

Chapter 3

Covariance in species patterning and environmental gradients in central Australian dunefields

Summary

1 Current evidence indicates that mulga-spinifex boundaries on central Australian mountain ranges relate foremost to a variety of edaphic (mainly soil-related) habitat variables. This provides support for the view that species' distributions in these mosaics principally reflect the combined influence of niche-differentiation and spatial variability. Certain other coexistence mechanisms, principally: fluctuating disturbance, competitive exclusion, facilitation and dispersal constraints, might also contribute to boundary regulation in this setting.

2 Further work is required to ascertain the universality of these themes for coexistence maintenance in mulga-spinifex mosaics across the range of central Australian landscapes.

3 Field surveys were conducted in mulga-spinifex mosaic habitats in central Australian dunefields to enable further characterisation of floristic patterns, and to directly relate observed patterns to environmental gradients.

4 Classification and ordination depicted the existence of three major dunefield mosaic assemblages that may be characterised as: Group A, non-spinifex mulga shrubland; Group B, mixed mulga-*Triodia basedowii* habitat (comprised of subgroups 2, 3, 4 & 5), and Group C, mixed mulga-*Triodia pungens* habitat (comprised of subgroups 6 & 7).

5 Dissimilarity analyses confirmed that mosaic boundaries are highly variable in character – in certain cases representing true compositional discontinuity and in others, more of a structural shift.

6 The results of direct gradient analysis provided strong indication that dunefield mosaic floristic patterns relate most closely to a topographically controlled gradient in soil texture, with 'non-spinifex' mulga occupying the heaviest textured swale soils and spinifex dominating the sandy dune slopes.

Examples of mixed mulga-spinifex habitat occurred in swales of intermediate clay content.

7 To account for this patterning, it was suggested that plants occupying the fine-textured swales do so principally by virtue of their greater ability to tolerate the water-limiting and hard setting soils there. It followed that the reported between-habitat separation of dunefield mosaic species was most easily explained by invoking the notion of independent niche distributions along this soil-texture gradient.

8 Importantly however, the edaphic model could not account for the exclusion of mulga species from areas upslope of their normal distribution or from sandier areas more generally. For this, a combination of fire effects and biotic interactions were regarded as being of greatest potential importance. Fire was likewise emphasised for its role in the maintenance of coexistence in spinifex habitat, principally through the process of competitive release.

3.1 Introduction

The research presented in the previous chapter was aimed at the identification of the major correlates of floristic patterning in mulga-spinifex mosaics on central Australian mountain ranges. The rationale for that study was that, in order to gauge the likelihood of mosaic coexistence breakdown, it is first necessary to gain a detailed understanding of the nature of habitat boundaries and of the factors currently contributing to their maintenance. Several mechanisms were proposed for coexistence regulation in this setting. As a generalised framework, it was suggested that floristic patterns in these mosaics can be most easily accounted for by invoking the related ideas of non-overlapping niche-space and habitat heterogeneity. This is because the results showed that shrub-grass alterations in this setting relate foremost to local- and regional-scale edaphic gradients. Other factors were also discussed in terms of their potential role for within- and between-habitat coexistence. These were: spatially and temporally variable disturbance, competitive exclusion, facilitation, and dispersal constraints. It was suggested however, that these processes might operate only on a spatially restricted scale in these mosaics. Overall, the study highlighted the need for experimentation to facilitate distinction between cause and correlation.

Before this is attempted though, it is first necessary to establish whether or not these processes are likely to influence patterning in mosaics across the range of central Australian landscape settings.

The widespread occurrence of mulga-spinifex mosaics throughout central Australian dunefields provides a good opportunity to take further account of their boundary properties and of the processes regulating mosaic coexistence. Earlier, Buckley (1979) provided a detailed account of edaphic and vegetation co-variation in central desert dunefields. His work demonstrated that variability in clay content influences dunefield plant distribution primarily through its control of water availability and soil profile penetrability. Accordingly, this author concluded that fire is of secondary importance in dunefield vegetation structuring. Importantly however, Buckley's study did not focus on mulga-spinifex boundaries *per se*, concentrating more on gradients from dune crests to sandy-clay spinifex swales. Later work by Allan & Southgate (2002) instead served to emphasise the role of fire for mulga boundary positioning in the frequently-fired sand country of the Tanami desert. It is apparent, therefore, that the lack of clarity regarding the formation and maintenance of mosaic boundaries is not particular to the mountain range setting.

This chapter examines the universality of the themes so far identified for mosaic regulation through an investigation of mulga-spinifex boundaries in central Australian dunefields. The main objective of this study is to build on the earlier research outlined above, and thereby extend knowledge of the relationship between mosaic vegetation and environmental variability. More specifically, this study seeks, through the use of numeric analysis, to further elucidate patterns of floristic variation in mulga-spinifex mosaics on central Australian dunefields, and to directly relate detected patterns to environmental conditions.

The questions addressed are:

1. What broad- and fine-scale floristic patterns characterise mulga-spinifex mosaics on central Australian dunefields?
2. What is the nature of habitat boundaries? Are most species confined to one or other habitat, or does shrub-grass patterning relate more to the abundance of dominant species across boundaries?

3. What factors most closely correlate with boundary positioning in dunefield mosaics?

3.2 Methods

3.2.1 STUDY SITES

Fieldwork was conducted in a selection of central Australian dunefield habitats, throughout 1999-2001. Sampling was spread across four sites: 1) Owen Springs property; 2) Orange Creek property, 3) Uluru-Kata Tjuta National Park; and 4) Yulara lease (Fig. 3.1). Known edaphic variation across mulga-spinifex habitat boundaries at Sites 3 & 4 relates to differences in soil texture and topographic position (Buckley 1979; Griffin 1984b). Here, two spinifex species – *Triodia basedowii* and *Triodia pungens* – each form mono-specific, spatially disjunct stands that directly abut mulga habitat at the dune-swale interface. The remaining sites are characterised by *Triodia basedowii* dunes and sandy rises and mulga swales.

3.2.2 SAMPLING DESIGN

Two attributes were used to stratify sampling:

- 1) vegetation structure (spinifex hummock grassland/mulga shrubland) and
- 2) time-since-fire (immature/mature with fully-formed canopy of structural dominant).

This stratification scheme, represented diagrammatically in Fig. 3.2, allowed for the allocation of survey samples to four mutually exclusive combinations of each habitat attribute. The survey aimed to achieve equal sampling for each of the four stratification classes. However, the intensity of within-class sampling was limited by sample availability. Table 3.1 lists the number of samples included for each class, and indicates *a priori* sample groupings. Sample placement was determined according to structural variation patterning visible on 1:50,000 aerial photographs.

3.2.3 DATA COLLECTION

As in the previously described study (Chapter 2) survey work took the form of quadrat-based sampling, involving full floristic documentation. Frequency was measured in accordance with the nested quadrat technique of Outhred (1984), the design of which was described in the previous chapter. Various environmental and disturbance attributes were recorded for each quadrat.

