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Patterns in the Composition and Distribution of the Vertebrate Fauna, Desert Uplands Bioregion, Queensland.

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in March 2004

for the degree of Doctor of Philosophy
in the School of Tropical Biology,
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(Alex Kutt) *(Date)*

Abstract

Approximately 20% of the Australian continent consists of tropical savanna rangelands, landscapes of dense native grass and scattered trees, dominated by cattle grazing. However a common problem in reviewing ecological patterns and processes of tropical savanna rangelands is the lack of adequate biological data for such conservation planning. James *et al.* (1995) and Fisher (2001a) recommended a framework for undertaking research in Australia’s rangelands including identifying spatial and temporal patterns of biota, quantifying the impact of pastoralism, developing concepts and tools for regional conservation planning and identifying the effects of fire. The primary objective of this study was, using the framework described above, to examine the patterns within, and environmental controls on, the vertebrate fauna assemblage in the Desert Uplands Bioregion.

The Desert Uplands Bioregion

The Desert Uplands is one of six tropical savanna bioregions that occur in Queensland. It is very poorly studied, with quite meagre information regarding its native biota. Its climate is semi-arid and the vegetation consists predominantly of *Acacia* and *Eucalypt* woodlands, ephemeral lake habitats and grasslands. Of the original 6.8 million hectares of vegetation cover in the Desert Uplands, by 1999 over 900,000 hectares, representing almost 14% of the bioregion, were cleared. National Parks and resource reserves in the Desert Uplands currently cover 182,100 hectares, or 2.6% of the bioregion. Including data from this study, 431 vertebrate species (24 amphibians, 229 birds, 61 mammals, 117 reptiles) have been recorded in the bioregion, and this total includes 59 species of conservation significance. Beef cattle grazing is the major form of primary production, with a majority of the land being leasehold (>70%).

Zoogeographic context

The broad zoogeographic context of the Desert Uplands bioregion was investigated by examining composition of the vertebrate fauna in comparison to neighbouring Queensland bioregions and those across the northern Australian tropical savannas.

Given its recognition as a discrete entity, the Desert Uplands Bioregion should support landscapes and biota that are distinct from neighbouring bioregions. The region also includes a number of recognised biogeographic barriers and the confluence of three major drainage basins. Correlation, ordination and variation in measures of Beta-diversity were used to investigate patterns in the variation in species richness, composition and environment.

This broad overview of bioregional patterns of vertebrate assemblages identified the Desert Uplands fauna as, on the one hand, being typical of semi-arid regions and, on the other hand supporting a fauna of intergradation and replacement. Both inland and coastal elements are represented. Historically, the frontier of marked climate gradients would have oscillated across the Desert Uplands, and the distribution of many vertebrate fauna examples suggests this bioregion is central to vicariant speciation. A number of species typical either of more mesic or xeric environments reaches the edge of their range within the Desert Uplands. Three endemic reptiles were recorded which suggests a degree of isolation and speciation in this landscape.

Vertebrate fauna composition patterns

A systematic quadrat-based vertebrate fauna survey of the Desert Uplands Bioregion was undertaken to investigate the patterns of distribution, composition and abundance of species, and the environmental factors that determine these. A standardised quadrat array was used as the basic sampling unit, stratified by regional ecosystems – unique combinations of land units, vegetation and soils. Generalised linear modelling was used to investigate the relationship of environmental factors to within-quadrat species richness and species abundance. Gradients in vertebrate composition were examined using multivariate classification and ordination, and correlation with environmental variables.

The Desert Uplands fauna consisted of a mix of vertebrate species some restricted to particular habitats and environmental extremes (e.g. hummock and tussock grasslands), and others, which were more catholic, forming indistinct and overlapping suites of woodland species. This latter group was characterised by a core assemblage complemented by a series of more patchily distributed species that responded in various

ways to subtle environmental shifts (e.g. in substrate type, ground and canopy cover). Models exploring variation in species richness identified a positive relationship with structural complexity of the vegetation. Overall the patterns of species composition and distribution were commensurate with those recorded in the Mitchell grass, *Acacia* and *Eucalyptus* woodlands across the northern tropical savannas.

Regional ecosystems and other surrogates of vertebrate fauna diversity

An essential component of biodiversity conservation is selecting areas where conservation management effort will be concentrated. As regional ecosystems are the primary classification used for conservation planning in the Desert Uplands, the adequacy of this land unit as a surrogates for vertebrate fauna composition and distribution, and in particular sites of high species richness or sites with a high number of species of conservation significance, was examined using correlation, analysis of variance and measures of habitat breadth. The surrogate value of other land classifications was also tested using analysis of similarity. The patterns of spatial fidelity between the richness and composition of flora and fauna assemblages recorded was investigated via linear and matrix correlation. A minimum-set algorithm was used to investigate complementarity between regional ecosystems, vertebrate fauna and plant taxa using the quadrat samples.

In general, regional ecosystems types were found to have a broad correspondence to fauna composition variation, though there was clear partitioning in species composition between the more distinctive regional ecosystem types (e.g. grasslands versus woodlands), and blurring between types that were structurally similar. The spatial fidelity between biotic assemblages at a quadrat level was also varied, but was strongest between related groups (all vertebrates and component taxa, all plants, and upper ground strata). The minimum-set algorithm indicated that selecting quadrats to reserve species-rich taxa (ground cover plants, birds) will capture a majority of other species, but does not necessarily guarantee these will fully reserve the complement of rare species. Where there was high disparity in species richness, composition and structural heterogeneity between sites, there was better complementarity. This suggests that site complementarity techniques may be inadequate as a planning tool for targeting rare, unusual, seasonal or intangible biotic assemblages.

Effects of grazing and fire on fauna and flora.

The impacts of pastoral land use and fire history was investigated within a single widespread regional ecosystem - open *E. similis* woodland with *Triodia pungens* ground cover. Many properties have long or permanently ungrazed paddocks within this vegetation type due to the presence of heartleaf poison bush *Gastrolobium grandiflorum*. Using a subset of standardised quadrat samples, the impact of fire age and grazing history and the interaction of these two processes on fauna and plant composition were examined. Statistical investigation included analysis of similarity and ordination, and generalised linear modelling was used to explore in detail the species and group response to the treatments and interaction terms.

Fire and grazing had a significant influence on the distribution and abundance of a number of fauna and flora species and guilds with the impact of both processes combining to mute or accentuate the measured species responses. Time since fire is the best predictor of vertebrate species composition, while for ants grazing class was superior. However for terrestrial species such as reptiles and small mammals, the grazing effects were quite marked. There were several fire and grazing increaser and decreaser species with an interaction between fire and grazing clearly evident for some species (*Pseudomys desertor* and *P. delicatulus*). Shifts in structure of plant communities partially accounted for these patterns. These results suggest that in tropical savanna pastoral landscapes both grazing and fire effects should be quantified to avoid measuring spurious species responses. There is often suggestion that intermediate grazing pressure causes neutral biodiversity impacts, irrespective of fire effects, however these results indicate that even light to moderate grazing may result in some community disarray.

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Chapter 1. Introduction.

Introduction

Approximately 20% of continental Australia consists of tropical savanna rangelands. These are defined as landscapes of dense native grasses and scattered trees, grazed by cattle, but where rainfall is too low to permit intensive agriculture (Harrington *et al.* 1984). Despite this geographical extent, there is perhaps some bias of ecological research to coastal and temperate environments due to the proximity to population centres and the presence of charismatic and species-rich ecological communities (compare papers in Ash 1996 with Hobbs and Yates 2000). Biophysical conceptual frameworks for rangeland management have been proposed (Morton 1990; Pickup and Stafford-Smith 1993; James *et al.* 1995), but with little subsequent specific bioregional research (Landsberg *et al.* 1997; Fisher 2001a). While some rangeland biota and assemblages are species rich and well studied (Dickman *et al.* 1999; Morton 1993; Fisher 2001a), on the whole data are deficient (Woinarski *et al.* 2001a).

In Australia there is explicit government policy that recognises the need for Ecologically Sustainable Development (Commonwealth Government 1996b) and specifically in rangelands (ANZECC and ARMCANZ 1999). Coupled with this is the goal of developing reserve systems that are comprehensive, representative and adequate for the protection of biodiversity (JANIS 1997). There is clear evidence that government targets proposed for remnant vegetation protection (10-30%) are too low and will lead to dramatic species loss (Barrett 2000; James and Saunders 2001). Therefore, off-reserve conservation is a vitally important adjunct to formal reserve systems (Hale and Lamb 1997; Queensland Government 2001). This requires practical guidelines, management techniques and policy conducive for pastoral land managers to improve the conservation gains in production environments (Lambeck 1999; BIOGRAZE 2000).

Conservation management in Australia is currently undertaken within a bioregion-planning framework (Thackway and Creswell 1995). Land classifications are commonly used as the foundation for selection of areas to reserve (Pressey 1994), and a system of land classification fundamentally underpins much conservation planning in Queensland (Sattler and Williams 1999). The objective of such planning is often to efficiently select areas for reserves in order to maximise representativeness of biota and landscapes (Vane-Wright 1991; Pressey *et al.* 1993). This process is heavily reliant on data on the biodiversity values of particular sites or regions (Prendergast *et al*. 1998), or where data are not available, the use of surrogates that represent spatial patterns of biodiversity (Flather *et al.* 1997). However the value of many surrogates for other aspects of biodiversity is uncertain. Few studies have examined the direct relationship of fauna distribution to *a priori* classifications (Pressey 1994).

