Variegated desert vegetation: Covariation of edaphic and fire variables provides a framework for understanding mulga-spinifex coexistence

CATHERINE E. M. NANO[1,2]* AND PETER J. CLARKE[2]

[1]*Biodiversity Conservation, Department of Natural Resources, Environment and the Arts, PO Box 1120, Alice Springs 0871, Australia (Email: catherine.nano@nt.gov.au); and* [2]*Botany, School of Environmental Sciences and Natural Resources Management, University of New England, Armidale, Australia*

Abstract   Mulga (*Acacia aneura* Mimosaceae) and spinifex (*Triodia* spp. Poaceae) habitats together characterize a large part of arid central Australia. Often very abrupt boundaries form between these two habitats, giving rise to a mosaic pattern of contrasting shrub-grass alterations across the landscape. Reasons for such patterning remain poorly understood though current niche-based views relate species' distributions to spatial resource gradients or to fire effects. Field survey work was conducted on central Australian mountain ranges to further quantify floristic, regeneration traits, and structural patterning across mulga-spinifex transitions and to test resource- and disturbance-models that explain these patterns. Compositional analysis demonstrated variability in transition type – in certain cases boundaries denoted true floristic discontinuity and in others, somewhat more of a structural shift. Moreover, it was shown that minimal between-habitat floristic overlap coincided with the occurrence of distinct edaphic changes, while greater compositional commonality occurred when soil gradients were more diffuse. This indicated that floristic patterning cannot be ascribed to any one single process. In the case of strong soil gradients, between-habitat segregation most likely resulted from resource-based niche differentiation; for weaker gradients, fire-frequency assumed greatest importance. Disturbance theory most readily accounted for the distribution of woody species' post-fire regeneration traits across habitat boundaries. The results also suggested that biotic factors – *viz* competition, facilitation and animal-mediated dispersal – may be of additional consequence for mulga-spinifex coexistence. Overall, the study served to emphasize the importance of multi-factor explanation for within- and between-habitat patterning in these mosaics. It also highlighted the need for experimentation to facilitate distinction between cause and correlation.

Key words: arid, boundaries, fire, grassland, shrubland.

INTRODUCTION

Desert landscapes characteristically support mosaics of structurally contrasting vegetation patches (Tongway & Ludwig 2001; Whitford 2002; Peters *et al.* 2006). In these variegated systems, woody-grassy transitions arise from a variety of disparate processes *viz* differential microhabitat tolerances (Montaña 1992; Dunkerly 2002); environmental drivers such as fire, grazing and major rainfall events (Wiegand *et al.* 2005; Kraaij & Ward 2006), and endogenous factors such as positive and negative feedbacks (Schlesinger *et al.* 1990; Tongway & Ludwig 2001). Another key characteristic of dryland systems is that they are often strongly affected by novel forms of disturbance, mainly because low moisture availability limits the rate of recovery following degradation (Peters & Herrick 2001). For these reasons, it can be very difficult to

accurately predict desert landscape responses to changed external drivers such as increased fire and grazing pressure or climate change. However, some general principles can be applied. Specifically, where vegetation transitions occur along abrupt environmental gradients, we can expect that successional dynamics will largely result in stand replacement because conditions for growth and survival do not occur in neighbouring habitat (see Loyd *et al.* 2000; Peters *et al.* 2006). Where these 'stationary transitions' (*sensu* Peters *et al.* 2006) dominate, it is unlikely that disturbance events will produce major changes in boundary position or in species composition. By contrast, transitions may be far more dynamic if they are controlled by external influences such as fire, grazing or rainfall (Callaway & Davis 1993). In the absence of edaphic control, patch boundaries may shift back and forth, reflecting the differential responses of the dominants to fluctuations in prevailing conditions (Peters *et al.* 2006). Alternatively, a directional change in a driver (e.g. increased landscape fire-frequency) may generate

permanent boundary changes that are maintained through time by the interaction of abiotic and biotic feedbacks (Peters *et al.* 2006). This latter scenario best accounts for the process of 'bush encroachment' in arid and semi-arid rangelands (e.g. see Schlesinger *et al.* 1990).

Large areas of arid and semi-arid Australia are dominated by mulga (*Acacia aneura*, Mimosaceae) shrubland and spinifex (*Triodia* spp., Poaceae) hummock grassland formations (see Johnson & Burrows 1994). These habitats regularly co-occur on mountain ranges, dunefields and sandplains (Perry *et al.* 1962) where they can form mosaics of distinct patches with visually abrupt boundaries (Bowman *et al.* 1994). Mulga and spinifex differ not only in terms of their physiognomy, but also in regard to their fire return intervals and fire response: mulga burns relatively infrequently and its dominant, *A. aneura*, has a low fire tolerance (see Hodgkinson & Griffin 1982; Griffin *et al.* 1983). Existing models for between-habitat dynamics correspond with Peters *et al.* (2006) *directional transition* concept, reflecting a long held (though as yet unsubstantiated) view that an increase in the extent and frequency of landscape wildfires is causing the expansion of spinifex and the concomitant retreat of mulga (see Griffin *et al.* 1983; van Etten 1987; Latz 1995; Allan & Southgate 2002). Two models for mulga contraction have been developed, both of which relate habitat distributions to the influence of fire on the patch dominants. The first predicts a conversion to spinifex at sites where post-fire soil erosion levels exceed thresholds for *A. aneura* reestablishment (see van Etten 1987; Bowman *et al.* 1994). This model is adapted from the framework for banded mulga that attributes patch establishment to soil resource redistribution (i.e. 'source-sink' movement); and patch maintenance to positive *A. aneura* soil feedbacks (see Tongway & Ludwig 1990). The alternative model aligns closely with the 'vital attributes approach' (Noble & Slatyer 1981) and the 'global model' for fire-dependent grasslands (Bond 2005; Bond & Keeley 2005; Bond *et al.* 2005). It predicts that fire-frequency will differentially affect the patch dominants because of their differing life histories and regenerative responses. Under high fire-frequencies, slow growing *A. aneura* will be disadvantaged because it faces an 'immaturity risk' (*sensu* Keeley & Fotheringham 2000) whereas C_4 *Triodia* grasses will be favoured by a reduction in shrub canopy effects. By these means shrubland can convert to grassland (van Etten 1987; Bowman *et al.* 1994; Latz 1995; Allan & Southgate 2002). An early analogue of this latter model is depicted in Noble and Slatyer (1981).

Existing evidence provides only equivocal support for directional mulga contraction. The study of van Etten (1987) of Western Australian mosaics is most convincing. He reported a minor historical retreat of mulga and documented the occurrence of floristically mixed transitions on undifferentiated soils. By contrast, the study of Bowman *et al.* (1994) of central Australian mosaics instead alluded to the predominance of stationary transitions. These latter authors reported temporally stable patterning and demonstrated compositional and soil covariance across structural gradients. However, their inability to separate cause and effect in relation to soil-vegetation patterning led them to suggest that directional changes via the mechanisms described above, may occur under certain exceptional circumstances.

While the importance of any number of alternative causes of mosaic patterning can only be properly resolved through experimentation, further quantification of species and environmental gradients is warranted given the widely varying results of the above-mentioned studies. The widespread occurrence of mulga-spinifex transitions throughout central Australia provides a good opportunity to test existing predictions for patch membership and boundary regulation by examining floristic patterns in a variety of situations in the one geographic region. The aim of this study was to compare species and species' trait patterning across mulga-spinifex boundaries and to test models that explain these patterns. The specific questions addressed were:

1. Do patch types defined by *A. aneura* or *Triodia* dominance also differ in species and life form composition?
2. Are transitions stationary or dynamic, that is, do boundaries mainly reflect resource or disturbance gradients?
3. Would an increase in landscape wildfires cause mulga contraction?