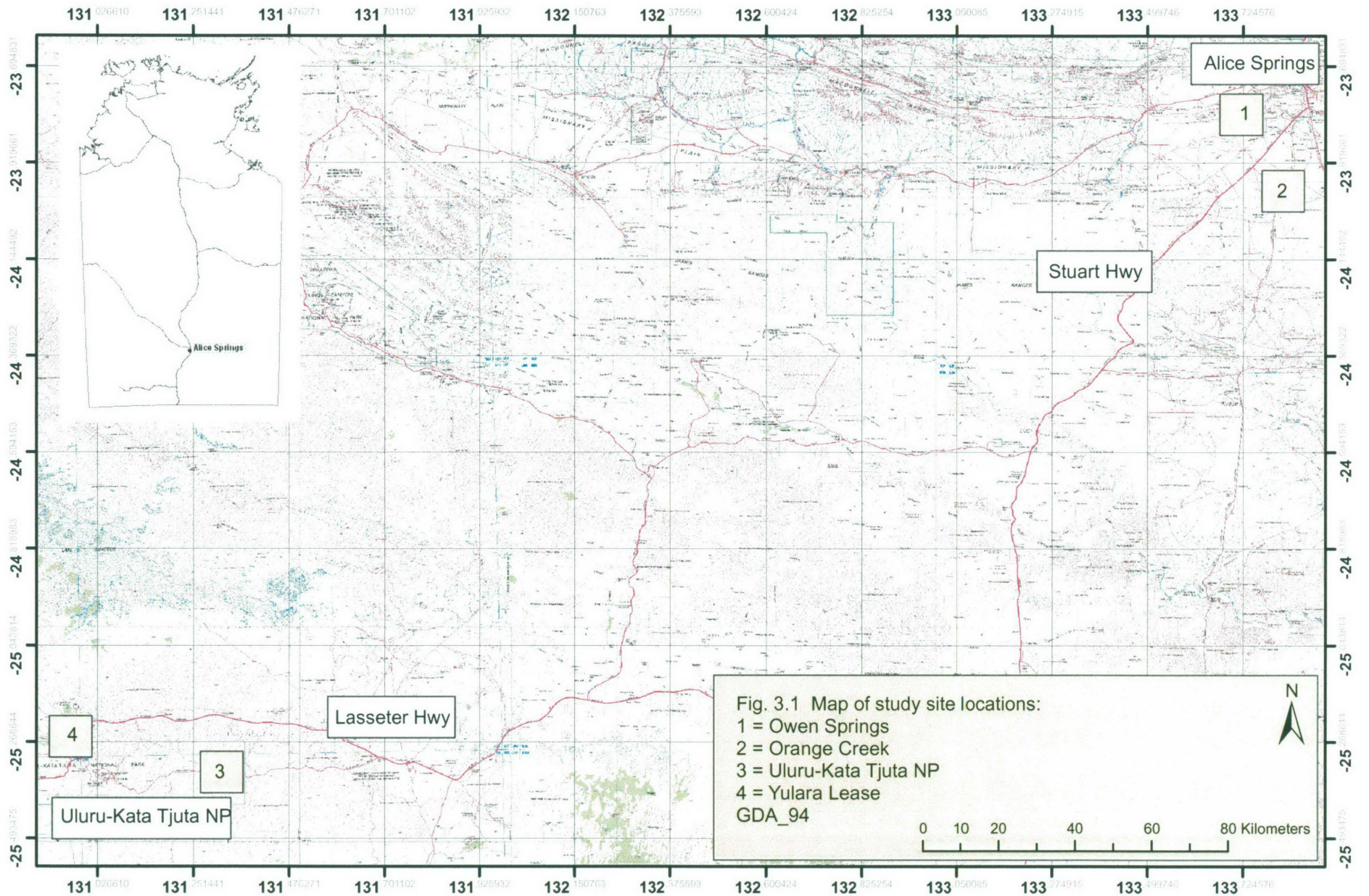


Fig. 3.1 Map of study site locations:
 1 = Owen Springs
 2 = Orange Creek
 3 = Uluru-Kata Tjuta NP
 4 = Yulara Lease
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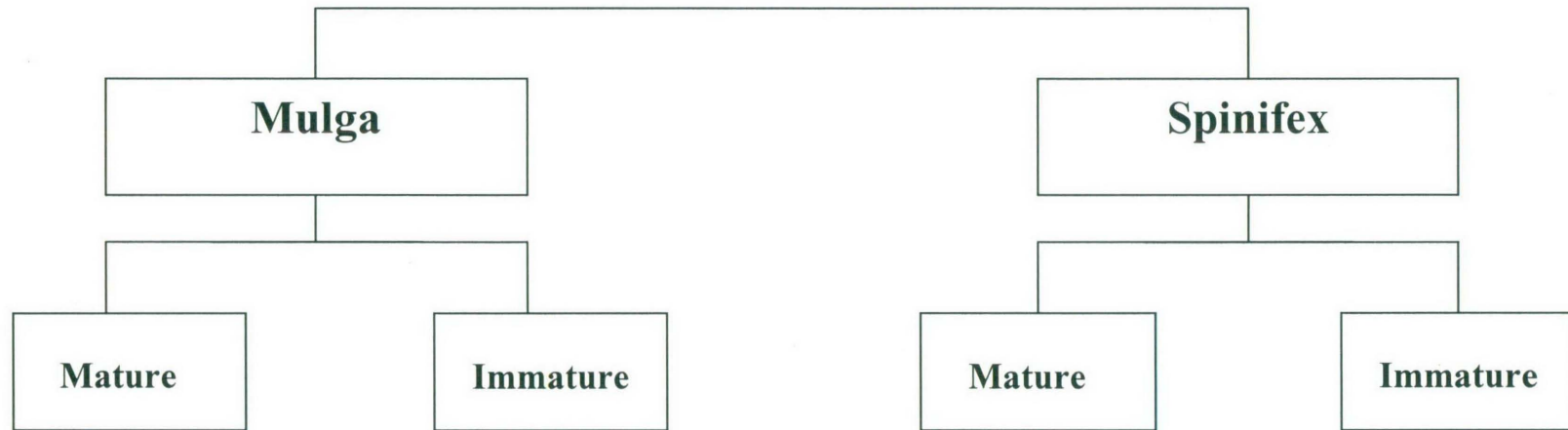


Fig. 3.2 Pictorial representation of survey design with sampling stratified over two variables: vegetation structural formation; and time-since-fire.

Table 3.1 Allocation of 28 samples of mulga-spinifex mosaics on central Australian dunefields to stratification categories: vegetation structure; and fire age. Symbols * = Study area 1 (Owen Springs), † = Study area 2 (Orange Creek), ~ = Study area 3 (Uluru-Kata Tjuta National Park); # = Study area 4 (Yulara Lease).

Stratification class I (Structural formation)	Stratification class II (Fire age of structural dominant)	No. samples	Site Nos.
Mulga shrubland	Mature	9	1*, 2*, 3*, 7 [†] , 8 [†] , 9 [†] , 15 [~] , 16 [~] , 17 [~]
	Immature	4	10 [†] , 11 [†] , 18 [~] , 19 [~]
Spinifex grassland	Mature	12	4*, 5*, 6*, 12 [†] , 13 [†] , 14 [†] , 20 [~] , 21 [~] , 22 [~] , 26 [#] , 27 [#] , 28 [#]
	Immature	3	23 [#] , 24 [#] , 25 [#] .

Soil characteristics were assessed by assaying one representative sample (at depths of 0-10 cm and ~50 cm) for pH and texture as *per* the methodology outlined in Chapter 2. Slope was recorded in the field with the use of a clinometer, and aspect with a compass. The process of data verification, outlined in the previous chapter, was again followed here.