A characteristic of the tropical savannas of northern Australian is the combination of climatic seasonality and gradual environmental variation over large geographic areas (Williams *et al.* 1996b; Ludwig *et al.* 1999b; Woinarski 1999b; Cook and Heerdegen 2001). Resources pulse in short intense wet seasons, then decline to an extended nadir through the dry season. In response, biotas are mobile and flexible, or contract to refugia or local extinction (Woinarski 1999a, b; Woinarski *et al*. 1992c; Franklin 1999). Savanna flora and fauna could be considered mutable, resource and climate-driven entities.

Objectives of Study

A problem that becomes apparent in any review of ecological patterns and processes in Australian tropical savanna rangelands is the lack of adequate biological data on patterns of biodiversity. This is especially true in northern Queensland. Regional fauna surveys for conservation planning have been sporadically conducted (see review in chapter 3; Kirkpatrick and Lavery 1979), but a large degree of this work has been opportunistic and descriptive in nature. Therefore much of the information is of little value in conservation planning, a process which requires accurate species localities and quantification of abundance and environmental pattern. In Queensland there is also a stark disparity between vertebrate fauna studies concentrating on the extensive savanna rangelands (see reviews in Sattler and Williams 1999; Woinarski *et al.* 2001a), and coastal and species-rich bioregions such as the Wet Topics that are very well studied (see review in Abrahams *et al.* 1995; Williams *et al.* 1996c).

James *et al.* (1995) recommended a framework for undertaking research and conservation planning in Australia's rangelands, with these four themes:

1. identifying spatial and temporal patterns of distribution of native biota;
2. quantifying the impact of pastoralism on native fauna;
3. identifying and controlling feral pest species; and
4. developing concepts and tools for regional conservation planning.

Fisher (2001a) suggests that in tropical savanna rangelands, a further theme should be added: identifying the effects of fire, and developing tools for its management.

The primary overarching objective of this study was to examine the patterns within, and environmental controls on, the vertebrate fauna assemblage in one of Queensland's tropical savanna bioregions: the Desert Uplands. This region embodies one of the classic dilemmas for rangeland managers in Queensland: the pace of development is outstripping the available knowledge of the ecology of the natural systems. Information for adequate and sustainable industry and conservation planning is lacking. In undertaking this study I examine three of the themes proposed above (excluding the question of feral pest species), but incorporating consideration of fire to the assessment of impacts of pastoralism. Though these are explicitly focussed on management, they also correspond to a hierarchy of processes considered to contribute to patterns of species-richness and diversity, namely: local ecological interactions and process, regional spatial and temporal variation in assemblage and environmental patterns, and broader biogeographic influences (Schluter and Ricklefs 1993).

The impact of feral cats on native fauna was also examined as part of the study, and a total of 194 catguts were collected over a 2-year period, consisting of 1300 prey items. However, due to constraints of time and thesis length, analysis and discussion of this data were excluded from the final dissertation and will be published separately at a later date.

Conservation planning in Queensland is currently focussed on regional ecosystems, a unit assumed to be a surrogate for fauna patterns (see chapter 4). The emphasis in the regional ecosystem approach on mapping vegetation (by dominant plant species) and geological and soil parameters is possibly due to widespread existing data primarily generated for agricultural needs (e.g. Turner *et al.* 1993), and high availability of aerial-photo and satellite imagery for remote interpretation of vegetation, geology and soil (Burrough and McDonnell 1998). The paucity of previous bioregional fauna surveys in northern Queensland suggests that these have been considered too expensive and time consuming. This is the challenge facing government agencies with inadequate resources and a business culture shift from long-term strategic biodiversity conservation to one of managerialism and the balance of political risk (Beckwith and Moore 2001). However, strategic protection of fauna species under high pressure of rapid landscape change still requires some primary data regarding habitat relationships and distribution, beyond simple retention rules or mapping of surrogates. Furthermore the choice of the Desert Uplands was not random. The bioregion was selected as a national priority for examination due to the rapid rate of tree clearing currently affecting the area, and the low level of reservation and (typically) meagre information regarding its native biota.

In conclusion there are four specific objectives of this study:

- What is the zoogeographic context of the Desert Uplands bioregion, in particular, is the fauna assemblage distinctive or comparable to other northern Australian bioregions, and has its geographic location (on a significant topographic discontinuity, the Great Dividing Range) influenced composition and pattern of vertebrate fauna?
- What are the regional patterns of spatial distribution of the fauna composition and assemblage, and what are the environmental determinants of these?
- How might the patterns of fauna and flora assemblage within regional ecosystems influence conservation planning in the bioregion, and are the patterns of biota complementary with existing land classifications?
- What is the influence of local scale interactions on the patterns of flora and fauna assemblage, in particular cattle grazing and fire, and how does this influence within-habitat variation?

Structure of Thesis

In the remainder of chapter 1, I provide an overview of the environment and landscapes of the Desert Uplands bioregion. I go on to describe the framework of conservation planning in Queensland - that is the system of bioregions, subregions, landzones and regional ecosystems. I also review the current state of regional ecosystem information available for the Desert Uplands, and existing information regarding flora and fauna, and biota of conservation significance. I briefly describe the nature of the pastoral industry in the bioregion.

In chapter 2 I present an overview of the Desert Uplands fauna, using data derived from the primary survey and a review of existing data sources. I collate all known, reliable and accurate records of vertebrate fauna for the bioregion including species recorded from this survey (chapter 3, 5). I examine the patterns of distribution and composition of vertebrate faunas throughout the Desert Uplands in comparison to neighbouring Queensland bioregions, and those across the northern Australia tropical savannas. In particular I review the evidence that the Desert Uplands bioregion contains a distinct vertebrate biota, and place this fauna in the context of larger biogeographic patterns of vertebrates across northern Australia.

In chapter 3 I describe the results of a systematic quadrat-based vertebrate fauna survey of the Desert Uplands and examine the patterns of distribution, composition and abundance of species recorded within the bioregion. I analyse the environmental factors that determine the distribution and relationships of assemblages within the regional ecosystems sampled and consider whether these assemblages vary in a predictable fashion. I also test possible predictors of local species richness across the range of quadrats sampled.

In chapter 4 I examine the question of whether regional ecosystems provided useful information on patterns of distribution, composition and species-richness in vertebrate and plant taxa. Using simple reservation scenarios I also test whether selection of reserves using regional ecosystems as surrogates of biodiversity pattern would be useful for conservation planning in the region.

In chapter 5 I examine the effect of local environmental change wrought by fire and grazing. I analyse whether the fire and grazing treatments have any measurable impact on vertebrate and invertebrate fauna and plant communities. I also examine the interacting effects between fire and grazing effects and the patterns of variation in the response of biota and how this matches data from existing studies.

In chapter 6 I synthesise the results presented in the previous chapters. I characterise the nature of the vertebrate fauna of the Desert Uplands, both in a historical context and via the current patterns of measured variation and composition in regards to environmental pattern. I suggest further work that might be required to advance our knowledge of the Desert Uplands Bioregion and to build on the work completed in this thesis.

The Desert Uplands Bioregion: an overview

Location, landscape and climate

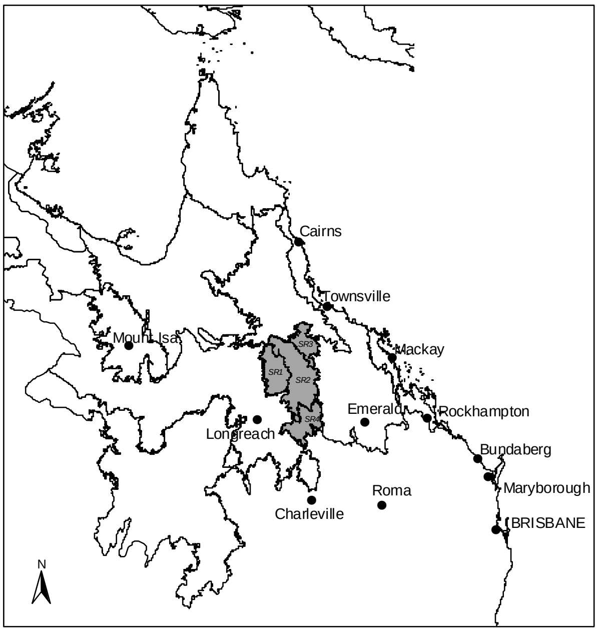
Australia has been divided into a number of bioregions (Thackway and Cresswell 1995) the intent being to provide a uniform framework for assessment of landscape conservation status and priorities for a national reserve system. This bioregionalisation was based on broad landscape patterns derived from major geological changes, climates and variation in flora and fauna assemblages (Sattler and Williams 1999).