METHODS

Study area

Sampling was carried out on central Australian mountain ranges west and south-west of Alice Springs in the Northern Territory, Australia. The region comprises both arid and semi-arid climates, and has on average fewer than 40 rain days in a year. Alice Springs, which is the closest major centre to the study sites, experiences an average of less than 280 mm of rainfall *per annum*. Overall, the climate may be regarded as extreme, being characterized by high (exceeding 30°C) daytime temperatures for much of the year, by low night time temperatures and regular frosts during the short winter months, and by highly erratic rainfall and occasional severe and protracted drought events (Bureau of Meteorology 2007).
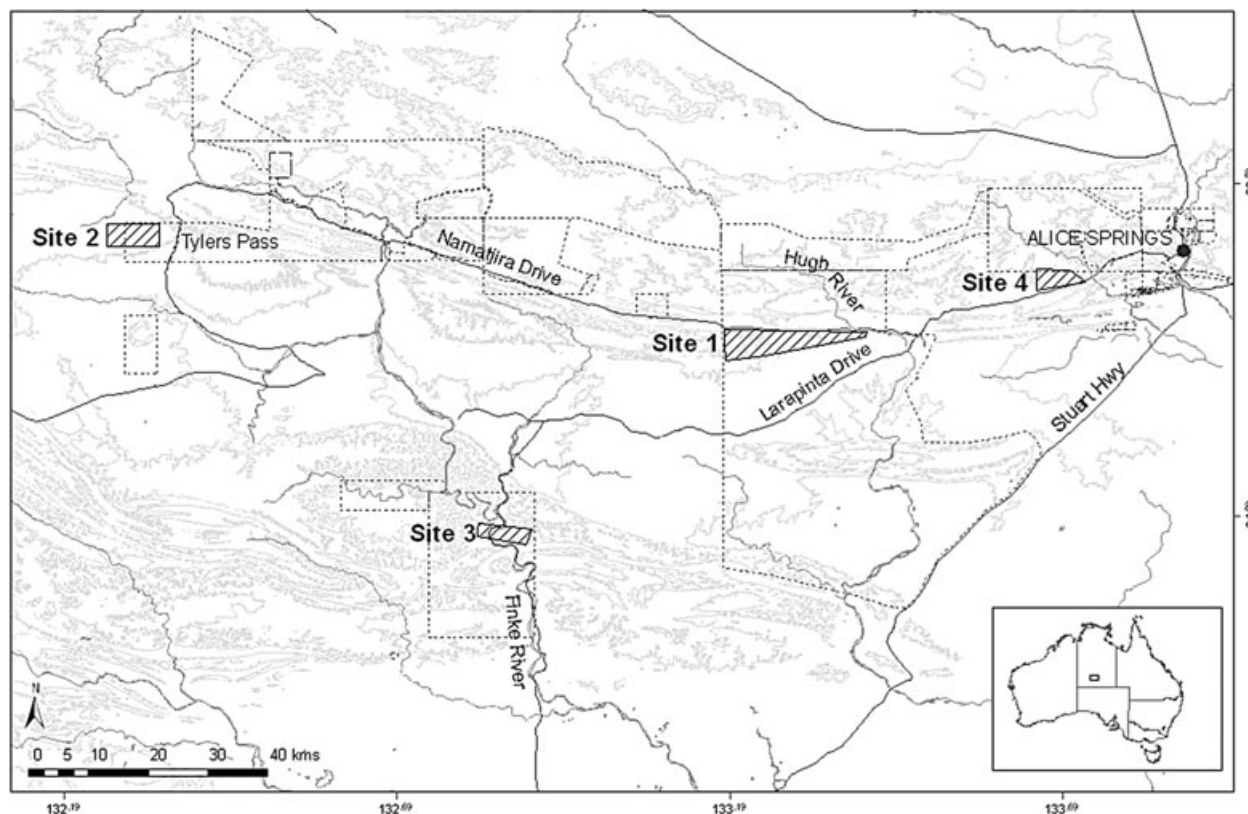
Fig. 1. Map of survey sites of mulga-spinifex mosaics on central Australian mountain ranges. Hashed lines denote approximate sample areas at each site, dotted lines denote conservation reserve tenure. Site 1 Brewer Conglomerate (Hugh River section); Site 2 Brewer Conglomerate (Tylers Pass section); Site 3 Finke Gorge sandstone; Site 4 Iwupataka granite hills.

Sampling design and site selection

Existing information indicated that the level of abiotic control of mulga-spinifex transitions may vary according to situation. Specifically, transitions on the Brewer Conglomerate hills are known to coincide with major soil changes (Bowman *et al.* 1994; B. Pitts 1994, unpub. report) that can in turn be directly linked to geomorphic gradients (see B. Pitts 1994, unpub. report). By contrast, at other sites, transitions occur on uniform parent material (Northern Territory Government unpublished data) and are therefore less likely to be directly controlled by intrinsic abiotic constraints. Four sites were chosen to encompass this expected variability (Fig. 1). These were spread over a wide area and different land tenures to enable general rather than site-specific conclusions to be drawn from this study. All sites were in close proximity to roads or major tracks. Sites 1 and 2 were expected to provide examples of transitions across contrasting soil types. They were each located on the low lying hills of the Brewer Conglomerate. Site 1 was positioned just west of the Hugh River on Owen Springs Reserve, and incorporated much of the sampling area included in the study of Bowman *et al.* (1994). The site included two large

(average map area 11.5 km^2) discrete mulga patches with abrupt canopy edges. At a finer scale, transitions form between *A. aneura* shrubland and either *Triodia brizoides* or *Triodia longiceps* hummock grassland. Site 2 was situated west of Tylers Pass and was separated from Site 1 by a distance of approximately 90 km. This area had not hitherto been sampled and included portions of the West MacDonnell Ranges National Park and Haast Bluff Aboriginal Land Trust. At this site, mulga characteristically occurred as numerous, small (some barely in excess of 0.1 ha) and discrete patches in a *T. brizoides* grassland matrix. Sampling at this site was spread across two sub-areas that were separated by a distance of 6 km. Sites 3 and 4 were expected to support transitions on undifferentiated soils. Site 3 was situated at Finke Gorge National Park, approximately 40 km southwest of Site 1 and contained mosaics on a low sandstone plateau. Site 4 provided examples of transitions on low granite hills. This site was located on the Iwupataka Aboriginal Land Trust, approximately 30 km northeast of Site 1. The configuration of mulga and spinifex patches at these two latter sites was similar to that at Site 1. In each case, sampling effort was concentrated around two large mulga patches and their neighbouring *T. brizoides* grasslands.

Aerial photographs were used to identify mature and regenerating mulga and spinifex patches at each site based on colour contrast and field experience. Thus, sampling could be stratified across habitat variables of expected level of soil differentiation (strong/weak abiotic gradients); vegetation structure (grassland/shrubland), and time since fire (mature/immature canopy). Sample plots were thereby allocated to one of eight mutually exclusive combinations of each habitat attribute. Sampling effort was ultimately weighted towards the Brewer Conglomerate sites in order to account for the greater variability in spinifex habitat that was encountered there.

