most support); and c. we based inference about variables for each species on their consistent presence and direction in well-supported models, and on the percentage of null model deviance explained by the models that contained those variables.

3. Results

Forty-eight woody and other long-lived perennial species were recorded. These included 14 species of *Acacia* (Mimosaceae), three species of eucalypt (Myrtaceae: *Corymbia* and *Eucalyptus*), three species of *Hakea* (Proteaceae) and three species of *Eremophila* (Myoporaceae).

The cover of long-lived plants excluding *A. aneura* and *T. pungens* did not differ significantly among vegetation types (Kruskall-Wallis $H_{2,105} = 0.35$, $P = 0.84$) (Fig. 2). The cover of these long-lived plants was not significantly related to the cover of *A. aneura* in shrublands plots ($r_s = 0.12$, $n = 42$, $P_{2\text{-tailed}} = 0.45$), but was positively related to

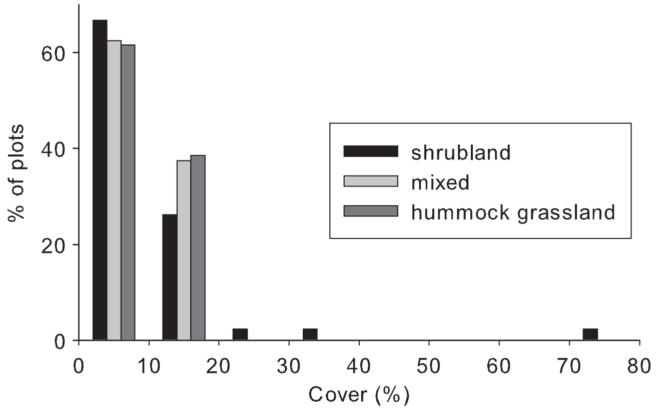

Fig. 2. The cover of long-lived plants other than *A. aneura* and *T. pungens* in three structural vegetation types, arranged in 10 percentile classes.

the cover of *T. pungens* in hummock grassland ($r_s = 0.33$, $n = 39$, $P_{2\text{-tailed}} = 0.04$).

The species richness (alpha diversity) of long-lived plants varied significantly between vegetation types at the plot level ($F_{2,102} = 8.0$, $P = 0.0006$), richness being significantly different (Tukey tests, $P < 0.05$) (less) in shrubland (mean 9.0 species) than in hummock grassland (11.8) or mixed (11.9) plots. However, at the landscape scale, hummock grassland and shrubland had similar species richness and mixed vegetation was at most only slightly more speciose (Fig. 3). Rarefacted gamma diversity (species richness of all vegetation types combined) was almost identical to that of mixed vegetation alone and scarcely greater than that of shrubland or hummock grassland (Fig. 3).

Three of the common species are obligate seeders as adults, and 12 are at most facultative resprouters (Table 1). Seven of these species (out of 11) had Grassland Association Indices of <0.5 and eight (out of 20) > 0.5, with no significant tendency for proportionally more fire-sensitive species (obligate seeders + facultative resprouters) to occur in shrubland than hummock grassland (one-tailed Fisher's Exact Test, $P = 0.19$).

Most common long-lived species (29 of 33) had a Grassland Association Index of less than 0.33 or greater than 0.67 (Table 1). More conservatively, significant (Bonferroni-corrected) association of 6 species with shrubland and 10 species with hummock grassland were demonstrated, though in only two of these was the preference absolute (Table 1). All species recorded in >5 shrubland or hummock grassland plots were also recorded in mixed plots.