In Queensland 13 bioregions are recognised, primarily developed by Stanton and Morgan (1977) and later refined by Sattler and Williams (1999). Six of these lie within the tropical savanna rangelands - environments of tropical grasslands with scattered trees, characterised by summer or monsoonal rainfall and dry winters (Solbrig and Young 1993). The Desert Uplands bioregion is one of these. It covers almost seven million hectares and borders the Mitchell Grass Downs to the west, the Brigalow Belt to the south and east, and the Einasleigh Uplands to the north (Figure 1.1). Its climate is semi-arid and the vegetation consists predominantly of *Acacia* and *Eucalypt* woodlands, ephemeral lake habitats and grasslands. It straddles the Great Divide between Charters Towers (20°4’41’’S, 146°15’14’’E), Hughenden (20°50’41’’S 144°11’55’’E) and

Blackall (24°25’27’’S, 145°27’54’’E). Elevation ranges from 780 m in the very north at White Mountains National Park, to less than 300 m in regions in the southwest. Typically the elevation is less than 400 m. Overall the bioregion has a summer dominant rainfall averaging between 350 and 600 mm annually (Figure 1.2). Rainfall variability is moderate to high in the eastern parts, and high in the west (Bureau of Meteorology 1989).

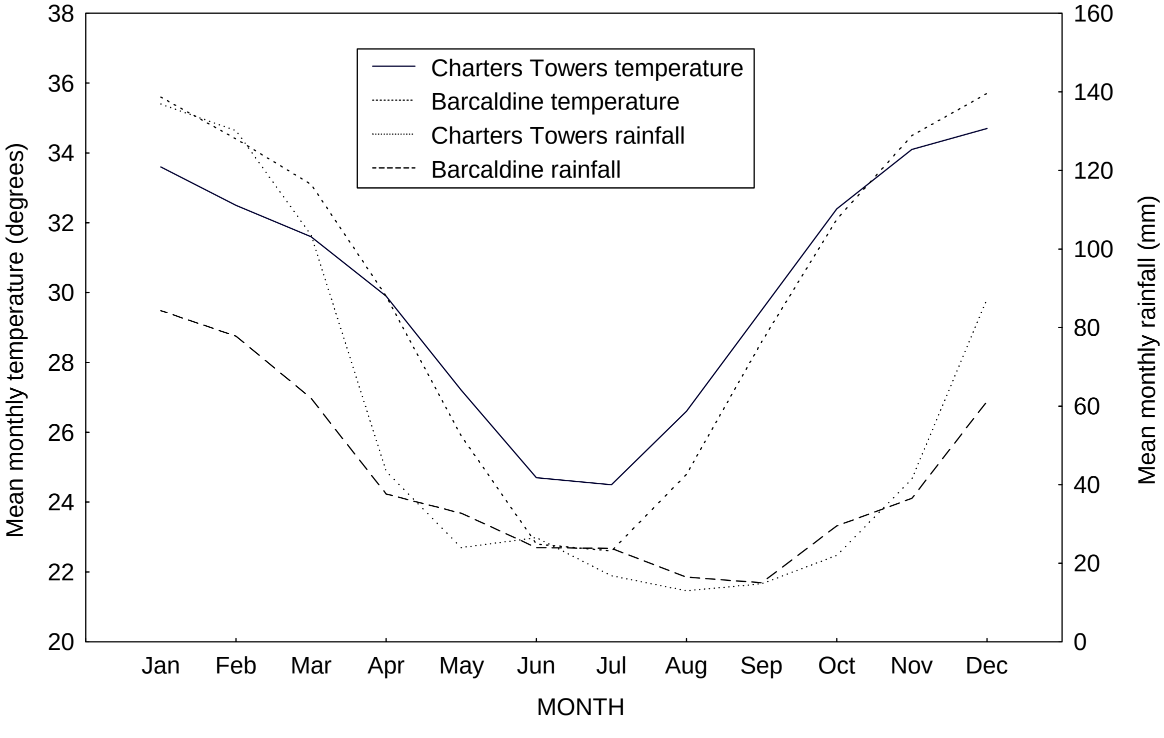
Red and yellow earths are the dominant soils of the bioregion, covering over 90% of its area (Isbell *et al.* 1967). These soils are generally infertile and prone to surface scalding. There are small areas of texture contrast and clay soils. Wetlands occur throughout the bioregion, though most are seasonal and are subject to high grazing pressures when dry. Spring-fed wetlands and those associated with riparian areas occur, as do closed depressions associated largely with the extensive sand sheets (Morgan *et al.* 2002). This latter type includes three of the largest wetlands: Cauckingburra Swamp, Lake Buchanan and Lake Galilee. These are recognised as nationally significant and listed on the Register of National Estate (AHC 1996) and the Directory of Nationally Important Wetlands.

Figure 1.1 Location of the Desert Uplands bioregion in Queensland (shaded), indicating the distribution of the four major sub-regions. SR 1 = Prairie-Torrens Creek, SR 2 = Alice Tableland, SR 3 = Cape-Campaspe Rivers, SR 4 = Southern Desert Uplands.



At a regional scale, the Desert Uplands provides a continuous north-south woodland corridor linking the woodlands and forests of the Einasleigh Uplands and Cape York Peninsula with the woodlands of the Carnarvon ranges. This ultimately connects with the woodlands and forests of the Great Dividing Range in New South Wales and Victoria (Morgan *et al.* 2002). To the west of the bioregion the Mitchell Grass Downs are timbered only along major water courses, while in the east the woodlands of the Brigalow Belt have been mostly fragmented by tree clearing. The Desert Uplands also lies on the eastern margin of the Great Artesian Basin, on the basal sandstones that extend down eastern Australia from the base of Cape York Peninsula to the north-western slopes of New South Wales. These sandstones form ranges and sandy plateaus that are largely undeveloped (Morgan *et al.* 2002).

Figure 1.2 Climate averages (temperature and rainfall) for Charters Towers and Barcaldine Post Offices. Data averaged for period 1882-1992. Charters Towers (20°4.68’ S, 146°15.68’ E) total mean annual rainfall is 659 mm. Barcaldine (23°33.26’ S, 145°17.29’ E) total mean annual rainfall is 501 mm.



The regional ecosystem concept

A regional ecosystem classification has been developed to assist the Queensland Environmental Protection Agency to plan for biodiversity both on and off reserve. This classification provides a foundation for the development of guidelines for clearing on leasehold lands under the Lands Act and more recently the Vegetation Management Act 1999 (VMA). The classification also helps guide pro-active conservation actions by government and non-government organisations (Morgan *et al.* 2002).

Regional ecosystems generally describe and map vegetation types that are consistently associated with a particular combination of geology, landform and soil (Sattler and Williams 1999). At present, definitions of regional ecosystems are biased towards plants, but it is expected that information about fauna will gradually be added as the knowledge base improves (Sattler and Williams 1999).

Each regional ecosystem is given a three-unit number. The first unit refers to a biogeographic region (the Desert Uplands = 10). The second unit refers to the land zone, which is a simplified geology/substrate-landform classification for Queensland. The third unit is the unique regional ecosystem number. Twelve different landzones are recognised for Queensland (Sattler and Williams 1999), and the Desert Uplands contains six: extensive sandy alluvial soils and alluvial clays (landzone 3); old higher clay sheets (landzone 4); sand plains and deep red earths (landzone 5); Tertiary duricrusts and small scarps (landzone 7); rugged sandstone ranges (landzone 10); and shale outcrop (landzone 9). There are also small areas of other landzones considered outliers of adjacent bioregions: basalts (outliers of the Einasleigh Uplands Bioregion), metamorphic rocks (outliers of the Brigalow Belt and Einasleigh Uplands Bioregions) and granitic rocks (outliers of the Brigalow Belt and Einasleigh Uplands Bioregions) (Morgan *et al.* 2002).

In Queensland there are currently two approaches to determine conservation priorities at the scale of regional ecosystems. The first uses ratings of Biodiversity Conservation Status applied by the Queensland Environmental Protection Agency. These reflect the original extent of a regional ecosystem, the degree to which it has been cleared, and the condition of what remains (Sattler and Williams 1999). The introduction of the

Queensland Vegetation Management Act (1999) established a second measure of ecosystem status across the state. This status, the VMA Conservation Status, reflects the original extent of a regional ecosystem and the degree to which it has been cleared. Generally speaking, regional ecosystems listed as "endangered" under the Vegetation Management Act cannot be cleared on either freehold or leasehold lands, while those listed as "of concern" cannot be cleared on leasehold or other crown lands. Three general categories exist, but with slightly different criteria for assessment under the EPA (additional degradation criteria) and VMA (simple area remaining rules).

- Endangered: if the remnant vegetation is less than 10% of its pre-clearing extent across the bioregion; or if 10-30% of its pre-clearing extent remains and the remnant vegetation is less than 10,000 hectares. The EPA also classifies a regional ecosystem as endangered if less than 10% of its pre-clearing extent remains unaffected by severe degradation and/or biodiversity loss or 10-30% of its pre-clearing extent remains unaffected by severe degradation and/or biodiversity loss and the remnant vegetation is less than 10,000 hectares or it is a rare regional ecosystem subject to a threatening process;

- Of concern: Remnant vegetation is 10-30% of its pre-clearing extent across the bioregion; or more than 30% of its pre-clearing extent remains and the remnant extent is less than 10,000 hectares. The EPA also classifies a regional ecosystem as of concern if 10-30% of its pre-clearing extent remains unaffected by moderate degradation and/or biodiversity loss; and

- No concern at present: if remnant vegetation is over 30 per cent of its pre-clearing extent across the bioregion, and the remnant area is greater than 10,000 hectares. The EPA also classifies a regional ecosystem as not of concern if the degradation criteria listed above for endangered or of concern ecosystems are not met.