Data collection

Vegetation was surveyed using the semi-quantitative frequency technique of Outhred (1984). The method involved the construction of a 0.1 ha quadrat, itself comprising 10 sub-quadrats with cumulative areas of 2, 4, 8, 16, 32, 65, 126, 255, 512 and 1022 m^2. Species scores reflect the sum total of their occurrences in each of the 10 sub-quadrats. The technique offers an advantage over standard frequency measures in that it provides an accurate and repeatable measure of species abundance patterns (see Morrison *et al.* 1995). For this study, we assumed that discontinuity in vegetation structure determines boundary location. To take full account of potential edge effects, samples were taken from patch edges (defined by the outer limit of the mulga canopy) and their interiors. Ultimately, 50 paired boundary plots and 23 (11 mulga, 12 spinifex) patch interior plots were included in the analysis. Localized site environmental attributes were measured *in situ*. Soil characteristics were determined by assaying one randomly selected sample (at depths of 0–10 cm and 50 cm) for pH, field texture (% clay), and calcium carbonate presence using the HCl reaction test (see McDonald & Isbell 1990). Soil-depth sampling involved driving a steel peg as far as possible into the ground and averaging scores over 9 sample points. Slope was recorded in the field with the use of a clinometer, and aspect with a compass. Aspect was ultimately scored as either predominantly north- (270–89°) or south-facing (90–269°). Slope position was recorded as lower, mid, or upper. A visual estimate of the variables % litter cover, the proportion of outcrop, rock and bare soil; and following Bowman *et al.* (1994) rock fragment distribution (% boulders >15 cm, % small rocks 1–15 cm, and % gravel <1 cm) was made for each quadrat. Geological units were derived from existing 1:250 000 maps layers. No direct measure of fire-frequency was available for the study sites but the likelihood of frequent fire in this system can be estimated from grass fuel loads (see Griffin & Friedel 1984). A fire-frequency index was constructed for each plot from the sum of hummock- and tussock-grass frequencies. Sites were additionally scored as recently burnt or long unburnt according to the presence/absence of a mature structural canopy. Nomenclature followed the checklist for Southern Bioregions of the Northern Territory (Kerrigan & Albrecht 2007).

Floristic and environmental relationships

To test for differences in species composition patterns between mulga and spinifex habitats, a sample × species frequency matrix was classified with the clustering techniques available in PATN V3.03 for Windows (Belbin, Griffith University & The University of Queensland 2004). The Bray-Curtis dissimilarity coefficient was used to calculate a sample association matrix and samples were clustered using the agglomerative polythetic clustering strategy (FUSE) with unweighted pair-group arithmetic averaging with β = −0.1. A similarity percentage analysis SIMPER (Clarke & Gorley 2001) was then used to determine the level of dissimilarity among the PATN-defined species groups and to determine which species contributed most strongly to within group similarity and to between group dissimilarity.

Soil texture, chemistry and depth variables were analysed according to predefined habitat type (mulga or spinifex) and to the PATN cluster divisions using generalized linear models (GLM). The analyses used a binomial error structure with a logit link function for the calcium carbonate variable and a normal error structure with an identity link function for the soil depth variable. A poisson error structure with a log link function was used for all other variables. *F*-tests were calculated from Pearson chi-squared, and where possible, *post hoc* tests were carried out using Bonferroni corrections. Plots of residuals were examined to detect any non-linear trends (see Quinn & Keough 2001). GLM were also used to test the main and interactive effects of habitat structure and canopy age on overall species richness and on *A. aneura* life-stage frequency using the classes: charred stumps; live >2 m; live 0.5–2 m and live <0.5 m.

The ordination technique of Canonical Correspondence Analysis (CCA) (ter Braak & Prentice 1989; ter Braak & Smilauer 2002) was used to directly relate environmental gradients to the floristic dataset. The Forward Selection procedure was used to reduce collinearity among the variables and to ensure that each variable made a statistically significant (as determined by partial Monte Carlo permutation tests) contribution to the model. Results are graphed as biplots, in which the length of the arrow and position of the arrow head indicate the correlation between the explanatory variable and the CCA axes. Three separate models

were produced: (i) with all significant variables included; (ii) with fire-frequency and fire-recency used as covariables; and (iii) with the most influential edaphic factors used as covariables. In addition, the frequencies of fire-killed (<30% resprout), facultative-resprouter (response changes in space and time), strong-resprouter (>70% resprout), and fire-stimulated woody and half-woody (suffruticose) species at each site were plotted as supplementary (passive) variables onto the CCA ordination. This was done to test contrasting views in the literature for the distribution of regenerative traits in the landscape in relation to fire and resource gradients. Data for resprouting ability were derived from the Northern Territory Herbarium database and from personal field observations of species' responses in these habitats. Species were categorized as fire-stimulated if their frequency in burnt plots was twice that in mature plots.

Models

A set of contrasting resource niche and disturbance niche models was constructed from the literature to explain changes in vegetation structure and species' fire response traits across mulga-spinifex transitions (Table 1). Each model had an explicit mechanism and a prediction that could be directly tested with CCA. Resource theory holds that in arid systems, fine-textured soils with high water-holding capacity favour shallow rooting grasses, and sandy loose soils favour deep rooting shrubs (Noy-Meir 1973; Squeo *et al.* 2007). We would further expect *A. aneura* to have high nutrient demands relative to *Triodia* (see Rice *et al.* 1994; Tongway & Ludwig 2001), meaning that mulga should be absent from extremely high pH soils that have low phosphorous and micronutrient levels (see Whitford 2002). Disturbance niche theory predicts that high fire-frequencies favour grasslands and lower fire-frequencies favour woody plant dominance (Bond *et al.* 2005). Lower fire-frequency in wooded habitat is attributed to negative shrub canopy effects on grasses (see Peterson *et al.* 2007). Resource and disturbance explanations for the partitioning of species' recovery traits are outlined in detail in Clarke and Knox (2002) and Clarke *et al.* (2005). In short, if resource gradients are important, we would expect a predominance of resprouting shrubs on fine-textured soils that hold moisture close to the surface, and in grassy habitats more generally where competition can be important. If by contrast, the disturbance niche is paramount, then the proportion of strong resprouters should increase, and the proportion of obligate seeders should decrease with fire-frequency.

RESULTS

Floristics

A total of 193 species was recorded across 73 samples in this study. Included were 25 mature and 10 immature mulga samples and 25 mature and 13 immature spinifex samples. Classification (Fig. 2) of the full data set depicted three broad mosaic assemblages that may be characterized as *T. brizoides* hummock grassland, *A. aneura* shrubland and *T. longiceps* hummock grassland. Three types of between-habitat patterning were evident from the dendrogram: (i) minimal floristic overlap between mulga and *T. longiceps* habitat; (ii) relatively high floristic commonality between mulga and *T. brizoides* habitat; and (iii) minimal floristic overlap between the two different spinifex habitats. This variability in between-habitat floristic dissimilarity suggests the co-occurrence of multiple transition types.

Truncation of the dendrogram at the 5-group level produced groups that could be more readily related to fire and intrinsic edaphic effects. Group 1 comprised 15 mature *T. brizoides* grassland samples on soils with granite, sandstone and quartzite parent materials. Also included was one sample of sparsely regenerating mulga with a dense *T. brizoides* understorey. Group 2 (seven samples) represented the recently burnt version of Group 1. Group 3 comprised eight mature and immature *T. brizoides* samples, all of which occurred on conglomerate saprolite. Group 4 comprised 34 mature and immature examples of *A. aneura* shrubland on granite, sandstone and quartzite lithologies. The frequency of *T. brizoides* was highly variable (range 0–10, average 4.53), while that of *T. longiceps* was mainly low (range 0–6, average 0.29). Regenerating mulga samples had a higher than average frequency of *T. brizoides* (5.44) and of *T. longiceps* (0.67). Group 5 comprised eight mature and immature *T. longiceps* grassland samples. All occurred on limestone soils that were overlaid with sandstone and quartzite scree. Both *T. brizoides* and *T. longiceps* were present mainly as seedlings in the regenerating grassland sites.

At the 5-group scale, site effects were apparent mainly in relation to the distribution of spinifex groups 5 and 3 – with both being confined to the Brewer Conglomerate hills (Sites 1 and 2). By contrast, Groups 1 and 2 were each recorded from three of the four sites, encompassing both the 'strongly' and 'weakly contrasting' sample areas. Patterning therefore did not reflect sample class allocation (i.e. strong/weak gradients) as *per* the original survey design. Also at this scale, there was no evidence for patch edge effects on group membership. Thus, the variables 'site', 'sample class' and 'quadrat position' were not included in the analyses.