3.2.4 DATA ANALYSES

Data matrices

Sample x attribute matrices were constructed for floristic, environmental and 'supplementary' data. The environmental matrix included a range of permanent and transient habitat attributes. Soil texture was scored according to increasing clay content with scores ranging from one through to six: 1 = 5-10%; 2 = 10-15%; 3 = 10-20%; 4 = 15-20%; 5 = 20-30%; and 6 = 30-35%. Aspect was transformed as $\cos(45 - \text{aspect value in degrees})$ in accordance with the recommendations of Ohmann and Spies (1998). The non-continuous attributes: fire recency, swale topographic position and land system were coded as categorical ('dummy') variables. For the supplementary matrix, species were assigned to one of 12 growth-form classes:

- | | |
|--|---------------------------------------|
| 1) Short-lived (<3 years) forb; | 7) Perennial hummock grass; |
| 2) Perennial forb; | 8) Short-lived (<3 years) half-shrub; |
| 3) Climber; | 9) Perennial half-shrub; |
| 4) Fern; | 10) Perennial shrub; |
| 5) Short-lived (<3 years) tussock grass; | 11) Mallee shrub; |
| 6) Perennial tussock grass; | 12) Perennial tree. |

Woody species were further categorised as: 1) obligate seeders, 2) facultative resprouters, and 3) resprouters, using the criteria and methodology outlined in Chapter 2.

Floristic composition patterns and environmental co-variance

Species composition patterns were examined with the ordination and clustering techniques outlined in the previous chapter, and again, (CCA) was employed as a method of inferring relationship between floristic patterns and environmental parameters.

3.3 Results

3.3.1 FLORISTIC PATTERNS

Compositional patterns

Classification (see Fig. 3.3) and ordination (see Figs 3.4 & 3.5) depicted the existence of three major dunefield mosaic assemblages which may be characterised as: Group A, non-spinifex mulga shrubland; Group B, mixed mulga-*Triodia basedowii* habitat (comprised of subgroups 2, 3, 4 & 5), and Group C, mixed mulga-*Triodia pungens* habitat (comprised of subgroups 6 & 7). Diagnostic species for each group and its respective subgroups are presented in Table 3.2. and detailed within- and between-group descriptions are presented in Appendix 3.1. An account of the major findings is presented in the following paragraphs.

The range of boundary types detected in this study mirrors that of the previous account of mountain range mosaics and includes: 1) minimal floristic overlap between mulga and spinifex habitats; 2) relatively high floristic commonality between mulga and spinifex habitats; and 3) minimal floristic overlap between two different spinifex habitats. Two of the broad-scale clusters (A & B), defined by the PATN analysis, form an immediate boundary. This equates to the Type I boundary described above. In this particular case, both habitats have equally high numbers of unique species and of species with far greater abundance in one or other habitat.

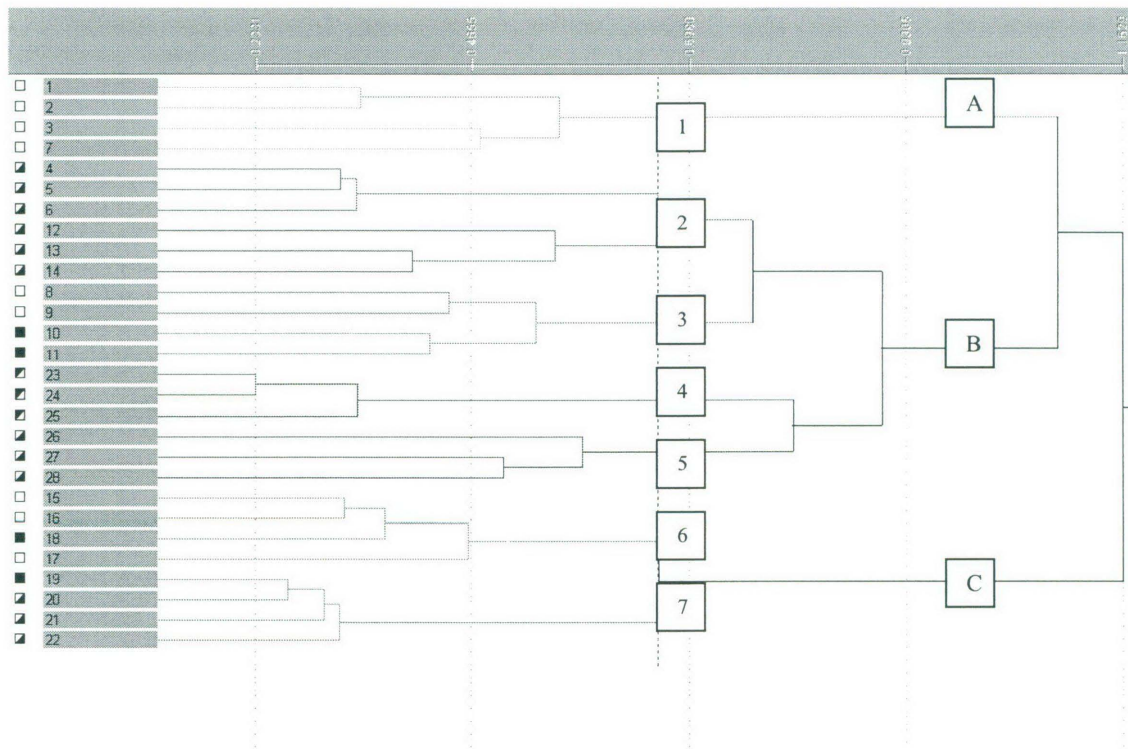


Fig. 3.3 Dendrogram showing classification of 28 samples based on floristic composition of mulga-spinifex mosaics on central Australian dunefields, cut at the seven-group level. Three major groupings are evident: Group A, *Acacia aneura* shrubland; Group B, *Acacia aneura* shrubland/ *Triodia basedowii* hummock grassland (with subgroups 2, 3, 4 & 5), and Group C, *Acacia aneura* shrubland/ *Triodia pungens* hummock grassland. Symbols show membership of the four *a priori* classes used to stratify sampling: □ = group 1, mulga-mature; ■ = group 2, mulga-immature; ▒ = group 3, spinifex-mature; ◻ = group 4, spinifex-immature.

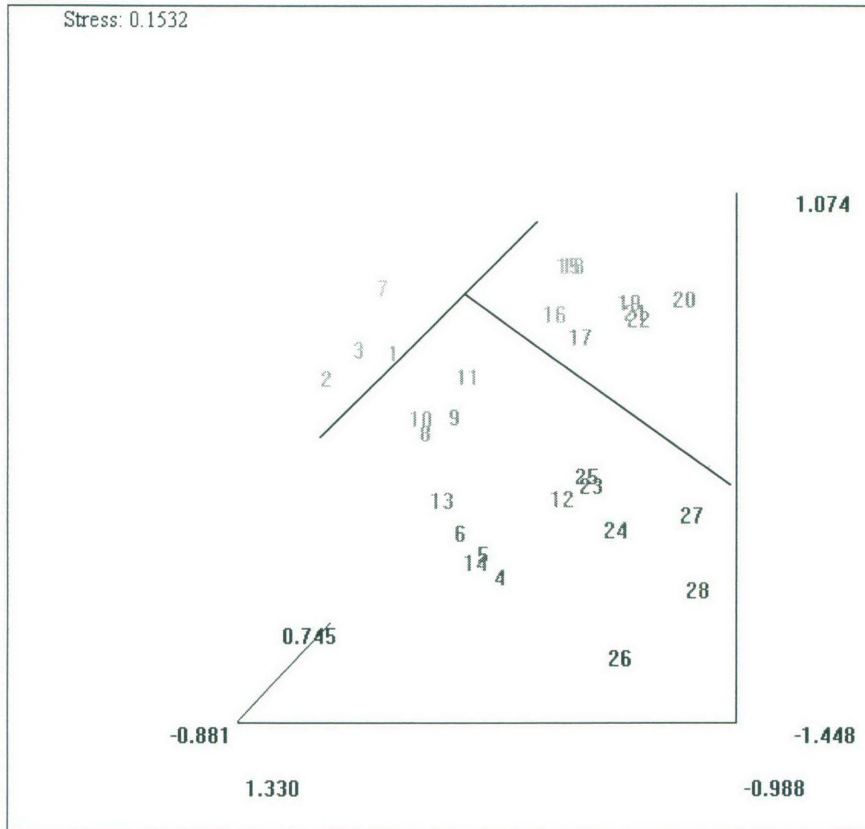


Fig. 3.4 Ordination diagram showing positioning of 28 samples based on floristic composition in mulga-spinifex mosaics on central Australian dunefields. Lines reflect major UPGMA divisions.