Subregional characteristics

The Desert Uplands bioregion has been divided into four subregions (or provinces) (see Figure 1.2): the Prairie-Torrens Creeks Alluvials, the Alice Tableland, the Cape-Campaspe Plains and the Southern Desert Uplands. Each subregion has a particular suite and pattern of landforms and soils that can be characterised and described within the landzones (Sattler and Williams 1999; Morgan *et al.* 2002).

Subregion One (Prairie-Torrens Creeks Alluvials) is dominated by extensive areas of alluvial sand and clay sheets, stripped lateritic plain and shales. The sandy soils and the skeletal soils generally carry White's ironbark *Eucalyptus whitei* woodlands, while clay soils have Mitchell grass *Astrebla spp* and blue grass *Dichanthium spp* grasslands or *Acacia cambagei* and *A. argyrodendron* low woodlands. Most watercourses draining this subregion originate within it and all are tributaries of the Thomson River and form part of the catchment of Lake Eyre (Sattler and Williams 1999; Morgan *et al.* 2002).

Subregion Two (the Alice Tableland) is the largest subregion of the bioregion and forms its central core. Deep red earths of an extensive and largely intact Tertiary plateau dominate it and carry open woodlands dominated by Yellowjacket *Eucalyptus similis,* with smaller areas of ironbark woodlands. The sandstone ranges support a variety of eucalypt woodlands and shrublands, and Lancewood *Acacia shirleyi* and Bendee *A. catenulata* low open forests. The subregion also contains the most well developed freshwater wetlands (Lake Moocha, Lake Thirlestone, Cauckingburra Swamp, Lake Galilee), extensive saline wetlands (Lake Buchanan and Lake Huffer), and a number of artesian mound springs and sandstone seeps. There are many endemic ecosystems associated with the lakes and their fringing dunes. Drainage is predominantly westward into the Lake Eyre Basin, or eastward into the Belyando River (Sattler and Williams 1999; Morgan *et al.* 2002).

Subregion Three (the Cape-Campaspe Plains) is in the northeast of the bioregion, between the Great Basalt Wall and the Cape River. It consists largely of an extensive undulating Cainozoic surface (red and yellow earths) in its northern part, and alluvial plains in the south. The climate and vegetation of the Cape-Campaspe Plains have similarities with that of the Brigalow Belt and the Einasleigh Uplands bioregions.

These landscapes carry woodland ecosystems dominated by ironbarks *Eucalyptus crebra* and *E. melanophloia*, Blackwood *Acacia argyrodendron*, Brigalow *A. harpophylla* and Blackbutt *E. cambageana*. Reid River Box *Eucalyptus brownii* woodland occurs on the texture contrast soils. In the north drainage is into the Burdekin River, and south into the Belyando River and then into the Burdekin River (Sattler and Williams 1999; Morgan *et al.* 2002).

Subregion Four (the Southern Desert Uplands) is dominated by deep sandy outwash, including sandy plains and alluvial fans, with clay plains or sandy alluvial terraces in the valley bottoms. These landscapes carry open woodlands dominated by Silver-leaved Ironbark *Eucalyptus melanophloia* or Poplar Box *E. populnea*. Alluvial clay plains usually have Brigalow *Acacia harpophylla* and Blackbutt *E. cambageana*, gidGee *A. cambagei* or Poplar Box *E. populnea* woodlands. Drainage is predominantly westward into the Lake Eyre Basin, although the eastern slopes of the subregion run into the Belyando River (Sattler and Williams 1999; Morgan *et al.* 2002).

Regional ecosystem types, extent and reservation

In the Desert Uplands, regional ecosystems were first described by Morgan (1999), based largely on land unit descriptions of the land system surveys of Perry *et al.* (1964), Gunn *et al*. (1967), Division of Land Utilisation (1978) and Turner *et al*. (1993), and the land unit survey of Lorimer (1999). A total of 75 regional ecosystems is currently recognised for the Desert Uplands. Twenty-one regional ecosystems are endemic to a single subregion: fifteen in the Alice Tableland, three in the Cape-Campaspe Plains, and three to the Southern Desert Uplands. A further 27 regional ecosystems occurring within the Desert Uplands are classified as outliers of the adjacent Mitchell Grass Downs, Einasleigh Uplands or Brigalow Belt bioregions (Morgan *et al.* 2002).

Using the more conservative EPA categorisation, 44 regional ecosystems are either endangered (n=15) or of concern (n=29) in the Desert Uplands, 27 of which now have a total extent of less than 10,000 hectares across the bioregion. Four "endangered" communities are subject to widespread clearing for pasture development, these being the *Acacia* woodlands and other timbered clay soils. The dominant extent of these "endangered" ecosystems is around Lake Buchanan and Lake Galilee, and associated with the spring systems along the western margin of the Alice Tableland (Morgan *et al.* 2002).

Of the original 6.8 million hectares of vegetation cover in the Desert Uplands, 900,000 hectares were cleared by 1999, representing almost 14% of the bioregion. Highest rates of clearing were in Subregion 4 (40% of 1 million hectares native vegetation cleared) and lowest in Subregion 2 (7% of 2.7 million hectares native vegetation cleared). In the 2-year period from 1997-1999 the clearing rate for the entire bioregion was 511,000 hectares, indicating that the majority of the clearing has been conducted recently (Wilson *et al.* 2002). Certainly since these figures were calculated in 1999, there will have been substantially greater amounts of native vegetation lost. The introduction of the Queensland Vegetation Management Act 1999 and threats of greater regulation on tree clearing by state and federal governments have caused many landholders to panic-clear beyond what they may have reasonably done otherwise.

National Parks and resource reserves in the Desert Uplands currently cover 182,100 hectares, or 2.6% of the bioregion. These parks include representation of 44 (59%) of the 75 regional ecosystems unique to the Desert Uplands. Moorrinya and Forest Den National Parks are in Subregion 1 (2.6% total area), White Mountains National Park is in Province 2 (3.9% total area) and Cudmore National Park is in Province 4 (1.8% total area). There are no parks in Subregion 3. Some selected data on regional ecosystems are presented in Table 1.1. The intent of these data is to provide examples of the regional ecosystem descriptions, and to indicate which regional ecosystems are most extensive (typical) in the Desert Uplands, which are most at threat from clearing, and which are best and worst represented in current reserves. Generally those regional ecosystems least threatened by clearing have high representation in National Parks, and those most widespread or most threatened are least represented.

Flora

The Queensland Herbarium has undertaken small-scale vegetation survey (1:250,000) in the Desert Uplands for regional ecosystem mapping. Twenty-nine rare and threatened plant species listed under the Queensland Nature Conservation Act 1992 are known to occur in the Desert Uplands. A further ten are believed to be new species (J. Thompson, Queensland Herbarium, 2002, pers. comm.), including two from the shores of Lake Buchanan. Artesian mound springs and two sandstone-based ecosystems have the greatest numbers of endangered species, while the highest total number of rare species occurs in riparian ecosystems. Twenty-two species of conservation significance are believed to be restricted to Subregion 2, the Alice Tableland (Morgan *et al.* 2002).

Table 1.1 Examples of regional ecosystems in the Desert Uplands. The top six in terms of area original extent (hectares), highest rate of clearing (lowest % remaining) and greatest extent protected within National Parks is tabulated.

Regional ecosystem	Description	Original extent	1999 extent	% remaining	Extent in NP	% extent in NP
10.10.1	(Low) woodland of *Acacia shirleyi* (with or without in the White Mtns) with very sparse tussock ground layer of usually *Cleistochloa subjuncea* or *Triodia* spp	92,176	91,968	99.8	**28,762**	**31.2**
10.10.2	Shrublands on shallow soils on sandstone plateaus.	20,599	2,0591	100.0	**16,625**	**80.7**
10.10.4	Open-woodland of *Eucalyptus miniata* and *Corymbia leichhardtii* or *C. lamprophylla* with mid-dense hummock grass ground layer of *Triodia bitextura*.	71,308	70,760	99.2	**15,916**	**22.3**
10.10.5	Open-woodland to woodland of *Corymbia trachyphloia* with or without *C. lamprophylla* usually with shrubby understorey.	57,108	56,965	99.7	**28,191**	**49.4**
10.3.19	Woodland of *Acacia cambagei* on lake-fringing dunes of Lake Galilee.	3,660	870	**23.8**	0	0.0
10.3.28	Open-woodlands to woodlands of *Eucalyptus melanophloia* with sparse grassy ground layer of predominantly tussock grasses.	**555874**	50,036	91.2	1,043	0.2
10.3.6	Open-woodland to woodland of *Eucalyptus brownii* with or without understorey of *Eremophila mitchellii* and with ground layer of tussock grasses.	**51,7559**	449,789	86.9	886	0.2
10.3.9	Open-woodland to woodland of *Eucalyptus whitei* with ground layer of tussock grasses.	**28,7733**	269,294	93.6	**11,756**	4.1
10.4.3	(Low) woodland of *Acacia harpophylla* ± *Eucalyptus cambageana* with very sparse grassy ground layer.	89,645	34,325	**38.3**	0	0.0
10.4.5	Low (open-) woodland of *Acacia cambagei* with very sparse tussock grass ground layer.	34,365	13,001	**37.8**	0	0.0