Table 1. Resource and disturbance models explaining habitat structure and woody species' fire trait distributions in mulga-spinifex mosaics

Model		Mechanism	Model prediction	Tests	Results
Resource productivity models					
(1) Soil moisture	Habitat structure	Soils without deep-profile moisture reservoirs restrict shrub persistence	Shrubland on sandier soils that allow for deep moisture percolation	CCA positive association of mulga shrubland with increasing soil texture	No support
	Fire-regeneration traits	Soils that do not retain moisture close to the surface restrict growth of species that allocate resources to storage organs	Resprouting will be more frequent in soils that retain surface moisture	CCA positive association of resprouting with decreasing soil texture	No support
(2) Soil depth	Habitat structure	Shallow soils restrict access to moisture of deep-rooted shrubs	Shrubs will be more frequent on deeper soils, grasses on shallower soils	CCA positive association of mulga shrubland with increasing soil depth	Conditional support
(3) Soil nutrients	Habitat structure	High pH and carbonated soils restrict shrub growth through reduced nutrient availability	Shrubs will be more frequent on neutral to acidic soils	CCA positive association of mulga shrubland with decreasing soil pH and carbonate presence	Conditional support
(4) Herbaceous competition	Fire-regeneration traits	Competition from grasses restricts shrub seedling recruitment in the post-fire environment	Resprouting will be more frequent in habitats that have higher herbaceous abundance	CCA positive association of resprouting with high graminoid frequency	Conditional support
Disturbance models					
(1) Fire-frequency	Habitat structure	Frequent fires inhibit shrub seedling recruitment to maturity (Global model)	Grassland will dominate areas with higher probabilities of frequent fire	CCA negative association of mulga shrubland with fire-frequency	Support
	Fire-regeneration traits I	Frequent fires inhibit shrub seedling recruitment to maturity	Resprouting will be more frequent in habitats with higher probabilities of frequent fire	CCA positive association of resprouting with fire-frequency	Support
	Fire-regeneration traits II	Frequent fires exhaust shrub seed banks	Fire-stimulated recruitment will be more frequent in habitats with lower probabilities of frequent fire	CCA negative association of mass recruitment with fire-frequency	No support

CCA, canonical correspondence analysis.

SIMPER pair wise group comparisons showed that mulga shrubland most closely resembled the composition of Group 1 (mature *T. brizoides*) (Table 2). The results showed further, that the respective dominants were the highest order contributors to between-group dissimilarity. Notably though, the two species varied greatly in terms of their proportional differences: *A. aneura* was more than six times more frequent in its own habitat while *T. brizoides* varied in abundance only by a factor of two. Combined, these data show that transitions between vegetation types 4 and 1 foremost reflect the varying abundance of *A. aneura*. In turn, key functional trait differences appear related to mulga canopy influences on disturbance frequency and resource availability. Mulga species contributing 50% of the 4:1 between-group dissimilarity included: facultative resprouter shrubs (e.g. *Eremophila latrobei* subsp. *glabra* and *Eremophila freelingii*); shade tolerant C_3 tussock grasses (e.g. *Digitaria brownii* and *Paspalidium constrictum*) and ferns (e.g. *Cheilanthes sieberi*
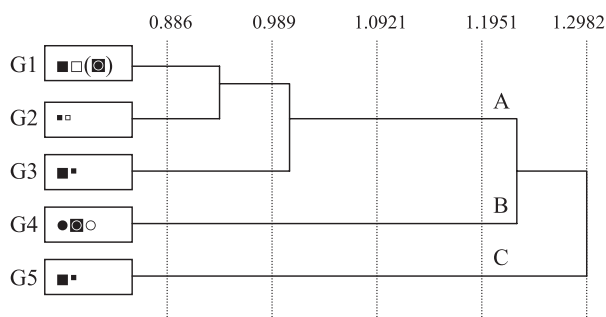
Fig. 2. Classification of 73 mulga and spinifex samples from central Australian mountain ranges. Three major clusters are evident: A = *T. brizoides* hummock grassland (with Groups 1, 2 & 3), B = *A. aneura* shrubland (Group 4) and C = *T. longiceps* hummock grassland (Group 5). *A priori* classes: ● mature mulga, ◉ immature mulga, ■ mature spinifex, ▪ immature spinifex from sites 1 & 2; and ○ mature mulga, □ mature spinifex; ▫ immature spinifex from sites 3 & 4. ( ) indicates 1 sample only from that class.

subsp. *sieberi* and *Cheilanthes lasiophylla*), as well as bird dispersed (berry producing) shrubs (e.g. *Enchylaena tomentosa* var. *tomentosa*). The fire-killed shrub *Acacia macdonnelliensis* was unique to mulga but was otherwise rare in the landscape. By contrast, numerous disturbance specialists including strong resprouters (e.g. *Senna glutinosa* subsp. *glutinosa* and *Eucalyptus gamophylla*) and fire-stimulated species (e.g. *Evolvulus alsinoides* var. *villosocalyx* and *Paraneurachne muelleri*) were either diagnostic of Group 1 or they did not occur in mulga. Fire-tolerant *Acacia* shrubs (e.g. *A. kempeana* and *A. bivenosa*) further distinguished Group 1 from mulga.

SIMPER showed that *A. aneura* was either completely absent from the remaining spinifex habitats or it occurred there in comparatively low abundance. The discrepancy between *A. aneura* frequency in mature (Group 1) and recently burnt (Group 2) *T. brizoides* habitat was particularly noteworthy, being in the order of 11 to 1 (Table 2). This is indicative of negative fire-recency effects on this species in Group 1–2 habitat. By contrast, the complete avoidance of Group 3 habitat by *A. aneura* may be more reflective of edaphic effects given that this group comprises burnt and mature samples. In each case, the list of subordinate mulga species contributing to between-group dissimilarity was essentially the same as that in the 4:1 comparison, providing further support for the importance of mulga canopy effects across the range of transition types. Fire-stimulated species (e.g. *Panicum effusum* and *Petalostylis cassioides*) distinguished Group 2 from mulga. By contrast, various alkaline soil specialists (see Latz 1995) (e.g. *T. longiceps*, *Eucalyptus socialis* subsp. *eucentrica* and *Sida* sp. Limestone) were diagnostic of, or were otherwise unique to Groups 3 and 5. Transitions involving mulga and spinifex groups 3 or 5 are therefore more likely edaphically controlled.

Floristic patterns in relation to environmental variables and fire age

Generalized linear models analysis showed that spinifex soils were more alkaline and more frequently carbonated at surface ($F_{1,71} = 31.9$, $P < 0.0001$ and $F_{1,71} = 24.1$, $P < 0.0001$) and at depth ($F_{1,71} = 39.2$, $P < 0.0001$ and $F_{1,71} = 8.7$, $P < 0.01$) than mulga soils. Soils were deeper ($F_{1,71} = 5.2$, $P < 0.05$) in mulga habitat, and trended towards an increase in clay content at surface and at depth ($F_{1,71} = 1.7$, $P > 0.05$ and $F_{1,71} = 2.9$, $P > 0.05$).

The five floristic groups differed widely in terms of their surface and deep-profile pH values ($F_{4,68} = 30.6$, $P < 0.001$ and $F_{4,68} = 38.1$, $P < 0.0001$) (Table 3). Groups 3 (*T. brizoides*) and 5 (*T. longiceps*) were each more alkaline at depth compared with all remaining groups (both $P < 0.0001$). Group 3 surface soils were also far more alkaline than those of all other groups ($P < 0.0001$), while Group 5 differed from Group 4 (mulga) in this same regard ($P < 0.0001$). In summary, Group 3 soils were extremely alkaline; Group 5 soils were neutral to alkaline on the surface and extremely alkaline at depth; and Groups 4, 1 and 2 were acidic throughout (Table 3). The five groups could also be distinguished on the basis of soil carbonate presence/absence at surface and at depth ($F_{4,68} = 48.5$, $P < 0.0001$ and $F_{4,68} = 36.2$, $P < 0.0001$). *Post hoc* tests were not possible, but Table 3 shows that Group 3 soil was consistently carbonated throughout the profile, while Group 5 was usually carbonated only at depth. Soils of the remaining groups were carbonate-free. Soil surface ($F_{4,68} = 2.9$, $P < 0.05$) and deep-profile ($F_{4,68} = 8.7$, $P < 0.0001$) texture values varied according to floristic group. Specifically, *T. longiceps* samples had the highest clay-content at surface and at depth, differing significantly from all other groups ($P < 0.02$ and $P < 0.001$), and *T. brizoides* Group 3 samples were sandier at depth ($P < 0.01$) than all other groups. Soil depth also varied according to floristic group ($F_{4,68} = 2.9$, $P < 0.05$) with Group 3 soils being the deepest. Floristically similar groups 4 (mulga) and 1 (*T. brizoides*) did not differ significantly in terms of their soil depth, chemistry and texture.