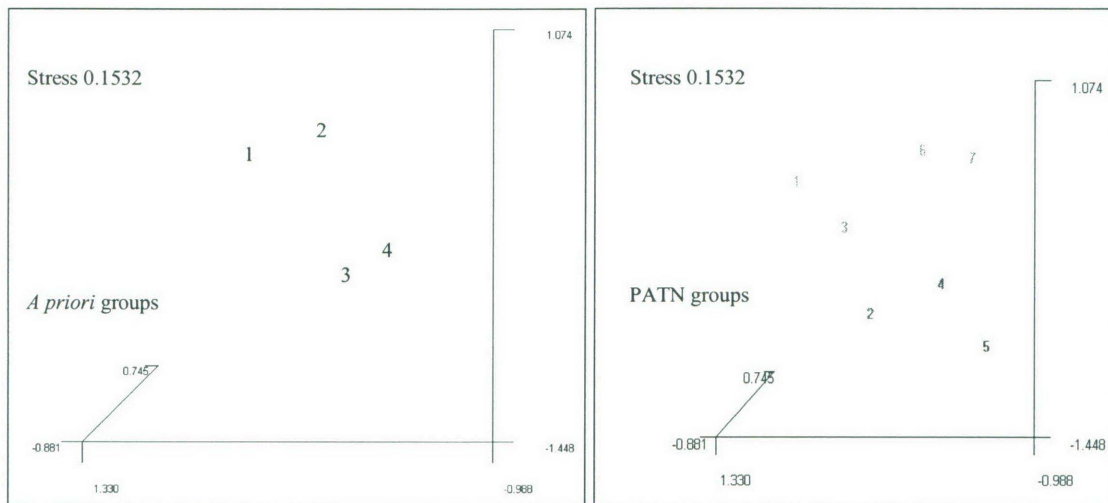


Fig. 3.5a and b. Ordination diagrams showing positioning of (a) the four *a priori* group centroids (1 = mulga mature; 2 = mulga immature; 3 = spinifex mature; & 4 = spinifex immature) and (b) the seven UPGMA cluster-centroids, based on floristic composition in mulga-spinifex mosaics on central Australian dunefields.

Table 3.2 Diagnostic species as identified by the SIMPER analysis of the broad- and fine-scale PATN floristic clusters.

PATN broad-groups	Diagnostic species	PATN fine-groups	Diagnostic species
A	<i>Aristida contorta</i> ; <i>Acacia aneura</i> ; <i>Enneapogon avenaceus</i> ; <i>Sclerolaena convexula</i> ; <i>Enneapogon polyphyllus</i> ; <i>Rutidosis helichrysoides</i> <i>Digitaria coenicola</i> ; <i>Abutilon otocarpum</i> ; <i>Rhodanthe charsleyae</i> ; <i>Triraphis mollis</i> ; <i>Sclerolaena costata</i> ; <i>Digitaria brownii</i> ; <i>Euphorbia drummondii s. lat.</i> ; <i>Boerhavia repleta</i> ; <i>Solanum quadriloculatum</i> ; <i>Aristida holathera var. holathera</i> ; <i>Minuria leptophylla</i> ; <i>Evolvulus alsinoides var. villosicalyx</i> ; <i>Cenchrus ciliaris</i> ; <i>Sida fibulifera</i> ; <i>Eragrostis laniflora</i> ; <i>Eragrostis barrelieri</i> .	1 = A	
B	<i>Triodia basedowii</i> ; <i>Aristida holathera var. holathera</i> ; <i>Eragrostis laniflora</i> ; <i>Solanum centrale</i> ; <i>Sida platycalyx</i> ; <i>Leucochrysum stipitatum</i> ; <i>Sclerolaena johnsonii</i> ; <i>Senna pleurocarpa</i> ; <i>Eriachne aristidea</i> ; <i>Calandrinia reticulata</i> ; <i>Enneapogon polyphyllus</i> ; <i>Acacia melleodora</i> ; <i>Ptilotus polystachyus</i> ; <i>Lechenaultia divaricata</i> ; <i>Calandrinia balonensis</i> ; <i>Euphorbia drummondii s. lat.</i> ; <i>Acacia aneura</i> ; <i>Aristida contorta</i> ; <i>Acacia murrayana</i> ; <i>Rulingia loxophylla</i> .	2	<i>Triodia basedowii</i> ; <i>Aristida holathera var. holathera</i> ; <i>Eragrostis laniflora</i> ; <i>Sida platycalyx</i> ; <i>Lechenaultia divaricata</i> ; <i>Eriachne aristidea</i> ; <i>Solanum centrale</i> ; <i>Ptilotus polystachyus</i> ; <i>Acacia murrayana</i> ; <i>Sclerolaena johnsonii</i> ; <i>Enneapogon polyphyllus</i> ; <i>Euphorbia drummondii s. lat.</i> ; <i>Acacia melleodora</i> .
		3	<i>Acacia aneura</i> ; <i>Triodia basedowii</i> ; <i>Aristida holathera var. holathera</i> ; <i>Leucochrysum stipitatum</i> ; <i>Lepidium phlebopetalum</i> ; <i>Sclerolaena johnsonii</i> ; <i>Sida platycalyx</i> ; <i>Enneapogon polyphyllus</i> ; <i>Rhagodia eremaea</i> ; <i>Euphorbia tannensis</i> subsp. <i>eremophila</i> ; <i>Eragrostis laniflora</i> ; <i>Muelleranthus stipularis</i> ; <i>Eriachne aristidea</i> ; <i>Monachather paradoxus</i> ; <i>Solanum quadriloculatum</i> ; <i>Euphorbia drummondii s. lat.</i> ; <i>Calandrinia balonensis</i> ; <i>Sclerolaena convexula</i> ; <i>Calandrinia reticulata</i> ; <i>Abutilon otocarpum</i> ; <i>Paspalidium reflexum</i> ; <i>Enchylaena tomentosa</i> ; <i>Tripogon loliiformis</i> .
		4	<i>Triodia basedowii</i> .
		5	<i>Triodia basedowii</i> ; <i>Senna pleurocarpa</i> ; <i>Aristida holathera var. holathera</i> ; <i>Rulingia loxophylla</i> ; <i>Eragrostis laniflora</i> ; <i>Aristida contorta</i> ; <i>Paraneurachne muelleri</i> ; <i>Dicrasyllis gilesii</i> .
C	<i>Monachather paradoxus</i> ; <i>Calandrinia reticulata</i> ; <i>Leucochrysum stipitatum</i> ; <i>Goodenia occidentalis</i> ; <i>Triodia pungens</i> ; <i>Eragrostis laniflora</i> ; <i>Aristida holathera var. holathera</i> ; <i>Waitzia acuminata</i> ; <i>Acacia aneura</i> ; <i>Amphipogon caricinus</i> ; <i>Velleia glabrata</i> ; <i>Stenopetalum anfractum</i> ; <i>Thyridolepis multiculmis</i> .	6	<i>Calandrinia reticulata</i> ; <i>Monachather paradoxus</i> ; <i>Acacia aneura</i> ; <i>Stenopetalum anfractum</i> ; <i>Leucochrysum stipitatum</i> ; <i>Thyridolepis multiculmis</i> ; <i>Goodenia occidentalis</i> ; <i>Waitzia acuminata</i> ; <i>Eragrostis laniflora</i> ; <i>Triodia pungens</i> ; <i>Maireana villosa</i> ; <i>Aristida holathera var. holathera</i> ; <i>Digitaria brownii</i> .
		7	<i>Leucochrysum stipitatum</i> ; <i>Triodia pungens</i> ; <i>Eragrostis laniflora</i> ; <i>Goodenia occidentalis</i> ; <i>Aristida holathera var. holathera</i> ; <i>Amphipogon caricinus</i> ; <i>Monachather paradoxus</i> ; <i>Velleia glabrata</i> ; <i>Calandrinia reticulata</i> ; <i>Acacia ammobia</i> ; <i>Brunonia australis</i> .