Regional ecosystem	Description	Original extent	1999 extent	% remaining	Extent in NP	% extent in NP
10.5.1	(Open-) woodland of *Eucalyptus similis* usually with *Corymbia brachycarpa* with sparse hummock grass ground layer of *Triodia pungens*.	**90,3128**	887,419	98.3	**16,229**	1.8
10.5.5	Open-woodlands to woodlands of *Eucalyptus melanophloia* with sparse grassy ground layer of *Triodia pungens* and/or tussock grasses.	**101,5345**	820,653	80.8	2,277	0.2
10.5.9	Open-woodland of *Eucalyptus quadricostata* and usually *Corymbia brachycarpa* and *C. leichhardtii* with sparse tussock grass ground layer.	7,048	7,048	100.0	3,405	**48.3**
10.7.10	Open-woodland of *Eucalyptus whitei* with sparse hummock grass ground layer of *Triodia pungens* and/or tussock grasses.	**380,504**	377,757	99.3	815	0.2
10.9.1	(Open-) woodland of *Acacia argyrodendron* with usually sparse grassy ground layer.	63,130	34,827	**55.2**	1,349	2.1
10.9.3	Low open-woodland to woodland of *Acacia harpophylla*	3,522	1,507	**42.8**	27	0.8
10.9.6	Low open-woodland to woodland of *Acacia cambagei* with very sparse tussock grass ground layer.	42,222	14,622	**34.6**	0	0.0

Vertebrate Fauna

The Desert Uplands bioregion has been very poorly surveyed for vertebrate fauna. The area was traversed by many early explorers (Landsborough 1862; Buchanan 1933; Mitchell 1969), and museum expeditions have passed through the northern reaches (Le Soeuf 1920; Wilkins 1929; Hall 1974). More recent surveys have included:

- a fauna survey of the Cape-Campaspe subregion in the Dalrymple Shire (Blackman *et al.* 1987);
- a survey of the distribution of arboreal fauna in the Prairie-Torrens Creek subregion (Munks 1993);
- a review of Pebble-mound Mouse *Pseudomys patrius* records and distribution (Van Dyck and Birch 1996);
- fauna lists for significant wetlands in the bioregion (Blackman *et al.* 1999);
- long term aerial monitoring of waterbird populations in a number of wetlands (R. Kingsford, NSW NPWS, unpubl. data);
- unpublished survey data for the southern Desert Uplands (Hannah and Thurgate 2001; Ludwig *et al.* 2000);

- specimen data from the Australian, South Australian and Queensland Museum collections database; and
- Birds Australia (Royal Australasian Ornithologists Union) Atlas data 1984 and 2001;

Some data also exist for the National Parks but these are either indicative species lists or observational species lists with little or no associated location, habitat or abundance information.

The database of vertebrate fauna records for the Desert Uplands bioregion compiled here and incorporating both primary and secondary data sources and all waterbird, bat and introduced species comprised 31,221 individual records of which 11 819 (8,277 birds, 546 amphibians, 1,233 mammals, 1,860 reptiles) were in unique localities. This totalled 431 species comprising:

- 24 amphibians (three families and nine genera) representing 20% of Queensland’s frog fauna. One species, the Cane Toad *Bufo marinus*, is introduced;
- 229 birds (63 families) representing 34% of Queensland’s avifauna;
- 61 mammals (19 families and 37 genera) representing 23% of Queensland’s mammal fauna. Seven of these are introduced species; and
- 117 reptiles (10 families and 51 genera) representing 26% of Queensland’s reptile fauna.

A total of 59 species recorded in the Desert Uplands have been identified to be of conservation significance, comprising 24 birds, one amphibian, 16 mammals and 18 reptiles. These are listed, together with the source of their status or the reason for their bioregional significance, in Table 1.2. Conservation status is derived from:

- Queensland Nature Conservation Legislation Amendment Regulation (No. 2) 1997;
- Commonwealth Environmental Protection and Biodiversity Conservation Act 1999;
- National Action Plans for marsupials and monotremes (Maxwell *et al.* 1996), reptiles (Cogger *et al.* 1993), shorebirds (Watkins 1993), birds (Garnett and Crowley 2000), rodents (Lee 1995), frogs (Tyler 1997) and bats (Duncan *et al.* 1999); and

- Atlas of Queensland’s Frogs, Reptiles, Birds and Mammals (Ingram and Raven 1991), which assesses the conservation status of the state’s vertebrate fauna using known population and distribution characteristics (Thomas and McDonald 1983).

In addition to species already listed as rare and threatened, a number of fauna species recorded in the Desert Uplands are considered to be of conservation significance due to their bioregional importance. These criteria include (from Morgan *et al.* 2002):

- the species is endemic to the Desert Uplands;
- the species is represented in the desert uplands by a disjunct population;
- the species has declined elsewhere in its range but still remains abundant in the Desert Uplands, or the species occurs in atypically high abundances in the bioregion compared to other parts of its distribution, suggesting the Desert Uplands is a significant population stronghold in Queensland; and
- the biology and distribution of the species is very poorly known and sampled across the state, and new records in the Desert Uplands represent important new localities.

Table 1.2 Vertebrate fauna species of conservation significance recorded in the Desert Uplands Bioregion.

Species	Common name	EPBC	NCA	AP	QM	DU
Birds						
Acanthiza pusilla	Brown Thornbill					B
Ardeotis australis	Australian Bustard			NT		
Burhinus grallarius	Bush Stone-Curlew			NT		
Chthonicola sagittata	Speckled Warbler			NT		
Climacteris picumnus	Brown Treecreeper			NT		
Emblema pictum	Painted Finch					B
Ephippiorhynchus asiaticus	Black-necked Stork		R			
Eremiornis carteri	Spinifexbird					B
Erythrura gouldiae	Gouldian Finch	E	E	E	E	
Falco subniger	Black Falcon					B
Geophaps scripta scripta	Squatter Pigeon	V	V	NT		
Lichenostomus leucotis	White-eared Honeyeater					B
Lophoictinia isura	Square-tailed Kite		R		R	
Melanodryas cucullata	Hooded Robin			NT		
Melithreptus gularis	Black-chinned Honeyeater		R	NT		
Neochmia ruficauda ruficauda	Star Finch	V	V		E	
Nettapus coromandelianus	Cotton Pygmy-goose		R	NT		
Poephila cincta cincta	Black-throated Finch	V	V	V	R	
Pomatostomus temporalis	Grey-crowned Babbler			NT		B
Rostratula benghalensis	Painted Snipe		R	V		
Stictonetta naevosa	Freckled Duck		R		R	
Tadorna radjah	Radjah Shelduck		R			
Tyto novaehollandiae kimberlei	Masked Owl	V	V	NT		
Amphibians						
Pseudophryne major	Large Toadlet					B
Mammals						
Aepyprymnus rufescens	Rufous Bettong			NT(lr)		
Chalinolobus picatus	Little Pied Bat		R	NT		

Species	Common name	EPBC	NCA	AP	QM	DU
Lagorchestes conspicillatus	Spectacled Hare-wallaby			NT		
Leggadina lakedownensis	Lakeland Downs Mouse				K	B
Nyctophilus gouldi	Gould's Long-eared Bat					B
Petauroides volans	Greater Glider			NT(lr)		
Petaurus norfolcensis	Squirrel Glider			NT		
Phascolarctos cinereus	Koala			NT		
Pseudomys desertor	Desert Mouse			K		B
Pseudomys patrius	Pebble-mound Mouse				K	
Sminthopsis douglasi	Julia Creek Dunnart	E	E	E	K	
Sminthopsis murina	Common Dunnart			NT		B
Trichosurus vulpecula	Common Brushtail Possum			NT(lr)		
Vespadelus baverstocki	Inland Forest Bat					B
Vespadelus finlaysoni	Inland Cave Bat					B
Zyzomys argurus	Common Rock-rat					B
Reptiles						
Acanthophis antarcticus	Common Death Adder		R	RK		
Anomalopus gowi	Speckled Worm-skink			RK		
Ctenotus capricorni	Capricorn Ctenotus		R	RK	K	
Ctenotus rosarium	Desert Uplands Ctenotus					B
Diplodactylus vittatus	Wood Gecko					B
Diporiphora winneckei	dragon					B
Egernia stokesii	Gidgee Skink					B
Lerista sp nov	Undescribed Mulch-slider					B
Lerista cinerea	Vine-thicket Fine-lined Slider		R	RK	K	
Lerista wilkinsi	Two-toed Fine-lined Slider		R	RK	K	
Paradelma orientalis	Brigalow Scaly Foot	V	V	V	V	
Pseudechis australis	King Brown/Mulga Snake		R	RK		
Pseudechis colletti	Collets Snake		R	RK		
Simoselaps warro	burrowing snake		R	RK	K	
Suta dwyeri	Dwyer's Snake					B
Tiliqua multifasciata	Centralian Blue-tongued Lizard					B
Tympanocryptis cephalus	Blotch-tailed Earless Dragon					B
Varanus mertensi	Mertens Water Monitor					B

Status sources:
EPBC = Commonwealth Environment Protection and Biodiversity Conservation Act 1999
NCA = Queensland Nature Conservation Legislation Amendment Regulation (No. 2) 1997
AP = Environment Australia Action Plan’s for Birds, Reptiles, Bats, Frogs, Rodents, Mammals
QM = Queensland Museum status (Ingram and Raven 1991)
DU = Bioregional importance or significance, this study
Status codes:
E = endangered, V = vulnerable, R = rare, RK = rare or insufficiently known, K = insufficiently known, NT = near threatened, NT(lr) = near threatened (least concern), B = bioregional.