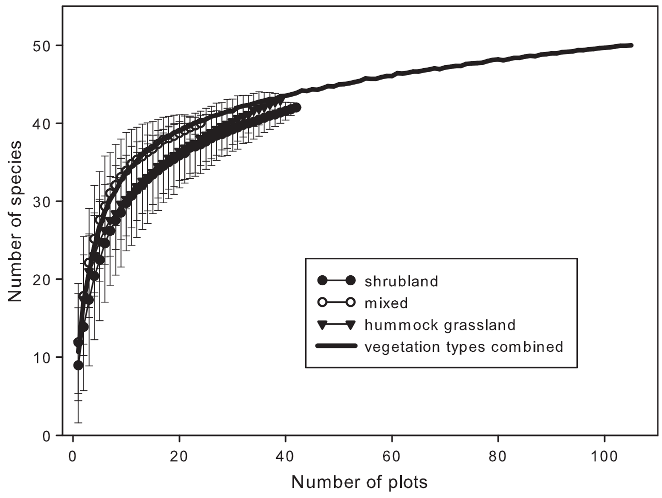

Fig. 3. Rarefaction curves (mean ± 95% CI) for long-lived plant species in three vegetation types in the southern Tanami Desert, and for the vegetation types combined (mean).

3.1. Species models

Surface soils displayed limited variation in texture, pH and bulk density but more extensive variation in surface cover of gravel and physical soil crusting (Table 2). Most (82%) of plots were burnt at least once during the 25-year period prior to assessment and 58% were burnt twice or more. Correlations amongst explanatory variables were weak ($r < 0.25$), with one exception: the number of fires was positively correlated with soil sandiness ($r = 0.48$, $P_{2\text{-tailed}} < 0.001$). As even the latter correlation was not overly strong, all variables were retained in the modelling process.

Credible models – those with a consistent core of explanatory variables amongst well-supported models – were developed for 17 of the 19 species evaluated (Table 3; Appendix). The percentage of null model deviance explained ranged from a little over 60% in *A. aneura* to less than 10% in three species, with a median of 16% (Table 3).

Nine species were associated with the number of fires (2 −ve, 7 +ve), eight with soil texture (2 less sandy, 6 sandier), five with pH (1 more acidic, 4 more alkaline), three with physical soil crust (2 with less, 1 with more) and one species was associated with less gravelly soils (Table 3). No associations with the bulk density of soil were identified.

T. pungens was associated with sandier soils and a greater number of fires whereas *A. aneura* was associated with the opposite gradient – less sandy soils and fewer fires, though also with less physical soil crusting (Table 3). Thirteen other species were also associated with one or more of the number of fires, soil texture or physical soil crusting.

4. Discussion

Despite great differences in physiognomy arising from the contrasting growth forms of two dominant species, the shrubland and hummock grassland on this Tanami Desert sandplain should be regarded as part of a floristic mosaic rather than a dichotomy. Our Grassland Association Index demonstrates that few common species display categoric or even especially strong association with vegetation type. Rarefaction curves demonstrate that, not only do shrubland and hummock grassland have almost identical levels of species richness at the landscape scale after controlling for sampling area, but that landscape diversity across vegetation types (gamma diversity *sensu* Whittaker, 1977) on this sandplain is scarcely greater than in either vegetation type alone – and almost identical to that of the small area of mixed vegetation. These results reinforce our previous finding that floristic differentiation of vegetation types as shown by ordination largely “collapses” when *A. aneura* and *T. pungens* are excluded from the analysis (Nicholas et al., 2009). Our results are also consistent with Nano and Clarke's (2008) more general evidence that floristic distinctions between *A. aneura* shrubland and *Triodia* hummock grasslands are weak at sites that lack a coincident edaphic boundary. Collectively, the evidence available from this and other study sites strongly supports the suggestion that hummock grassland and mulga shrubland at this site are alternative stable states (Table 4).

Despite the antagonistic nature of their occurrence (Murphy et al., 2010; Nano and Clarke, 2010), *T. pungens* occurred at low density in 43% of shrubland plots and *A. aneura* at low density in 15% of grassland plots. Nevertheless, the edaphic and fire history correlates of the presence/absence of these key species describes essentially the same multi-variate gradient – soil texture, physical soil crusting and frequency of fire – as we have previously

Table 1
Growth form, resprout strategy and association with hummock grassland plots of 33 long-lived plant species.