Seven groups were distinguished at the finer-scale of division:

i. Group A, = subgroup 1 (Fig. 3.6) ‘non-spinifex’ mulga shrubland: This cluster comprised four samples distributed across two sites (Owen Springs and Orange Ck). Neither of the *Triodia* species recorded in this study contributed to within-group similarity.

ii. Group B, Subgroup 2 (Fig. 3.7) comprised six samples from Sites 1 (Owen Springs) & 2 (Orange Creek), all of which were dominated by mature stands of *Triodia basedowii*. The fire tolerant shrubs *Acacia murrayana* and *Acacia melleodora* characterised the shrub layer.

iii. Group B, Subgroup 3 (Fig. 3.8) comprised four samples from Site 2 (Orange Creek), all of which were characterised by mixed stands of *T. basedowii* and *Acacia aneura*. Two of the samples supported regenerating mulga, and two supported mature mulga. Many of the remaining highly diagnostic species were sandy soil specialists: *Aristida holathera* var. *holathera*, *Leucochrysum stipitatum*, *Sclerolaena johnsonii*, *Eriachne aristidea*, *Calandrinia reticulata* and *Calandrinia balonensis*. Also included were the chenopod shrubs *Rhagodia eremaea* and *Enchylaena tomentosa*.

iv. Group B, Subgroup 4 (Fig. 3.9) comprised three samples from Site 4 (Yulara lease), all of which were characterised by immature stands of *T. basedowii*. The group was characterised by various fire encouraged species: *T. basedowii*, *Senna pleurocarpa*, *Aristida holathera* var. *holathera*, *Paraneurachne muelleri*, *Rulingia loxophylla* and *Dicrastyliis gilesii*.

v. Group B, Subgroup 5 (Fig. 3.10) comprised three samples from Site 4 (Yulara lease), all of which were characterised by mature stands of *T. basedowii*. One species, *T. basedowii*, contributed most of the within-group similarity. This indicated that species richness was very low, and that most of the constituent species did not occur in more than one sample.

vi. Group C, Subgroup 6 (Fig. 3.11) comprised four samples from Site 3 (Uluru National Park). The majority of these were characterised by mature stands of mulga with a low abundance of *Triodia pungens* in the understorey. The remaining sample was dominated by regenerating mulga, with a slightly higher abundance of *T. pungens* compared with the mature mulga samples.

vii. Group C, Subgroup 7 comprised four samples from Site 3 (Uluru National Park). The majority of samples were characterised by mature stands of *T. pungens*, though one also had regenerating mulga with a *T. pungens* understorey. Included in the group of diagnostic species was the dune specialist *Acacia ammobia*.

Two variations of Type I boundaries were recorded for the fine-scale clusters. The first involved subgroups 1 (non-spinifex mulga) and 2 (*T. basedowii* hummock grassland), both of which occurred in the northern-most study sites (Sites 1 & 2). In this instance, boundaries were marked by structural variation, as illustrated by the highly variable abundance of the two dominants (*A. aneura* and *T. basedowii*), as well as by compositional discontinuity, given the high numbers of species that were unique to one or other habitat (see Appendix 3.1). The second Type I variant involved subgroups 1 (non-spinifex mulga) and 3 (mixed mulga-*T. basedowii*). In this case, boundaries did not represent a structural shift given that the between-habitat abundance of the shrubland dominant *A. aneura* did not vary. Instead, the two habitat types were distinguished foremost by the greater abundance of *T. basedowii* in group 3, and by the high number species that were unique to either habitat.

Two variants of Type II boundaries were likewise apparent. The first occurred between Uluru mulga and spinifex habitats. In this case, very few species were unique to, or had twice their abundance in, either of the two habitat types. Instead, the boundaries mainly represented structural shifts, given that both of the dominants had comparatively low abundances in neighbouring habitat. The second Type II boundary involved subgroups 3 (mixed mulga-*T. basedowii*) and 2 (*T. basedowii*). In this case, the abundance of spinifex did not vary considerably across habitat boundaries and few species were unique to spinifex habitat. By contrast, the between-habitat abundance of *A. aneura* varied by a factor of two, and many mulga species were entirely absent from spinifex habitat. One Type III boundary was sampled (subgroups 4 & 5), with differences apparently relating foremost to fire effects.

3.3.2 FLORISTIC PATTERNS IN RELATION TO ENVIRONMENTAL VARIABLES

Constrained ordination

The preliminary analysis of all samples using DCA indicated that the first axis gradient length of the species data was long (>3 SD), thereby justifying the use of the

Fig. 3.6 PATN Group A, Subgroup 1: non-spinifex mulga shrubland. This cluster comprised four samples distributed across two sites (Owen Springs and Orange Ck). Neither of the *Triodia* species recorded in this study contributed to within-group similarity.

Fig. 3.7 PATN Group B, Subgroup 2: mature *Triodia basedowii*. This cluster comprised six samples from Sites 1 (Owen Springs) & 2 (Orange Creek). The fire tolerant shrubs *Acacia murrayana* and *Acacia melleodora* characterised the shrub layer.

Fig. 3.8 Group B, Subgroup 3: mixed stands of *T. basedowii* and *Acacia aneura*. This cluster comprised four samples from Site 2 (Orange Creek).

Fig. 3.9 Group B, Subgroup 4: immature stands of *T. basedowii*. This cluster comprised three samples from Site 4 (Yulara lease).

Fig. 3.10 Group B, Subgroup 5: mature stands of *T. basedowii*. This cluster comprised three samples from Site 4 (Yulara lease).

Fig. 3.11 Group C, Subgroup 6: mature stands of mulga with very low *Triodia pungens* abundance. This cluster comprised four samples from Site 3 (Uluru National Park).