Pastoralism in the Desert Uplands

Pastoralism in the Desert Uplands has a long history (Smith 1994), the first leases being settled in the 1850’s and 1860’s in the north-east (Natal Downs, Mirtna) and south-west (Bowen Downs, Aramac). Particularly in the more productive “downs” country to the west, historically many areas were grazed by sheep (Smith 1994), though there was a shift to cattle in the open woodlands near the turn of the nineteenth century (Bennett 1928). Beef cattle grazing is now the major form of primary production, though much of the region is considered of low potential for pastoralism due to relatively low rainfall, poor soils and vegetation considered of low general palatability (e.g. *Triodia*) compared to tussock grasses (Rolfe *et al.* 2000). Approximately 1,200 individual lots have been identified in the Desert Uplands region, amalgamated into 320 properties. A majority (>70%) of the land is leasehold, with most of the freehold land concentrated in Subregion 4 in the south. Only 15% of the properties are greater than 25,000 hectares in size.

The grazing industry is based largely on the extensive use of natural rangelands, and in 1999 nearly 87% of the Desert Uplands remains dominated by native vegetation (Morgan *et al.* 2002). While there are issues of declining pasture productivity, woody regrowth and soil degradation, the bioregion remains in relatively good condition compared to bioregions to the south and east (Morgan *et al.* 2002). However the combination of changing markets requiring better finished cattle, deterioration of real rates of financial return and shift to drought resilient stock, has increased pressure to improve productivity of cattle via tree-clearing and sowing of introduced pastures (Rolfe *et al.* 2001). Though much of the bioregion is still intact, the southern portion of the bioregion has been subject to some of the highest clearing rates in Australia (Fairfax and Fensham 2000; Rolfe *et al.* 2001).

There are several regional planning processes currently underway in the Desert Uplands, including the preparation of Local Government Plans under the Integrated Planning Act, a local build-up and development strategy and various natural resource strategies (Morgan *et al.* 2002). Community-based committees, as required by the Vegetation Management Act 1999, are undertaking the current development of Regional Vegetation Management Plans, for the Northern and Southern Desert Uplands planning areas. This is currently the most important planning process for the bioregion in that it will set the development protocols and minimum retention rates for regional ecosystem clearing (Morgan *et al.* 2002). The Regional Vegetation Management Plans plan must consider both the pressures for land development, and protection and conservation and biodiversity values. The final plans are likely to have significant long-term influence on the management of the natural resources and biodiversity in the Desert Uplands Bioregion.

Chapter 2. The Desert Uplands Bioregion: broad zoogeographical context.

Introduction

There have been long held views that the species diversity of a location is a product of its climate, geography and history (Wallace 1876; Willis 1922). It is currently recognised that resource and competitive controls cannot be deftly separated from overarching biogeographic history, both being equally significant in patterning local and regional diversity (Williams *et al.* 2002c). As such the examination of the zoogeography of continental or bioregional biota is primary to understanding smaller scale patterns of composition and distribution (Ricklefs and Schluter 1993).

The key stages in the evolution and eventual realisation of the extant Australian fauna have been widely reviewed (papers in Part 1 of Keast 1981; Frakes *et al.* 1987; Archer *et al.* 1998; Frakes 1999). The last 100 million years are considered the most defining, in particular the slow migration of Australia north to its current position coincident with alternating cycles of warm and wet (greenhouse), and cool and dry (icehouse) climates (Frakes *et al.* 1987). This geophysical and climatic footprint has partly determined current fauna distribution patterns though controls of biotic distribution and diversity are numerous and overlapping, with cause and effect often intertwined. These have variously been considered to be vegetation patterns (Kikkawa and Pease 1982; Cody 1993), climatic gradients (Nix 1982), cycles of widespread aridity and presence of nutrient deficient soils (Beadle 1981; Morton 1993), the prevalence of fire (Kershaw *et al.* 2002), the existence of refugia and barriers such as the Great Dividing Range (Schodde 1982) and dispersal corridors and land bridges (Winter 1997). The relative influence of each has been widely debated. For example 11 factors have been identified as possible promoters of Australian lizard diversity, these ranging from geographic to habitat elements, yet at best multiple causality is proposed (Morton and James 1988; Pianka 1989; Morton 1993).

The patterns of flora and fauna have been characterised via a range of phytogeographic and zoogeographic analyses. Spencer (1896) used distributions of fauna to divide Australia into three subregions - Torresian, Bassian and Eyrean - a system robust enough to be still in use today (Crisp *et al.* 1999; Fisher 2001a). More recently Burbidge (1960) revised the categories to reflect vegetation patterns, and Schodde (1989) further split these into Torresian, Eyrean, Bassian, Tumbunan and Irian zones that reflect more recent understanding of vegetation origins and plate tectonics (Figure 2.8). There is reasonable congruence of distinct fauna assemblages with these regions for some groups, (e.g. birds, Cody 1993; mammals, Winter 1997) though in others the patterns are more complex and idiosyncratic (e.g. desert lizards, Cogger and Heatwole 1981; Pianka 1981). There are myriad other schemes (Archer and Fox 1984; Crisp *et al.* 1999).

The literature describing the biogeography and evolution of Australia’s current biota is extensive, not the least being the exhaustive overviews provided by numerous authors in Keast (1981), Barker and Greenslade (1982), Archer and Clayton (1984) and Dyne and Walton (1987). More recently, advances in molecular studies using mitochondrial DNA have identified deep genetic differentiation in species that lack any external phenotypic variation across vicariant boundaries (Joseph *et al.* 1995; Moritz *et al.* 1997) subverting some previous interpretations. A contemporary revision of the biogeography of Australian fauna that incorporates molecular data is overdue.

The biogeographic patterns of parts of north-eastern Queensland have received specific attention, in particular the diverse and endemic-rich Wet Tropics bioregion (see review and references in Williams *et al.* 1996c). Repeated cycles of refugial isolations and expansion, invasion of biota from New Guinea and south-eastern Australia, and local extinction have patterned the fauna in this region (Williams and Pearson 1997; Winter 1997). A steep topography has resulted in sharp altitudinal gradients and montane isolation in some fauna (Nix and Switzer 1991). Biogeographic patterns in tropical savannas of northern Australia have also received recent consideration. In contrast to north-eastern Queensland, the tropical savannas are patterned by a series of broad latitudinal bands along climatic (essentially rainfall) gradients (Bowman *et al.* 1988; Whitehead *et al.* 1992; Fisher 2001a). The topography is uniform and hence turnover in faunal assemblages is gradual, though there is an abrupt vegetation/soil boundary coincident with the start of the Mitchell Grass Downs Bioregion (Barkly Tablelands) that is considered to be coincident with the Torresian/Eyrean interzone (Nix 1982; Fisher 2001a).

By virtue of its recognition as a discrete entity, the Desert Uplands bioregion should support landscapes and biota that are distinct from neighbouring bioregions (Thackway and Creswell 1985). The high number of endemic regional ecosystems suggests this is at least partly true (chapter 1, Morgan *et al.* 2002), though this inference may be circular as in most cases regional ecosystems are by definition already unique to bioregions. A number of authors have reviewed patterns of species distribution that incorporate facets of the bioregion's geography. In studies of the distribution of avifauna, Schodde and Mason (1980) and Ford (1986) recognise regions (north-eastern and central-eastern Queensland) and barriers (Carpentaria, Burdekin-Lynd) that transect and delineate the Desert Uplands (Figure 2.7). Additionally, Schodde and Mason (1999) considered major continental drainage basins coupled with broad habitat types as appropriate distribution delimiters of Passerine taxa and ultrataxa. The Desert Uplands also lies on the confluence of three major drainage basins the Flinders River flowing to the Gulf, the Burdekin River flowing to the east coast and Torrens Creek feeding into the Lake Eyre Basin (Figure 2.6). The Great Dividing Range runs down the centre of the Alice Tableland Sub-region, corresponding with a broad zone of Torresian/Eyrean intergradation (Figure 2.6). Furthermore, north-south and east-west rainfall, topographic and temperature gradients further suggest that there may be associated distinctive patterns of gradual turnover in the biota in this region (Figures 2.3-2.5).

In this chapter I examine the zoogeography of the Desert Uplands bioregion. I collate all known, reliable and accurate records of vertebrate fauna for the bioregion including the results of my own survey (chapter 3, 5). In particular I examine the patterns of distribution and composition throughout the Desert Uplands in comparison to neighbouring Queensland bioregions and those across the northern Australia tropical savannas. The questions asked are:

- what is the degree of distinctiveness or endemism of the fauna assemblage of the Desert Uplands, and is this comparable to other bioregions in Queensland? Furthermore how comparable is the Desert Uplands to climatically similar but geographically separated bioregions across the northern tropical savannas?;
- are subregions (see chapter 1), a useful representations of biotic variation within a bioregion?; and
- given continental-scale data suggests the Desert Uplands is situated at a geographic and climatic crossroads (straddling the Great Dividing Range and at the boundary of three of northern Australia's major catchments), is this reflected in the distribution of vertebrate fauna? In addition, if there are distinct patterns of species turnover or unusual distributions, is this change gradual or stepped?