Generalized linear models analysis showed that species richness was enhanced in recently burnt spinifex but did not vary according to fire age in mulga ($F_{1,69} = 5.419$, $P < 0.05$). Analysis of *A. aneura* life-class frequency also revealed the importance of habitat and fire age on the distribution of this species. Seedlings, charred stumps and mature shrubs (2–6 m) were more frequent in mulga than in spinifex ($F_{1,69} = 56.44$, $P < 0.0001$; $F_{1,69} = 79.8$, $P < 0.0001$ and $F_{1,69} = 146.9$, $P < 0.0001$), the latter being absent from spinifex altogether. Not unexpectedly, seedlings and charred stumps were more frequent in immature habitat ($F_{1,69} = 4.993$, $P < 0.05$; $F_{1,69} = 24.41$, $P < 0.0001$),

Table 2. Species contributing up to 50% of the average Bray-Curtis between-group dissimilarity (using SIMPER analysis); and woody species with a summed average frequency >1 that are unique to or absent from mulga

Life form	Fire response	Species	Mean species frequency				
			G1	G2	G3	G4	G5
Tree	r	*Corymbia opaca*	0.19	0.29	*2.1*	*0*	0.13
	r	*Hakea lorea* subsp. *lorea*	0.31	0.14	0.38	0	0.63
Mallee shrub	r	*Eucalyptus gamophylla*	0.38	0.71	0	0	0
	r	*Eucalyptus socialis* subsp. *eucentrica*	0	0	0	0	**2**
	r	*Eucalyptus trivalvis*	0	1	0	0	0
Shrub	k	*Acacia aneura*	**1.1**	*0.1*	*0*	7	*0.8*
	v	*Acacia bivenosa*	**2.7**	**4.4**	**2.6**	0.2	**2.8**
	v	*Acacia kempeana*	**2.3**	0.29	1	**1.9**	**1**
	r	*Acacia spondylophylla*	0	**3.6**	0	*0*	0
	r	*Acacia victoriae* subsp. *arida*	0	0	0.38	0	0.13
	v	*Eremophila freelingii*	0.5	*0*	0.1	**3.2**	**0.8**
	v	*Eremophila latrobei* subsp. *glabra*	0.4	*0*	*0*	**2.6**	0
	v	*Eremophila latrobei* subsp. *latrobei*	*1*	0.3	*0*	**4.2**	0
	r	*Gossypium sturtianum* var. *sturtianum*	0	**3.7**	0.75	0	0
	r	*Hibiscus solanifolius*	0	**4.1**	*0*	*0*	0
	v	*Indigofera* sp. MacDonnell Ranges	0.44	**2.9**	0.25	0.6	0.5
	k	*Maireana georgei*	**1.8**	0	0	1.3	0.25
	k	*Melhania oblongifolia*	0	1.29	**3**	0.2	0
	v	*Scaevola spinescens*	**3.2**	0.43	0	0.7	0
	v	*Senna artemisioides* nothosubsp. *artemisioides*	**2**	1.29	**2.1**	**1.4**	0.13
	r	*Senna glutinosa* subsp. *glutinosa*	**1.94**	**1.29**	0.13	0.3	**4**
Half shrub		*Abutilon fraseri* subsp. *fraseri*	0.06	0.6	0	**2.2**	1.4
	r	*Anemocarpa saxatilis*	0.06	0.57	1.63	0	0
	k	*Enchylaena tomentosa* var. *tomentosa*	*0.9*	*0.4*	*0.5*	**2.5**	*0.4*
	v	*Evolvulus alsinoides* var. *villosicalyx*	**2.1**	**6.3**	1	**1.7**	0.63
	r	*Haloragis uncatipila*	0.19	1.43	1.5	0	0
	r	*Hibiscus sturtii* var. *grandiflorus*	0.38	**5.1**	0	1.2	0.38
	v	*Maireana villosa*	0.1	*0*	*0*	**2.2**	0
	r	*Petalostylis cassioides*	0.13	**3.9**	0	*0*	0
		Phyllanthus lacunellus	0.06	**3.6**	0	*0*	0
		Ptilotus schwartzii var. *schwartzii*	**1.56**	**3.4**	0.13	1.3	0
	r	*Ptilotus sessilifolius*	0	0.29	**1.75**	0	0.25
	r	*Sida* sp. Limestone	0	0	1.38	0	0
	k	*Sida filiformis*	**3.7**	**1.9**	0.4	**5.4**	**2.5**
Forb		*Euphorbia centralis*	0	0	**3**	0.3	0
		Ptilotus clementii	0	1.29	**2.5**	0.1	0.13
		Salsola tragus	0	0	**4**	0.2	0
		Solanum ellipticum	0	1.43	**3.9**	0.9	0
		Swainsona phacoides	0	0	**2.4**	0	0
		Trichodesma zeylanicum var. *zeylanicum*	0	**1.86**	**3.9**	0.1	0.13
		Zygophyllum tesquorum	0	0	**2.1**	0	0
Fern		*Cheilanthes lasiophylla*	**2.5**	*0*	*0*	**5.3**	*1*
		Cheilanthes sieberi subsp. *sieberi*	0.3	*0*	*0*	**2.6**	0
Hummock grass		*Triodia brizoides*	**9.9**	**9.3**	**10**	4.5	*0*
		Triodia longiceps	0	0	0	0.3	**10**
Tussock grass		*Digitaria brownii*	*0.3*	*0.3*	*0*	**3.5**	*0*
		Enneapogon polyphyllus	0.13	0.86	**2**	**2.2**	0.5
		Eriachne mucronata	**1.9**	**1.71**	0	0.9	0.38
		Panicum effusum	0.13	**4.3**	0	0.1	0
		Paraneurachne muelleri	**2.6**	**5**	0.13	0	1.38
		Paspalidium constrictum	*0.1*	*0.1*	*0*	**2.6**	0
		Tripogon loliiformis	0.06	0	0	**2.1**	0.6
SIMPER pair wise average dissimilarity			G1	G2	G3	G4	G5
		G1		75.3	78.5	77.5	85.2
		G2			79.9	86.8	89.9
		G3				89.5	94.5
		G4					89.2

Numbers in bold indicate diagnostic species by group. Italicized numbers indicate discriminating species for mulga and spinifex group pair wise comparisons. G1-3 *T. brizoides* (spinifex); G4 *A. aneura* (mulga); and G5 *T. longiceps* (spinifex). Fire response: *r* > 70% resprout; v = response varies in space and time; k < 30% resprout.

Table 3.   Mean (±standard error) soil pH, CaCO₃, texture and depth values across the five PATN groups

Soil variable	G1	G2	G3	G4	G5
Soil pH (S)***	5.9 (0.2)	6.0 (0.3)	8.8 (0.1)	5.4 (0.1)	7.3 (0.4)
Soil pH (D)***	6.3 (0.2)	6.4 (0.2)	8.9 (0.1)	5.7 (0.1)	8.5 (0.3)
CaCO₃ frequency (S)***	0.0 (0.0)	0.0 (0.0)	100 (0.0)	0.0 (0.0)	12.5 (0.1)
CaCO₃ frequency (D)***	0.0 (0.0)	0.0 (0.0)	87.5 (0.1)	2.9 (0.03)	37.5 (0.2)
Soil depth (cm)*	9. (1.0)	9.4 (1.6)	12.9 (2.1)	11.8 (0.7)	7.3 (1.1)
Clay content class: 1–9 (S)*	2.4 (0.3)	1.9 (0.1)	2.6 (0.4)	2.9 (0.2)	3.9 (0.8)
Clay content class: 1–9 (D)***	5.2 (0.6)	6.1 (0.9)	3.8 (0.6)	6.6 (0.4)	9.0 (0.0)

Significance levels *$P < 0.05$; ***$P < 0.001$. G1–3 *T. brizoides;* G4 *A. aneura*; and G5 *T. longiceps*. S = surface, D = depth.