Fig. 3.6

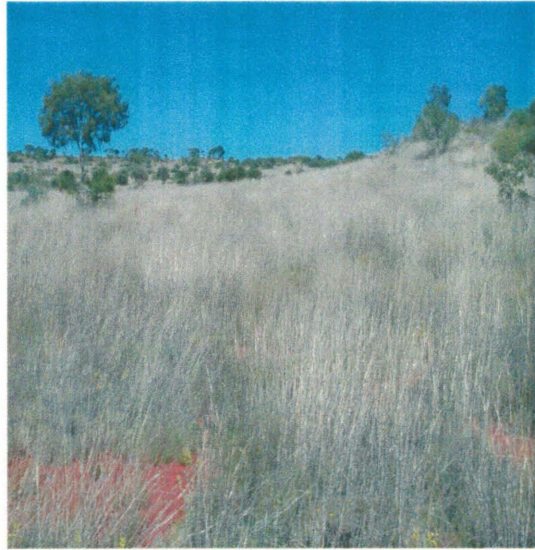


Fig. 3.7



Fig. 3.8



Fig. 3.9



Fig. 3.10



Fig. 3.11

unimodal model CCA for analysis (ter Braak & Smilauer 1998). The resultant model explained 72.6 % of the variation in the floristic data, with the first two axes accounting for 48.3 %. Monte Carlo tests indicated that the first, and all canonical axes of the CCA were highly significant ($P = 0.002$) with 499 permutations under a reduced model). Forward selection revealed that four variables were significant (Table 3.3).

The first axis of the site x environmental variables biplot (Fig. 3.12) was principally characterised by topographic position and soil texture. This axis illustrated a gradient from high *A. aneura* abundance (subgroups 1, 3 & 6) in swales and on fine-textured soils to high spinifex abundance on coarse-textured soils on dune slopes. The inter-set correlations of environmental variables (CoE) (Table 3.4) indicated that swale position was the strongest gradient on the first axis (CoE 0.7444), followed by soil texture at depth (CoE 0.6193), and at surface (CoE 0.5469). The first axis also correlated with aspect (CoE -0.5144) and slope (CoE -0.5616), with spinifex sites having higher values of each measure. Fire recency (CoE -0.2747) had only moderate bearing, relating principally to floristic variability among burnt and unburnt *Triodia basedowii* samples (Subgroups 4 & 5). Inter-set correlations indicated that Landsystem (CoE 0.3669) was one of the strongest gradients along the second axis. This axis also clearly depicted correlation between samples of Site 1 (Owen Springs) and increased soil pH (surface CoE 0.5554, depth CoE 0.489).

The first axis showed strong patterning of species' attributes in relation to habitat gradients (Fig. 3.13). Particularly noteworthy, was the correlation of resprouter richness with spinifex samples (Subgroups 2, 4 & 5). The same pattern was depicted for hummock grasses and perennial forbs. By contrast, obligate seeders and short-lived half-shrubs were negatively correlated with spinifex, being most closely associated with non-spinifex mulga. For most other groups – facultative resprouters, climbers, perennial half-shrubs, short-lived and perennial tussock grasses, short-lived forbs, trees and mallee shrubs – higher richness correlated with the position of the mixed mulga-spinifex cluster (Subgroup 3). Patterning in perennial shrubs did not appear to be habitat related.

Table 3.3 Significance of environmental variables as determined by the Monte Carlo Test (199 permutations) in the CCA analyses. Significance $P < 0.05$ (in bold font).

Variable	F	P
Aspect (degrees)	0.86	0.636
Fire recency	1.51	0.086
% Litter cover	1.39	0.108
pH Depth	0.94	0.532
pH Surface	1.13	0.29
Slope value	1.7	0.002
Soil texture Depth	2.19	0.002
Soil texture Surface	1.23	0.242
Topographic position: Swale	3.01	0.002
Landsystem: Ewaninga	3.15	0.002

Table 3.4 Inter-set correlations from the CCA analyses.

Variable	AX1	AX2
Aspect (degrees)	-0.5144	0.0348
Fire recency	-0.2747	-0.2066
% Litter cover	0.1819	0.3024
pH Depth	0.0392	0.489
pH Surface	0.1282	0.5554
Slope value	-0.5616	0.2261
Soil texture Depth	0.6193	-0.4065
Soil texture Surface	0.5469	-0.0864
Topographic position: Swale	0.74444	-0.1894
Landsystem: Ewaninga	0.3669	0.6687

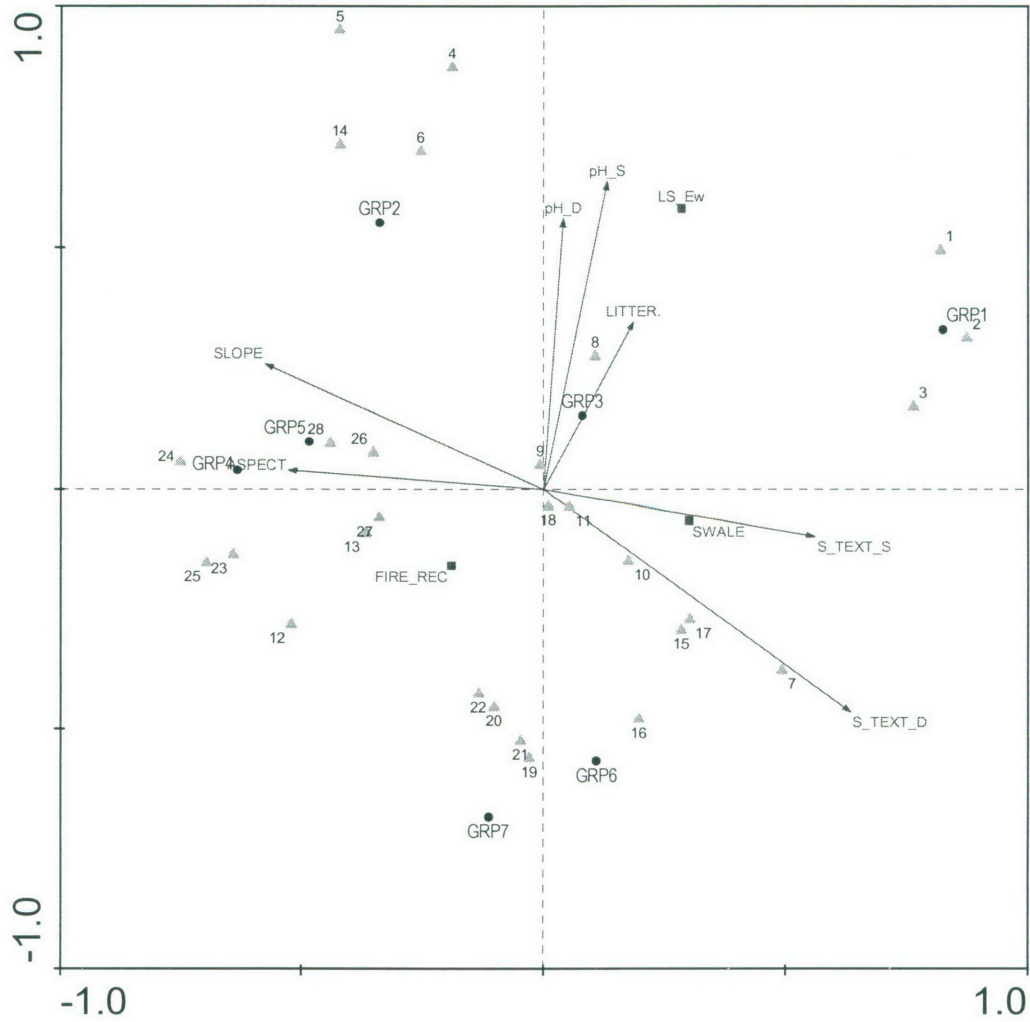


Fig. 3.12 Site x environmental variables biplot using data from 28 samples of mulga and spinifex habitat on central Australian dunefields. Arrows represent continuous environmental variables. Increasing arrow length denotes a stronger correlation with environmental gradients. Categorical variables are indicated by a square symbol with more important variables being further from the origin. Numbers and triangle symbol indicate site position in ordination space. PATN fine-scale clusters (GRP1-7) are plotted as passive variables. Aspect = aspect (degrees); Fire_res = fire recency; Litter = % litter cover; pH_L = pH at depth; pH_S = pH at surface; Slope = slope value; Text_D = soil texture at depth; Text_S = soil texture at surface; SWALE = swale topographic position; LS_Ew = Ewaninga Landsystem of Perry *et al.* (1962).