I address these questions through a sequence of related data explorations that include:

- compilation of species lists for a series of adjacent and related bioregions in northern Australia, and collation of a range of climate, vegetation and landscape data for these bioregions. From this, the relationship between variation in taxa richness for each bioregion and these environmental factors is examined using Spearman rank correlation;
- exploration of the pattern of composition of vertebrates in each bioregion via ordination;
- examination of the relationship between climate, vegetation and landscape factors for each bioregion with the pattern of ordination using principal axis correlation. This identifies the significant major axes of environmental change, and allows scrutiny of the patterns of fauna variation along these gradients;
- examination of the shift of vertebrate composition across the bioregions using weighed mean ordination scores for selected vertebrate genera. This indicates the relative influence of the vertebrate group on the ordination pattern, and suggests which may be characteristic, or species-rich within a particular bioregion. Spearman rank correlation of selected genera with environmental factors is also undertaken;
- using a measure of Beta-diversity, examination of the patterns of species turnover for vertebrate groups between all bioregions considered, and within the subregions

of the Desert Uplands. Constellation diagrams are used to illustrate the similarity and difference between the Desert Uplands and other bioregions; and

- using only reliable and comprehensive point locality data for Queensland, examination of the pattern of distribution for a subset of related species with both an Eyrean and Torresian/Bassian origin, and the nature of the distribution in relation to the geographic location of Desert Uplands Bioregion.

Methods

Sources of fauna data

The distribution of vertebrate fauna was examined across a series of tropical savanna bioregions (Figure 2.1). The delineation of these bioregions has been derived from broad landscape patterns using underlying patterns of geology, soils, landform, climate and changes in floristic and faunal assemblages (Thackway and Cresswell 1995; Sattler and Williams 1999). Apart from the Desert Uplands (DEU), adjacent bioregions in Queensland running in a series from coast to arid inland were included: Wet Tropics WET; Einasleigh Uplands EIU; Northern Brigalow Belt NBB; Mitchell Grass Downs MGD; and Channel Country CHC. Data for a series of climatically similar northern tropical savanna bioregions running west into the Northern Territory were also compiled: Gulf Fall and Uplands GFU; Gulf Coastal GUC; Sturt Plateau STU; Daly Basin DAB; and Ord-Victoria Plains OVP. The Mitchell Grass Downs (MGD) is distributed in both Queensland and the Northern Territory. Boundaries used were taken from the Interim Biogeographical Regionalisation of Australia (chapter 1, Thackway and Cresswell 1995; Sattler and Williams 1999). The subregional boundaries for the Desert Uplands are derived from Queensland Environmental Protection Agency data (Sattler and Williams 1999; Morgan *et al.* 2002; Chapter 1, Figure 1.1).

Because of the weak and inconsistent spread of fauna distribution data in Queensland (Sattler and Williams 1999), only adequately surveyed adjacent bioregions were included in the analysis. As such the Northwest Highlands (NWH) and Gulf Plains (GUP) were excluded. Only presence or absence of fauna species within each bioregion was identified, regardless of apparent or known abundance of the species, as survey effort in each was inconsistent and variable in spread and effort. Appropriate standardisation of the data was not possible. Apart from the Desert Uplands, within-bioregion (sub-regional) fauna data distribution was also unknown.

The terrestrial vertebrate fauna data for each of the bioregions was collected from a variety of sources including:

- primary survey (this thesis, chapter 3);
- unpublished survey data for the southern Desert Uplands (Hannah and Thurgate 2001; Ludwig *et al.* 2000);
- Queensland Museum collections database;
- Northern Territory Fauna Database (Parks and Wildlife Commission, Northern Territory Department of Infrastructure, Planning and Environment);
- Wildnet fauna database (Queensland Environmental Protection Agency)
- Birds Australia (RAOU) Atlas 1984;
- published data sources for the Northern Brigalow Belt bioregion, (Lavery 1968; Lavery and Johnson 1968; Lavery and Johnson 1974; Lavery and Seton 1974; Hannah and Thurgate 2001), Wet Tropics (Williams *et al.* 1996c), Channel Country (McFarland 1991), Mitchell Grass Downs (Johnson 1997; Fisher 2001a); and
- unpublished data sources such as Dalrymple Shire Fauna Survey and Emerald Shire Fauna Survey (Queensland Parks and Wildlife Service).

In the final data set some taxa were excluded from the bioregional species lists for analysis; waterbirds, waders and seabirds of the families Ardeidae, Anatidae, Anhingidae, Anseranatidae, Charadriidae, Ciconiidae, Fregatidae, Gruidae, Haematopodidae, Jacanidae, Laridae, Pelecanidae, Phalacrocoracidae, Podicipedidae, Rallidae, Recurvirostridae, Rostratulidae, Scolopacidae, Sulidae, Threskiornithidae; bats; and marine mammals. This was due to inconsistent, poor and biased data collection, extremely seasonal migratory behaviour or irrelevance to terrestrial patterns. Introduced species were also excluded.

Climatic, geographic and other environmental data

General geographic (Thackway and Cresswell 1995), climate (BIOCLIM, Nix 1986, Hutchinson 1991) and vegetation data (Fox *et al.* 2001) were collated for each bioregion to examine the gradients and correlations underlying species richness and composition patterns. These data were extracted from GIS interrogation using Arc View 3.2. Data included:

- geographic data: area (log transformed), latitude (maximum, minimum, range), longitude (maximum, minimum, range), altitude (maximum, minimum, range), average distance to coast;
- climate data: mean temperature (wettest quarter, annual range, annual, driest quarter, seasonality), mean rainfall (warmest quarter, coldest quarter, rainfall range, rainfall mean, rainfall seasonality); and
- vegetation data representing the number and percentage area of broad vegetation groups (Fox *et al.* 2001) within each bioregion (Table 2.2).

Bioregion richness

For each bioregion a composite list of species indicating taxa, family and genera was tabulated, excluding the species groups mentioned above. The number of “unique” species was identified - that is, species recorded within only that bioregion. This is not strictly a measure of species endemism as only a subset of bioregions across northern Australia is under consideration here.

Figure 2.1 Location of biogeographic regions mentioned in text and analysis. Bioregion boundaries from Thackway and Cresswell (1995) and Sattler and Williams (1999). Bioregion codes are given in the Methods text.

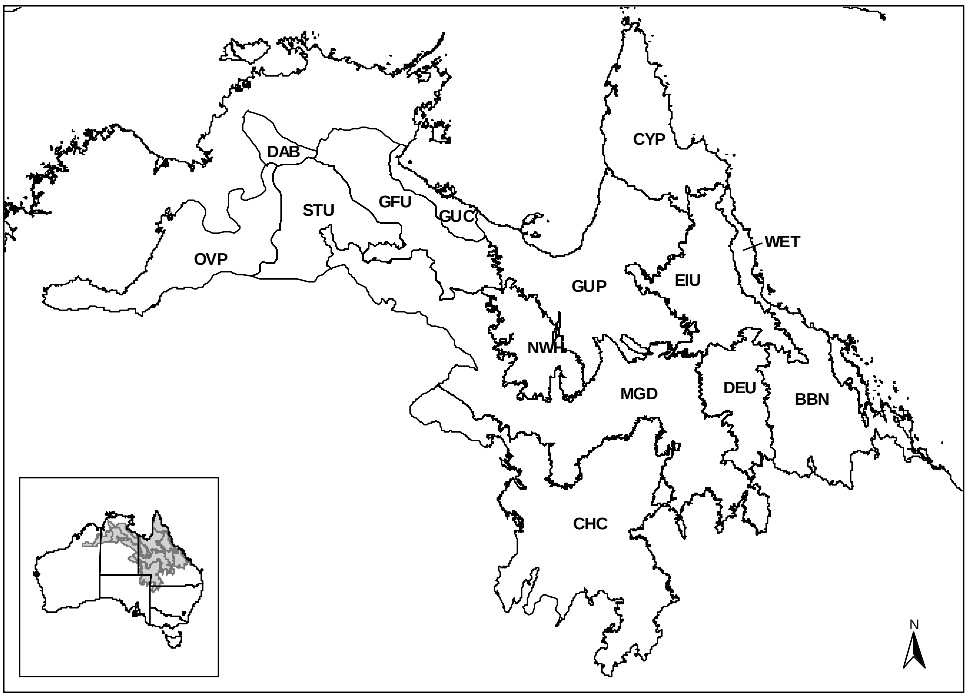


Figure 2.2 Mean annual rainfall for northern Australia with bioregion boundaries superimposed. Rainfall in millimetres. Data from Bureau of Meteorology (www.bom.gov.au) and are based on the standard 30-year period 1961-1990.