Table 4.   Results of ordinations by canonical correspondence analysis (CCA) for species-environmental correlation coefficients

Species environmental coefficients	Model I (all significant variables included)		Model II (Fire-frequency & recency as covariables)		Model III (Geology & soil chemical properties as covariables)	
	Marginal effects lambda	Conditional effects	Marginal effects lambda	Conditional effects	Marginal effects lambda	Conditional effects
Aspect (degrees)	0.15	0.028*	0.11	0.022*	0.12	0.03*
CaCO₃ (surface)	0.32	0.002**	0.31	0.002**	CoV.	CoV.
Fire-recency	0.15	0.002**	CoV.	CoV.	0.16	0.002**
Fire-frequency index	0.19	0.002**	CoV.	CoV.	0.19	0.002**
% Outcrop	0.11	0.024*	0.11	0.014*	0.08	0.01*
Sandstone	0.21	0.002**	0.22	0.002**	CoV.	CoV.
% Stones	0.15	0.028*	0.13	0.016*	0.09	0.022*
pH depth	0.29	0.002**	0.28	0.002**	CoV.	CoV.
Slope value	0.13	0.042*	0.14	0.058 NS	0.08	0.058 NS
Soil depth	0.14	0.02*	0.13	0.01*	0.09	0.01*

*$P < 0.05$; **$P < 0.01$; NS, not significant, Monte-Carlo permutation tests. CoV., indicates that the environmental variable was treated as a covariable.

while mature shrubs were more frequent in mature habitat ($F_{1,69} = 22.01$, $P < 0.0001$). Juveniles (<2 m) showed an interaction of habitat and fire age effects ($F_{1,69} = 8.124$, $P < 0.01$), being more frequent in immature than in mature mulga but not varying according to fire age in spinifex.

Monte Carlo tests indicated that the first, and all canonical axes of all three CCA models were highly significant ($P = 0.002$ with 499 permutations under a reduced model). CCA using significant edaphic and fire-related variables (Table 4) produced a model that explained 70.2% of the variation in the floristic data, with the first two axes accounting for 45.3%. The first axis of the site × environmental variables bi-plot (Fig. 3a) illustrated a gradient from high mulga abundance on low pH and non-carbonated soils to spinifex dominance on stonier, higher pH and, in the case of Group 3 samples, strongly carbonated soils. Fire-frequency (as implied by ground fuel loads) correlated with the gradient from shrubland to grassland though this variable was of reduced consequence relative to the soil parameters (Table 5). Likewise, fire-recency had only moderate influence. Sandstone and carbonate presence were the most influential variables

along the second axis. The first axis showed strong patterning of species' fire-response attributes in relation to habitat gradients. Particularly noteworthy was the correlation of strong-resprouter frequency and fire-stimulated frequency with spinifex samples. By contrast, variable-resprouter frequency and weak-resprouter frequency were positively correlated with mulga.

Canonical Correspondence Analysis with fire-frequency and fire-recency included as covariables explained 81.2% of the variation in the floristic data, and the first two axes accounted for 53.1% of this variation. The forward selection results deviated from those of the previous analysis only in that in this case, slope was not significant (Table 4). Likewise, patterning along Axes 1 and 2 (Fig. 3b, Table 5) did not vary from that of the first CCA, indicating the overriding importance of edaphic variability for species' patterning in these mosaics. Species' attribute patterns closely resembled those of the first model.

The third CCA model, with soil chemical properties and geology included as covariables, explained 77.1% of floristic variation, with the first two axes accounting for 47.3%. In this model, Axis 1 was most strongly
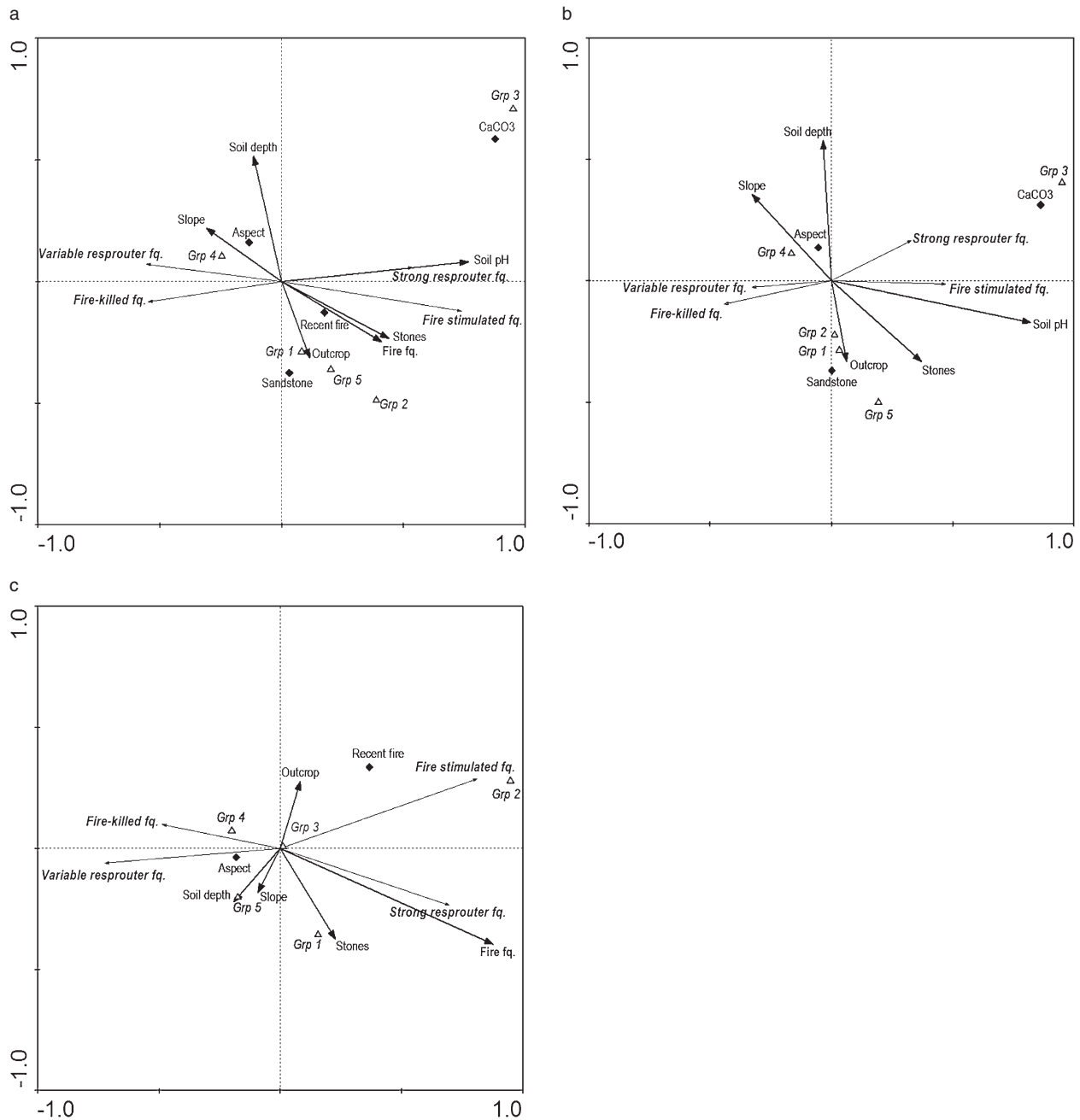
Fig. 3. Site x environmental variables biplot using data from 73 samples of mulga and spinifex habitat on central Australian mountain ranges. (a) all significant environmental variables included; (b) with fire frequency and fire-recency included as covariables; and (c) with soil chemical properties and geology included as covariables. Thick arrows represent continuous environmental variables. Increasing arrow length denotes a stronger correlation with environmental gradients. Categorical environmental variables are indicated by a diamond symbol, with more important variables being further from the origin. Thin arrows represent continuous passive variables and the PATN fine-scale clusters (Grps 1–3 = *T. brizoides*; Grp 4 = mulga; Grp 5 = *T. longiceps*) are indicated by a triangle symbol. Strong resprouter fq. is the proportion of woody species classified as resprouters (>70% resprout); Variable resprouter fq. is the proportion of woody species classified as variable resprouters (response varies in space and time); Fire-killed fq. is the proportion of woody species that are killed by fire (<30% resprout), and Fire-stimulated fq. is the proportion of woody species that have enhanced recruitment in the post-fire environment.