Species	Growth form	Resprout strategy	Number of plots			Grassland Association Index	*P*
			Shrubland ($n = 42$)	Mixed ($n = 24$)	Grassland ($n = 39$)		
Acacia cuthbertsonii	SH	S,F	8	2	0	0.000	0.006
Psydrax attenuata	TR/SH	R	19	8	0	0.000	<0.0001*
Spartothamnella teucriiflora	SH	F	13	5	0	0.000	0.0001*
Rhyncharrhena linearis	WV	R	17	6	1	0.060	<0.0001*
Eremophila gilesi	SH	F	15	7	1	0.067	0.0002*
Acacia aneura var. *tenuis*	TR/SH	S	42	24	6	0.133	<0.0001*
Rhagodia eremaea	SH	F	12	5	3	0.212	0.021
Tinospora smilacina	WV	R	8	5	2	0.212	0.090
Enchylaena tomentosa	SH	S,F	7	3	2	0.235	0.15
Acacia kempeana	SH	S,F	16	13	5	0.252	0.018
Eremophila latrobei	SH	R	36	22	18	0.350	0.0003*
Senna artemisioides	SH	F	37	22	35	0.505	1.0
Ptilotus obovatus	LP	F	17	10	17	0.519	0.82
Atalaya hemiglauca	TR	R	8	6	13	0.636	0.20
Acacia ancistrocarpa	SH	R,S	2	1	4	0.683	0.42
Triodia pungens	HG	F	18	24	39	0.689	<0.0001*
Acacia tenuissima	SH	n.r.	10	8	22	0.703	0.003
Anthobolus leptomerioides	SH	R	11	10	25	0.710	0.0008*
Eremophila longifolia	TR/SH	R	6	6	14	0.715	0.038
Hakea chordophylla	TR	F	5	5	14	0.751	0.017
Acacia adsurgens	SH	S	6	9	17	0.753	0.006
Acacia pruinocarpa	SH	n.r.	7	16	21	0.764	0.0009*
Gossypium australe	SH/LP	F	9	9	31	0.788	<0.0001*
Corymbia opaca	TR	R	5	8	19	0.804	0.0005*
Hakea macrocarpa	TR	R	7	9	27	0.806	<0.0001*
Acacia ligulata	SH	S,R	4	5	18	0.829	0.0003*
Acacia estrophiolata	TR	F,S,R	2	1	10	0.843	0.011
Codonocarpus cotinifolius	TR	R	1	6	5	0.843	0.10
Acacia inaequilatera	TR/SH	S,R	3	7	21	0.883	<0.0001*
Acacia colei	SH	S	1	2	8	0.896	0.012
Acacia coriacea	TR/SH	R,F	3	6	24	0.896	<0.0001*
Santalum lanceolatum	TR/SH	R	1	3	13	0.933	0.0002*
Eucalyptus gamophylla	SH	R	0	1	7	1.000	0.004

Only species found in >5 shrubland or hummock grassland plots are included. Growth form: TR = tree; SH = shrub; WV = woody vine; HG = hummock grass; LP = long-lived perennial. Resprout strategy: S = seeder; F = facultative resprouter; R = resprouter; n.r. = not recorded. Association ranges from 0 to 1. *P* values are from two-tailed Fisher's Exact Tests comparing presence/absence in shrubland and hummock grassland plots; * = significant at $P < 0.05$ after application of a step-wise Bonferroni correction for multiple testing (threshold $P = 0.0029$). The horizontal lines separate species with a strong association with shrubland (GAI < 0.33) and with hummock grassland (GAI > 0.67) from species with relatively neutral association.

described as characterising the distribution of physiognomic vegetation types at this site (Nicholas et al., 2009). *T. pungens* occurs on relatively degraded and more frequently-burnt soils than *A. aneura*. Although the effects of the identified variables in our models are additive, they are also consistent in overall direction – sandier soils are more frequently burnt ($r = 0.48$). More frequent burning in a semi-arid landscape is likely to contribute to the degradation of soils by engendering erosion and the creation of hydrophobic (physical, not biological) soil crusts (Ravi et al., 2010). It is an appropriate simplification, therefore, to describe a simple but subtle gradient in the general favourability of growing conditions on the mulga-spinifex sandplain.