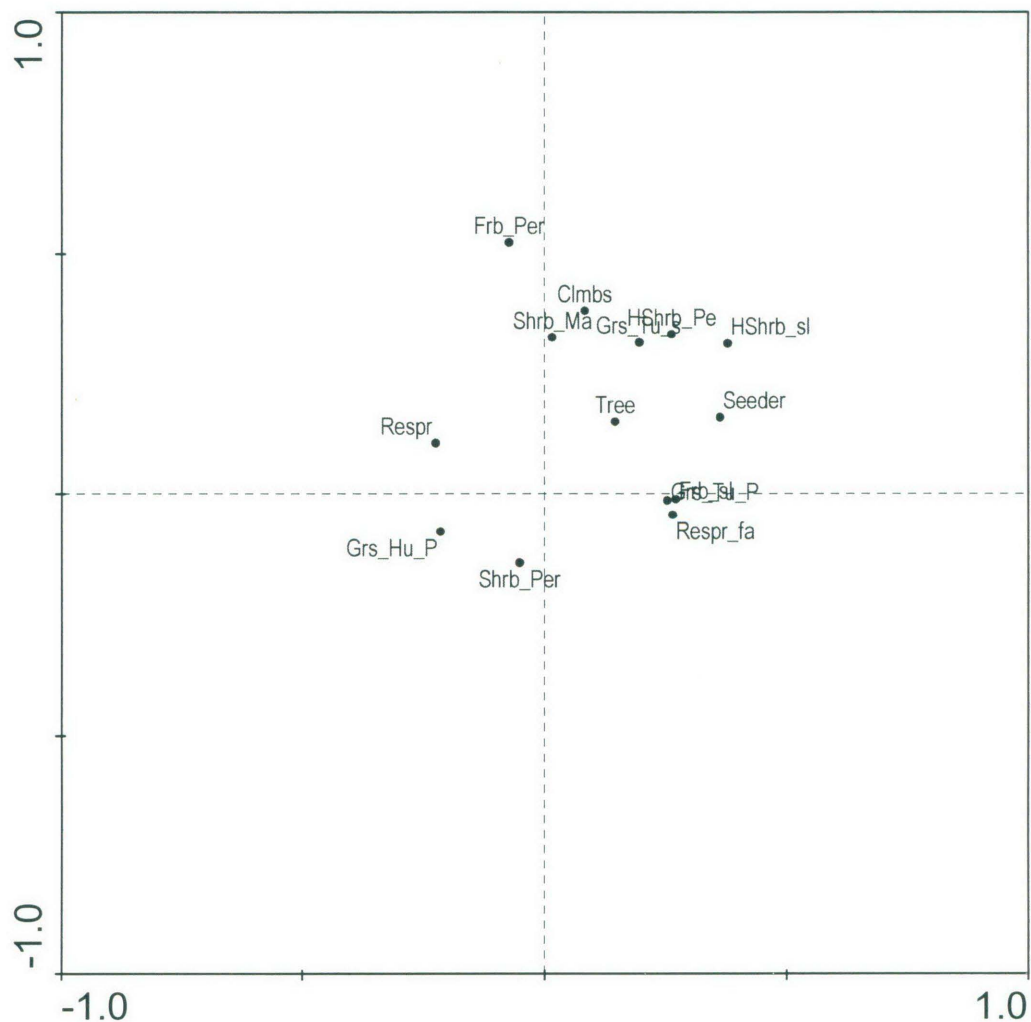


Fig. 3.13 Scatterplot of species' attributes plotted as supplementary data in relation to environmental variables in the analysis of 28 samples of mulga and spinifex habitat on central Australian dunefields. Climbs = climbers; Grs_Tu_P = perennial tussock grasses; Grs_Tu_s = short-lived tussock grasses; Frb_Per = perennial forbs; Frb_sl = short-lived forbs; Tree = trees; Shrb_Ma = mallee shrubs; Shrb_Per = perennial shrubs; HShrb_sl = short-lived half shrubs; Grs_Hu_P = perennial hummock grasses; Seeder = obligate seeders; Respr_fa = facultative resprouters; Respr = resprouters.

3.4 Discussion

3.4.1 FLORISTIC PATTERNS WITHIN- AND BETWEEN-HABITAT BOUNDARIES

Distribution and abundance of species

The results of this study support those of the previous examination of mountain range mosaics, in that they emphasise the highly variable nature of mulga-spinifex boundaries. In this study, two of the broad-scale clusters (A & B) defined by the PATN analysis formed an immediate boundary that equates to the Type I category, involving little floristic overlap between mulga and spinifex habitats. At this broad scale, therefore, dunefield boundaries closely resemble Bowman *et al.*'s (1994) account of between-habitat relations for mountain range mosaics. Fine-scale dunefield boundaries do, however, vary from mountain range boundaries in their detail. Two variations of Type I boundaries were recorded in this instance: one involving subgroups 1 (non-spinifex mulga) and 2 (*Triodia basedowii* hummock grassland), marked by structural variation as well as by compositional discontinuity; and the second involving subgroups 1 and 3 (mixed mulga-*T. basedowii*), that were distinguished foremost by the greater abundance of *T. basedowii* in group 3, and by the high number of species that were unique to either habitat. Two variants of Type II boundaries were likewise apparent: the first involving Uluru mulga and spinifex habitats, where very few species were unique to, or had twice their abundance in, either of the two habitat types; and the second involving subgroups 3 (mixed mulga-*Triodia basedowii*) and 2 (*Triodia basedowii*), marked primarily by the variable abundance of *A. aneura* and the high number of unique mulga species. One example of Type III boundaries was obtained, with differences apparently relating foremost to fire effects. This is discussed in greater detail below.

Recognition of this high level of variability in the character of mosaic boundaries provides some means of gauging the likelihood of fire-induced landscape-wide dunefield mosaic coexistence breakdown. According to these floristic results, the uniform contraction of mulga and concomitant expansion of spinifex seems unlikely. The greatest risk of coexistence breakdown occurs in relation to subgroups 3 & 2. Here, mulga contraction could quite easily occur in the context of high fire frequency, given that *A. aneura* is intolerant of repeated firing, and that there exist no physiological barriers to spinifex occupancy of subgroup 3 habitat. In this situation,

the fire-induced loss of *Acacia aneura* and associated unique fire-sensitive mulga species represents the essential step in the conversion of shrubland to hummock grassland. In the case of other dunefield boundaries, however, it is apparent that certain physiological barriers would first need to be overcome if spinifex was to increase its abundance in neighbouring mulga habitat. This applies particularly to subgroups 1 & 3 given that *Acacia aneura* and *Triodia basedowii* co-occur in equally high abundance in Subgroup 3, yet the latter contributes very little to Subgroup 1 compositional similarity, and is in fact absent from many subgroup 1 samples. The likelihood of spinifex encroachment from subgroup 3 into subgroup 1 habitat is therefore probably low.