correlated with fire-frequency (Fig. 3c, Table 5). Fire-recency had some, though far reduced effect. Overall, Axis 1 depicted a gradient from infrequently burnt mulga shrubland to frequently burnt spinifex grassland. Fire-recency effects characterized Axis 2, with recently burnt (Group 2) and mature (Group 1) *T. brizoides* clusters having the greatest spatial separation. In this model, the frequencies of fire-

Table 5. Results of ordinations by canonical correspondence analysis (CCA) for eigenvalues and interset correlations of environmental variables with the first two axes of CCA

	Model I (all significant variables)		Model II (Fire-frequency & recency as covariables)		Model III (Geology & soil chemical properties as covariables)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.389	0.259	0.345	0.244	0.216	0.124
Correlation coefficients	0.925	0.911	0.942	0.885	0.841	0.829
Gradient length	3.429	3.661				
Interset correlations						
Aspect	−0.3441	0.4075	−0.1752	0.4129	−0.4355	−0.0857
CaCO3 (surface)	0.7341	0.4829	0.8534	0.2908	CoV.	CoV.
Fire-frequency index	0.379	−0.2252	CoV.	CoV.	0.7433	−0.33
Fire-recency	0.2913	−0.2083	CoV.	CoV.	0.5679	0.5125
Sandstone	0.0519	−0.6184	0.0038	−0.7009	CoV.	CoV.
% Outcrop	0.1064	−0.2853	0.059	−0.2945	0.076	0.2482
pH (depth)	0.7083	0.0741	0.7783	−0.1533	CoV.	CoV.
Slope value	−0.2858	0.1997	−0.3098	0.3166	−0.087	−0.1704
Soil depth	−0.1073	0.469	−0.0329	0.5131	−0.1708	−0.1945
% Stones	0.4062	−0.2125	0.3586	−0.3019	0.2297	−0.3723

CoV. indicates that the environmental variable was used as a covariable.

stimulated and strong-resprouter shrubs were closely aligned along Axis 1 and were positively associated with increasing fire-frequency. Fire-stimulated recruitment varied along Axis 2 primarily in relation to fire-recency effects in spinifex.

DISCUSSION

What is the nature of mulga-spinifex transitions?

We found that patch types defined according to *A. aneura*, *T. brizoides* or *T. longiceps* dominance differed in floristic composition and life history traits. This means that the different patch types provide contrasting habitats for subordinate mosaic species, either because of intrinsic abiotic variability or because the dominants differentially affected habitat conditions. Importantly though, the results also showed that the degree of between-habitat floristic overlap varied by patch type combination: in certain cases boundaries reflected abrupt compositional discontinuity and in others, somewhat more of a structural shift. This variability was evident at both broad (i.e. 3-group) and fine (5-group) scales. Our data showed, therefore, that mulga-spinifex mosaics comprised different transition types. Regarding the latter type, *A. aneura* distribution was the primary determinant of boundary location given that the other patch dominant *T. brizoides* was far less often confined to its own habitat. The finding represents a major deviation from Bowman *et al.* (1994) who reported only the first transition type.

Do mulga-spinifex transitions reflect resource niche partitioning?

Our results showed that mulga-spinifex transitions were strongly correlated with changes in physical environmental factors. Aligning with Bowman *et al.* (1994), we documented a generalized gradient from mulga shrubland on deeper and more acidic soils; to spinifex grassland on carbonated alkaline soils. It may be assumed, therefore, that the juxtaposition of contrasting soil types has given rise to this variegated landscape patterning. This aligns with Whitford's (2002) view of the overarching influence of soil properties on structural patterning in deserts. The demonstrated association of shrubland with deeper, more nutrient-rich soils is in keeping with explanations for mulga grove–intergrove patterning (Tongway & Ludwig 2001). The results did not, however, comply with the inverse texture hypothesis given that mulga was weakly associated with the functionally drier, finer-textured soils and was therefore not directly limited by water availability. This deviation possibly relates to other factors associated with clay soils such as mechanical constraints on root growth (see Sperry & Hacke 2002).

Importantly, the combination of analyses presented in this study reveals a greater level of complexity beyond that reported in the study of Bowman *et al.* (1994). Most notably, the results of analysis at the 5-group level showed that floristic dissimilarity between mulga and spinifex was highest where there were major soil changes. Specifically, we propose that stationary transitions occurred on different soils between mulga and *T. brizoides* Group 3 and between mulga and *T. longiceps* habitats. We further suggest that soil variability has

given rise to stationary transitions between *T. longiceps* and *T. brizoides* dominated grasslands, and between the different *T. brizoides* habitats (groups 3 and 1–2). It is likely that these transitions are mediated by the interaction of inherent soil texture and nutrient constraints and plant resource acquisition traits, and that they will therefore remain stable through time (see Peters *et al.* 2006). By contrast, we propose that 'dynamic' transitions occurred on undifferentiated soils between *A. aneura* and *T. brizoides* Group 1–2 habitat. Importantly though, we expect that boundary changes would only occur over long time scales (i.e. many decades) owing to limits on primary productivity.

The results also allow consideration of the role of resource-gradients in the distribution of species' post-fire regenerative traits. Across the range of CCA analyses presented, there was a consistent association of fire-killed and variable resprouter frequency with mulga shrubland and of strong resprouter frequency with spinifex grassland. Two resource-niche models for resprouting were tested in this study. The first relates resprouter frequency to soil type, with the expectation that sandy-soils restrict the growth of species that allocate resources to storage organs. In this case, however, the soil texture hypothesis had low explanatory power in that CCA indicated that soil texture had little overall effect. The second model for the distribution of response traits attributes the lack of shrub seedling recruitment in grasslands to competition from grass adults in the post-fire environment. While CCA analysis demonstrated a positive association of resprouting with grassland dominance, care needs to be exercised in the application of competition theory owing to the greater propensity of these particular *Triodia* species to regenerate from seed rather than from vegetative buds. By this reasoning, there is a greater potential for fire-killed species to persist in these grasslands than in others characterized by resprouting grass species. Overall, this study provided little direct support for the role of the resource-niche in the partitioning of species' regenerative traits.

Would boundaries shift as a result of a disturbance mediated reduction in resource patchiness?

The first model of Bowman *et al.* (1994) ascribes mulga contraction to fire-induced soil erosion. It suggests that fire can disrupt a feedback process whereby the presence of mulga leads to deeper soils that better support mulga dominance. It is in this way akin to various existing models for desertification (see Schlesinger *et al.* 1990; Bhark & Small 2003) or 'landscape dysfunction' (Tongway & Ludwig 1997) in other dryland systems. The results of this study did not, however, lend support to this model in this particular setting. At the

broadest level of comparison, the soil depth differential between shrubland and grassland habitat coincided with edaphically controlled differences in soil chemistry and was therefore unlikely to be a consequence of *A. aneura* dominance. At the 5-group level, *Triodia* group 3 occurred on the deepest soils, meaning that the basic premise of the model was again not supported. Overall these results did not provide support for the concept of a directional expansion of spinifex in response to fire-driven soil changes. This means that other possible post-fire changes must be examined in relation to the process of mulga contraction.