Table 2
Edaphic and fire history attributes of the study plots.

Variable	Median	10th–90th percentile	Range
Soil texture	Sandy-loam	Loamy sand – Sandy clay loam	Sandy – Sandy clay loam
pH	6.9	6.5–7.3	6.0–7.6
Bulk density (g cm^{-3})	1.51	1.41–1.61	1.3–1.66
Surface gravel (% cover)	2	0–11	0–40
Physical soil crust (% cover)	27	14–48	9–75
No. of fires in 25 years	2	0–4	0–4

The extent to which this gradient existed *a priori*, possibly as a consequence of micro-topographic variation leading to accumulation of fine sediment in depressions, or is a product of feedback loops with vegetation, remains unclear. Contrasts in soil infiltrability can be a key driver of vegetation patterns in semi-arid regions (Mills et al., 2009), though both *A. aneura* and *T. pungens* are highly drought resistant. Further, both *T. pungens* by virtue of its fire-tolerance, flammability and tolerance of extremely harsh growing conditions, and *A. aneura* by virtue of fire suppression and nitrogen fixation, are capable of "engineering" the conditions that they favour.

Cover of long-lived plants excluding the dominants didn't differ between vegetation types even though that in hummock grassland was more likely to have been depressed by recent fire. Mutual depression by and recovery from fire could account for the positive correlation between the cover of *T. pungens* and other long-lived species in hummock grassland, though it is also possible that more productive sites had higher cover of both plant groups.

Contrary to expectation, most common species on the sandplain displayed associations with gradients in one or more of the same three environmental parameters that describe the shrubland-hummock grassland dichotomy, and were thus at least partly associated with the derived gradient we have described. Associations with soil texture or the number of fires were particularly prominent. The two species associated with less frequent fire, *A. aneura* and *Acacia kempeana*, are not resprouters as adults. Furthermore, fires in mild fire-weather may burn leaf litter on the

Table 3
Summary of binomial habitat selection models for 19 common species on a Tanami Desert sandplain.

Species	No. of plots	Key predictor variables (direction of association)	%DE
Psydrax attenuata	27	Texture (less sandy)	20.4
Acacia aneura var. *tenuis*	72	Texture (less sandy), no. of fires (−), physical soil crust (−)	60.6
Acacia kempeana	34	pH (−), no. of fires (−)	15.0
Eremophila latrobei	76	Physical soil crust (−)	14.0
Senna artemisioides	91	pH (+)	5.8
Ptilotus obovatus	44	pH (+)	8.1
Atalaya hemiglauca	27	–	
Triodia pungens	81	Texture (sandy), no. of fires (+)	24.3
Acacia tenuissima	40	No. of fires (+)	11.7
Anthobolus leptomerioides	46	Texture (sandy), pH (+)	15.6
Eremophila longifolia	26	No. of fires (+)	5.2
Acacia adsurgens	32	No. of fires (+), physical soil crust (+)	15.7
Acacia pruinocarpa	44	Texture (sandy)	13.5
Gossypium australe	49	No. of fires (+)	38.2
Corymbia opaca	32	–	
Hakea macrocarpa	43	Texture (sandy)	22.8
Acacia ligulata	27	No. of fires (+), gravel (−)	16.7
Acacia inaequilatera	31	Texture (sandy), pH (+)	24.3
Acacia coriacea	33	No. of fires (+), texture (sandy)	25.3

No. of plots are those in which the species was present. Key predictor variables are as identified in more detail in Appendix. %DE is the % of deviance explained by the most well-supported model. Species are ordered as in Table 1, i.e. from most strongly associated with shrubland to most strongly associated with grassland, the horizontal line separating species with Grassland Association Indices < and >0.5.