For the remaining boundaries, between-habitat sorting might also relate to the influence of biotic factors. As explained in the preceding chapter (see Booth *et al.* 2003), it has been suggested that the level of habitat ‘invasibility’ reflects the extent to which native species pre-empt resource uptake and thereby prevent closely related (or otherwise, ecologically equivalent) potential invaders from gaining a foothold. This might well account for the absence (or otherwise very low abundance) of various spinifex *Acacia* species (e.g. *A. ligulata*, *A. ammobia*, *A. murrayana* and *A. melleodora*) from mulga habitat. It may also explain the segregation of other congeneric species pairs across mulga-spinifex boundaries. Prominent examples include: *Sclerolaena convexula* (mulga) and *S. johnsonii* (spinifex); *Digitaria brownii* (mulga) and *D. ammophila* (spinifex); *Aristida contorta* (mulga) and *A. holathera* var. *holathera* (spinifex); *Indigophora linnaei* (mulga) and *I. psammophila* (dune); and *Goodenia heterochila* (mulga) and *G. occidentalis* (dune). Also, in the case of these latter boundary types, facilitation by *A. aneura* may play a role in the determination of species’ distributions. Again (see previous chapter), obvious examples include the heightened abundance of species with bird-dispersal syndromes, e.g. *Rhagodia eremaea*, *Einadia nutans* subsp. *nutans* and *Enchylaena tomentosa* in mulga habitat.

Distribution of growth-form groups

The results of this study indicate that for the majority of growth form groups, richness increases with a rise in *A. aneura* dominance. They therefore add weight to the supposition put forward in Chapter 2 that there is a greater level of niche differentiation in mulga habitat than in spinifex habitat, and that diversity maintenance in mulga is therefore less likely to be closely dependent on the process

of fire-initiated competitive release. The greater richness of tussock grasses in mulga habitat is also a common theme of the two studies. It seems highly likely therefore, that niche segregation along habitat gradients is an important component of mosaic coexistence maintenance in both mountain range and dunefield settings.

3.4.2 FLORISTIC PATTERNS IN RELATION TO ENVIRONMENTAL GRADIENTS

Edaphic gradients

The results presented here indicate that mulga-spinifex alterations in central Australian dunefield mosaics coincide foremost with topographically correlated gradients in soil texture. Aligning directly with existing accounts of dune-swale gradients (e.g. see Perry & Lazarrides 1962; Griffen 1984b), this study reports a generalised shift from non-spinifex mulga shrublands on the finest-textured swale soils characteristic of the Ewaninga Landsystem, through to spinifex dominated grasslands on sandier dune slopes. Examples of mixed mulga-spinifex habitat occur on swale soils of intermediate clay content. According to Buckley (1979), variability in clay content influences dunefield plant distribution primarily through its control of water availability and soil profile penetrability. This means that plants occupying the fine-textured swales do so principally by virtue of their greater ability to tolerate water-limiting and hard setting soils. As a consequence, the between-habitat separation of dunefield mosaic species reported here is most easily explained by invoking the notion of independent niche distributions along the soil texture gradient. Importantly, though, this model does not account for the exclusion of species from areas upslope of their normal distribution or from sandier areas more generally. For this, other governing factors must be considered.

Fire effects

The results presented in this study are consistent with the predictions of the global model for the coexistence of fire-dependent ecosystems and adjacent forests, which attributes the persistence of the former to their greater flammability and hence, their shorter fire-return intervals (Bond *et al.* 2005). As already outlined, this model holds that fire-sensitive habitats are distinguished from neighbouring vegetation foremost by their inability to cope with recurrent fire events. At the time of survey, four samples of regenerating mulga with a spinifex understorey were achieved, yet no examples of spinifex-free immature mulga could be obtained. It is regarded here, that

this patterning is reflective of the differing degrees of flammability of the two mulga types (i.e. subgroups 1 & 3). The second criterion of the global model was also met, as demonstrated by the results showing the close affiliation of obligate seeders and facultative resprouters with mulga habitat, and the greater richness of resprouters in spinifex habitat. It is probable therefore, that dunefield mosaic patterning results from the combined influence of edaphic constraint and fire effects. Specifically, it is proposed that *Triodia* is excluded from fine-textured soils by fundamental niche constraints (see above discussion), while fire effects, possibly in combination with species' interactions, mediate the persistence of *A. aneura* on dune slopes and in sandier swales where flammable *Triodia* occurs in high abundance. In terms of the remaining constituent mulga and spinifex species, it is expected that their distribution would likewise be influenced by the combined effects of regeneration niche and disturbance niche constraints (see detailed discussion in previous chapter). Experimentation is required to test these ideas.

Fire-recency effects were again evident, primarily in terms of within-habitat spinifex richness and composition patterns. In this study, burnt and mature examples of Site 4 (Yulara) *Triodia basedowii* had very low floristic commonality, with richness in the former far outweighing that in the latter. Numerous recognised fire-encouraged species (e.g. *Aristida holathera* var. *holathera*, *Goodenia gibbosa*, *Scaevola parvifolia*, *Yakirra australiensis*, *Paraneurachne muelleri*, *Rulingia loxophylla*, *Senna pleurocarpa* and *Corchorus sidoides*) were either unique to, or were far more abundant in the burnt sites. Again, this patterning can be most easily explained by invoking the notion of disturbance-mediated competitive release for coexistence maintenance in spinifex habitat. And in this study, as in the last, it was demonstrated that regeneration in mulga does not seem to follow the same course, given that burnt and unburnt mulga from Site 2 formed one cohesive cluster and that the two burnt mulga samples from Site 3 had little floristic commonality with each other, one aligning with the remaining mature mulga samples and the other with the spinifex samples. This finding adds weight to the supposition put forward in Chapter 2 that the two habitats have widely divergent regeneration patterns.

3.4.3 CONCLUSION

The work presented in this chapter indicates that while mulga-spinifex mosaics differ in detail in the mountain range and dunefield settings, there is a high level of commonality in terms of the processes regulating boundary formation and maintenance. Specifically, it was shown here that patterning in dunefield mosaics correlates foremost with edaphic gradients, namely topographically influenced shifts in soil texture. To account for this patterning, it was suggested that plants occupying the finer-textured swales likely do so principally by virtue of their ability to tolerate water-limiting and hard-setting soils. This in turn implies that species characteristic of upslope positions or sandier swales are prevented from occupying areas outside of their current range by fundamental niche constraints. Importantly though, the edaphic model could not account for the exclusion of species from areas upslope of their normal distribution, or from sandier areas more generally. For this, fire effects were regarded as being of greatest likely importance, given that many mulga species are intolerant of the repeated firing that occurs in spinifex habitat. Fire was likewise emphasised for its role in the maintenance of within-habitat coexistence in spinifex, principally through the process of competitive release. Evidence was again provided for the additional influence of biotic factors, namely competition, facilitation, and dispersal constraints on patterning in these mosaics. Combined, the two studies provide strong indication that coexistence in mulga-spinifex mosaics is regulated by a range of factors and, possibly, by their interactive effects. They thus highlight the need for experimentation to determine the actual mechanisms involved in species sorting, and to establish when in the life cycle these mechanisms operate. The following chapters examine the influence of a range of biotic and abiotic constraints on recruitment success within- and between-habitat boundaries by way of addressing this issue.