Does current patterning reflect the disturbance niche?

In their account, Bowman *et al.* (1994) reported that contrary to the predictions of theory, mulga and spinifex are not end components of a fire gradient from long undisturbed shrubland to frequently burnt grassland. Accordingly, they argued that these habitats have independent post-fire recovery paths, thereby explaining the abrupt floristic changes across habitat boundaries, and the non-significant contraction of mulga in recent history. Certain of our data lend weight to this view. Specifically, they indicated that some transitions (i.e. those involving groups 4 & 3 and 4 & 5) were most probably edaphically controlled, meaning that successional dynamics would ultimately lead to stand replacement (see Peters *et al.* 2006). The data also showed that all of the *A. aneura* life-classes were more closely associated with mulga than with spinifex. This is inconsistent with the type of patterning that would result from a recently initiated wide-scale retreat of mulga – which scenario would instead likely produce more mixed patterning especially in relation to regenerating and fire-killed classes.

Importantly though, our study differed from that of Bowman *et al.* (1994) in being able to present additional data that are more consistent with models for dynamic between-habitat relationships. For example, we documented the occurrence of structurally and compositionally mixed habitats that can be interpreted as intermediate fire successional stages (e.g. regenerating mulga with a dense *T. brizoides* understorey). Further, the *A. aneura* life-class data are of additional relevance in that they demonstrated the presence of <2 m individuals and charred stumps in spinifex (albeit at a far reduced frequency than in mulga), and the simultaneous absence of live adults in that habitat. This indicated that while this species can in certain circumstances establish in neighbouring habitat, it will rarely persist to maturity there, most likely due to fire effects. The discrepancy between *A. aneura* frequency in long unburnt (Group 1) and recently burnt (Group 2) *T. brizoides* habitat provided additional evidence for the

negative effects of fire on the distribution of this species. And finally, strong support for dynamic transition models was provided by the third CCA that identified fire-frequency, as derived from ground fuel load estimates, as the single most important factor associated with the gradient from shrubland to grassland. Combined, these results showed that in cases where shrub-grass transitions did not reflect dramatic microhabitat changes (e.g. between groups 4 and 1), boundary positioning was primarily dependent on the level of fire recurrence. While advocating the use of this dynamic model, Bowman *et al.* (1994) could not apply it directly to their results because of the consistently strong floristic–edaphic covariance they encountered.

Evidence further indicated that the distribution of fire-response traits can be best explained by disturbance niche theory. Specifically, CCA consistently showed that the proportion of strong resprouters increased along the fire-frequency gradient. Importantly, however, the positive association of fire-stimulated recruitment with increasing fire-frequency indicated that a persistence/recruitment trade-off is unlikely to operate in these mosaics. Instead, the results demonstrated that while many mulga species were non-sprouters, they were not 'obligate seeders' in that they did not exhibit obligate fire-stimulated recruitment. In this way, mulga qualifies as a fire-independent ecosystem (*sensu* Bowman 2000), differing from spinifex not just in terms of fire-recurrence and -recovery rates (see Bowman *et al.* 1994), but also in regard to its non-reliance on fire for within-habitat regenerative processes.

Would changed fire-frequency cause directional boundary shifts?

It has been emphasized throughout this discussion that certain boundaries were more reflective of *A. aneura* canopy development than of abrupt floristic and edaphic discontinuity. The result is of immediate relevance to the discussion of possible future mulga contraction. Here, for example, it would be easy to foresee a boundary shift in the direction of mulga in response to heightened fire-frequency given that *A. aneura* is among those species least capable of withstanding repeated fire exposure. In this context, the loss of *A. aneura* would represent the critical step in the conversion of shrubland to hummock grassland. This model deviates from that of Bowman *et al.* (1994) in that its depiction of mulga contraction is not necessarily permanent, and it does not require the novel incursion of spinifex species through the creation of novel post-fire 'niche opportunities' (*sensu* Shea & Chesson 2002). In this way, it aligns most closely with the definition of Peters *et al.* (2006) of *shifting transitions* in that it implies that prevailing site conditions (in this

case fire-return intervals) temporarily favour one patch dominant over the other. Importantly, this model can also readily account for situations where changed fire patterns may generate long-term changes in boundary location. For example, a shifting transition may become directional if positive fire feedbacks establish and create flow on effects such as *A. aneura* seed bank depletion. However, like the model of Bowman *et al.* (1994), this new model has little current application in the central Australian context in the absence of direct evidence for widespread mulga contraction.

Importantly though, this alternate view of fire-mediated *A. aneura* segregation accounts for the rarity of mulga-*T. brizoides* mixes in the central Australian landscape in spite of the overlapping edaphic tolerances of the structural dominants. It thereby raises the possibility that with reduced firing, mixed patch types could potentially dominate the landscape, while the segregation of mulga and spinifex species across physiological niche thresholds (e.g. extremely high pH and strongly carbonated soils) would be comparatively rare.

Do other factors influence habitat membership?

This study additionally alludes to the importance of biotic interactions for coexistence in these mosaics. This relates principally to the importance of competitive effects in grassland habitat. Applying disturbance theory (see Chesson 2000), the reported lower overall species richness in mature- than in immature-spinifex may be explained by the increasingly negative influence of *Triodia* dominance with time since fire. By contrast, the equivalent species richness in regenerating and mature mulga suggests that this habitat type is possibly less reliant on disturbance for the circumvention of competitive exclusion. The results of the CCA are of additional relevance to this discussion of competitive effects in spinifex in that they showed that this habitat was characterized by strong resprouters that have disturbance-enhanced recruitment. This is highly suggestive of the importance of the trait combination of persistence and event-dependent recruitment (most prominent in the *Acacia* species *A. bivenosa* and *A. spondylophylla*) as a means of reducing the risk of extirpation from this highly competitive and fire-prone habitat.

It is possible too, that as the mulga dominant, *A. aneura* may have contributed to habitat membership by precluding the establishment of spinifex *Acacia* species with similar resource requirements. And further, canopy effects in mulga habitat might in some cases have caused the reduction in *Triodia* abundance across habitat boundaries. This is in keeping with the notion of resource-controlled wooded formations *as per* the global fire model (see Bond 2005). Future

experimental emphasis on these issues may therefore prove instructive. Conversely *A. aneura* may have influenced species' distributions by enhancing moisture, shade and nutrient availability. This form of facilitation by shrubs has been recorded in a number of other desert environments (e.g. see Fridley 2003; Schenk *et al.* 2003). The predominance of shade-tolerant C_3 tussock grasses and ferns in mulga habitat is a potentially good example of this process. And further, the enhanced abundance of berry producing chenopod shrubs in mulga may have resulted from the provision of multiple perch sites for fruit-eating birds by *A. aneura*. This type of dispersal-mediated floristic patterning was documented by Yeaton (1978) in Chihuahuan Desert shrublands. Again though, experimentation is required to ascertain the relative contribution of these factors to mosaic patterning.

Do existing models account for boundary regulation?

The various models examined in this study each provided some insight into the likely reasons for floristic, functional trait and structural variability in mulga-spinifex mosaics. Importantly though, none could independently account for all patterning. Instead, the results strongly pointed to the co-occurrence of different transition types that are controlled by a variety of contrasting processes – including edaphic constraint, fire and biotic interactions – and potentially, their interactive effects. This result mirrors the increasing emphasis on multi-causal explanation for community assembly (Weiher *et al.* 2004), and indeed, community 'disassembly' (*sensu* Worm & Duffy 2003) in the wider ecological literature. It is expected, therefore, that a more inclusive approach will be of greater value in the formulation of predictive models for mulga-spinifex distribution shifts, and for understanding Australian desert plant community dynamics more generally.

ACKNOWLEDGEMENTS

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