ground under mature *A. aneura* stands without damaging the shrub layer (Griffin and Friedel, 1984). Less predictably, two species associated with more frequent fire are also not resprouters: *Acacia adsurgens* is a seeder and *Gossypium australe* a facultative resprouter (for the latter, see also Williams et al., 2002). We are unaware of any publications about the life history of these species, but both are relatively fast-growing, the Northern Territory plant attributes database (see *Methods*) indicating that they commence producing seed in the field 1–3 and 1–5 years respectively after germination. Contrary to the hypothesis that seeders may be associated with less fire-prone shrublands, it is possible that fire triggers germination in these species, that the time from germination to seed production is sufficiently short that follow-up fires are rarely problematic even in fire-prone grasslands, and even that the resprouting habitat may be necessary to persist in shrubland in the face of competition from *A. aneura* and lack of disturbance. In addition, we have demonstrated weak associations with pH in five species notwithstanding limited variation around neutral in the range of pH found in surface soils.

Table 4
Criteria and evidence that the shrublands and grasslands of the southern fringe of the Tanami Desert in central Australia are Alternative Stable States. The criteria are based on Connell and Sousa (1983) as modified by Peterson (1984) and Sousa and Connell (1985). Studies marked * were conducted in our study area.

Criterion	Evidence
Alternative states are in the same environment – or derived from the same environment via feedback loops	-Partial overlap in sub-soil niche (*Bowman et al., 2007) -Partial overlap in surface soil niche (*Nicholas et al., 2009) -Extensive floristic overlap between vegetation types (*Nicholas et al., 2009; *this study) -*Acacia aneura* and *Triodia* modify soils in the direction of observed differences (see text) -Competitive exclusion of *A. aneura* by *Triodia* (Nano and Clarke, 2010) -*A. aneura* and *Triodia* influence fire frequencies in opposite directions (*Bowman et al., 2008; *Nicholas et al., 2009; Murphy et al., 2010)
Perturbation is a “pulse”	-Fire can eliminate *A. aneura*, especially if repeated (Start et al., 1991; *Bowman et al., 2008)
Alternative states are self-sustaining for >1 generation	-Stability over 52 years based on aerial photography (*Bowman et al., 2008) -Stability over several thousand years inferred from isotopic analysis of subsoils (*Bowman et al., 2007)

Of course, correlation isn’t proof of causation. Facilitation and competition are two processes that can shape the realised niche of a species, generating environmental correlations that may differ from the fundamental niche. Trees that invade grasslands may facilitate the establishment of a range of other woody species (Barnes and Archer, 1999; Shararn et al., 2009). However, at the plot scale, shrubland in our study had significantly fewer species than hummock grassland or mixed vegetation, suggesting that *A. aneura* is highly competitive and not generally facilitative, although other explanations are possible. *A. aneura* can and often does achieve remarkably high canopy cover for a shrub in a semi-arid environment (25–55% at this site, Nicholas et al., 2009), so it is plausible that asymmetric competition for moisture limits the ability of other species including *Triodia* to occur in these shrublands. In Patagonian steppe, shrubs have conflicting effects on grass seedlings, providing shade that enhances their survival, but competing for moisture and so decreasing their survival (Aguiar and Sala, 1994; Aguiar et al., 1992). However, competitive dominance by *A. aneura* is contrary to the experimental findings of Nano and Clarke (2010) for a sanddune-swale environment. Nano and Clarke’s finding relates to *Triodia* seedlings, and it is possible that dominance of the taller *A. aneura* over *Triodia* may occur as *Triodia* matures and becomes more sensitive to shading. Given the great range of environmental settings in which *A. aneura* and *Triodia* spp. occur, experimental transplantings across a broad range of these settings may well shed further light on the processes driving this key interaction in the ecology of central Australia.

This semi-desert sandplain is an ideal proving ground to explore ASS theory and tree–grass interactions because: a. vegetation types reflecting two fundamentally different lifeforms present abrupt boundaries; b. floristic difference between vegetation types are minor; c. the environment is remarkably uniform; d. fire is a demonstrably important source of disturbance; and e. the historical context is known.

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Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jaridenv.2011.06.016.

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