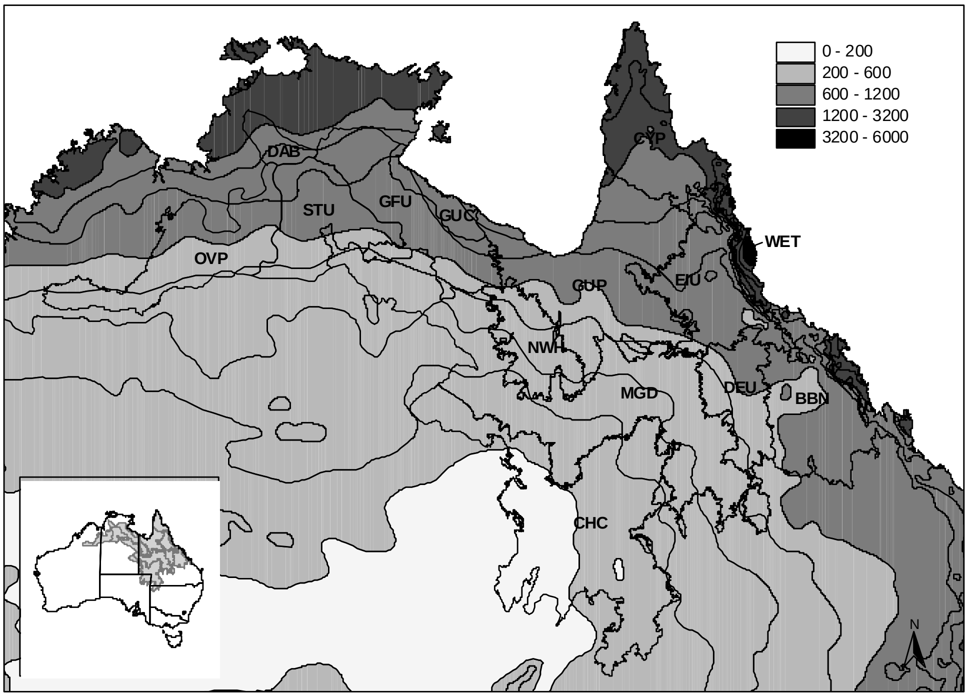


Figure 2.3 Mean annual maximum temperature for northern Australia with bioregion boundaries superimposed. Temperature in degrees Celsius. Data from Bureau of Meteorology (www.bom.gov.au) and are based on the standard 30-year period 1961-1990.

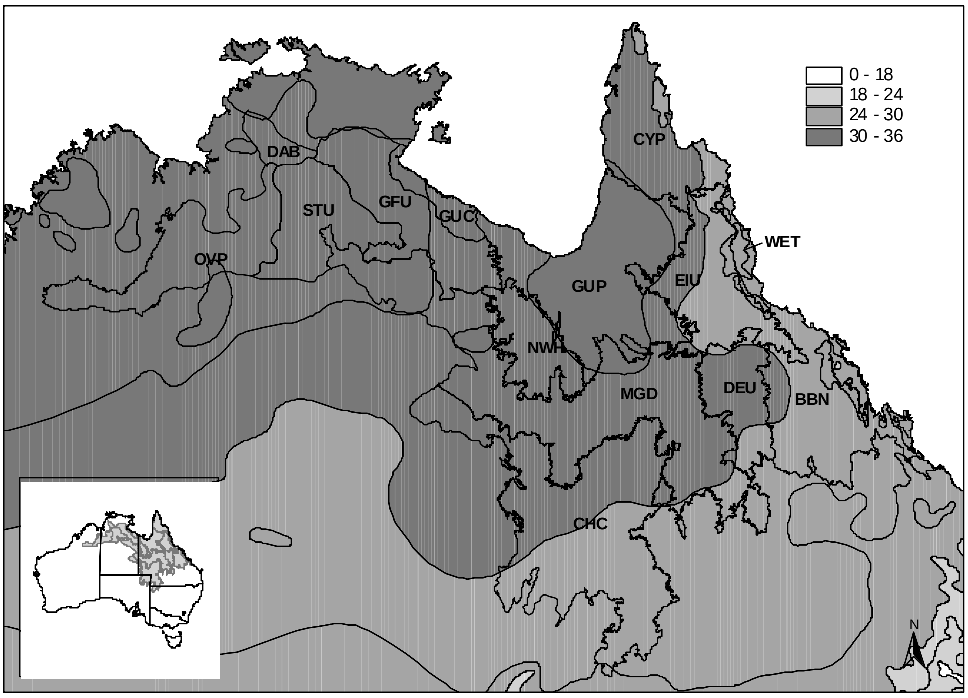


Figure 2.4 Mean annual minimum temperature for northern Australia with bioregion boundaries superimposed. Temperature in degrees Celsius. Data from Bureau of Meteorology and are based on the standard 30-year period 1961-1990.

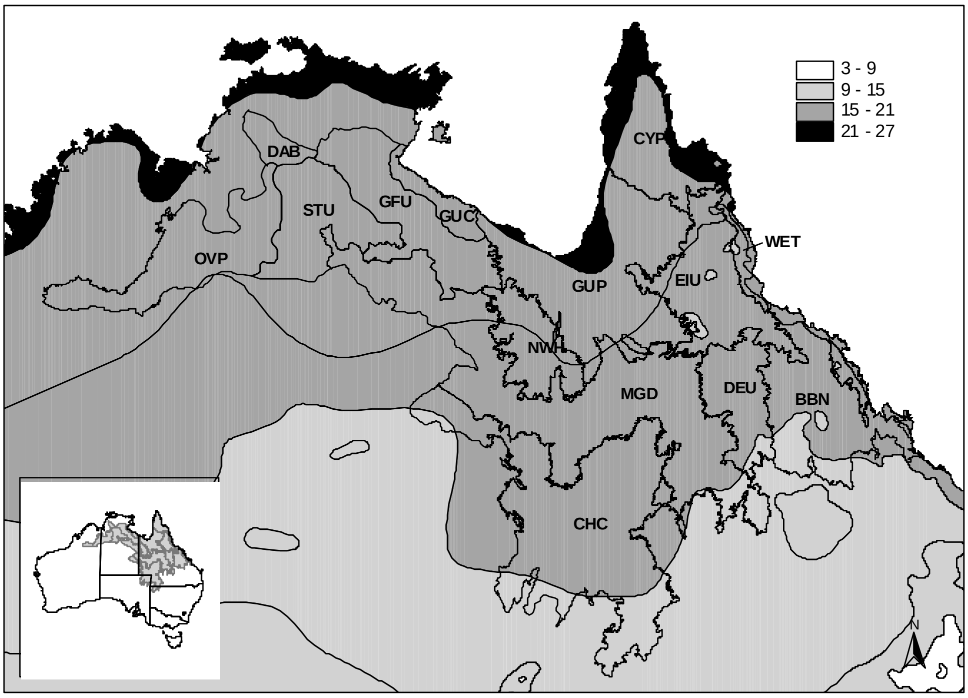


Figure 2.5 Digital elevation model for northern Australia with bioregion boundaries superimposed. Dark shading indicates higher elevation and lighter shading, lower. DEM data from www.auslig.gov.au/meta. Shading in 250m intervals. Black >1000m, white 0 m.

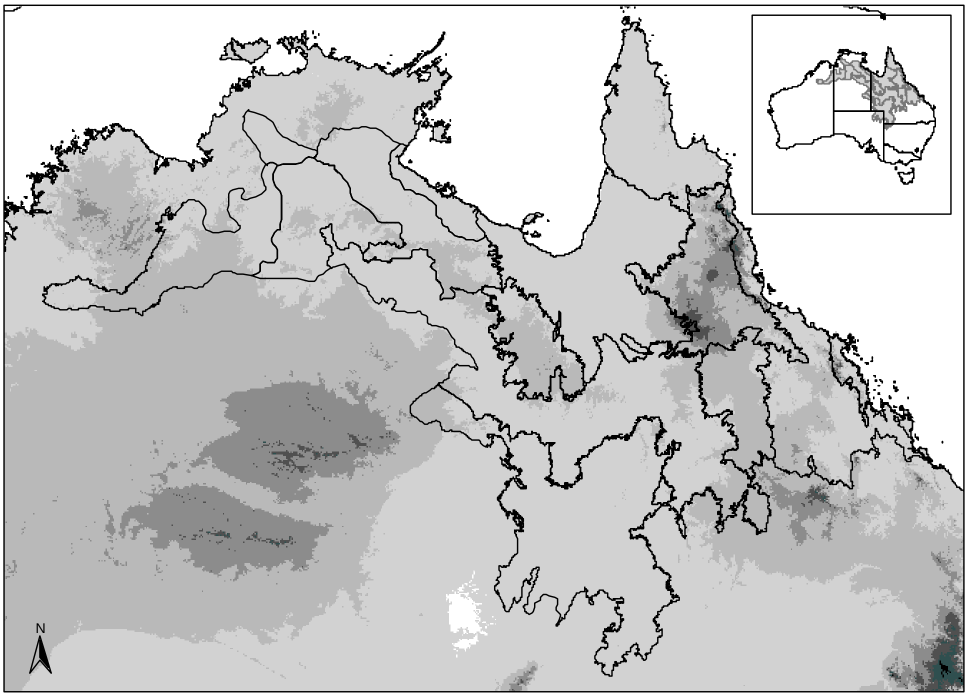


Figure 2.6 Major drainage systems, catchment boundaries and location of Great Dividing Range. Bioregion boundaries superimposed. Drainage data from, www.auslig.gov.au/meta.

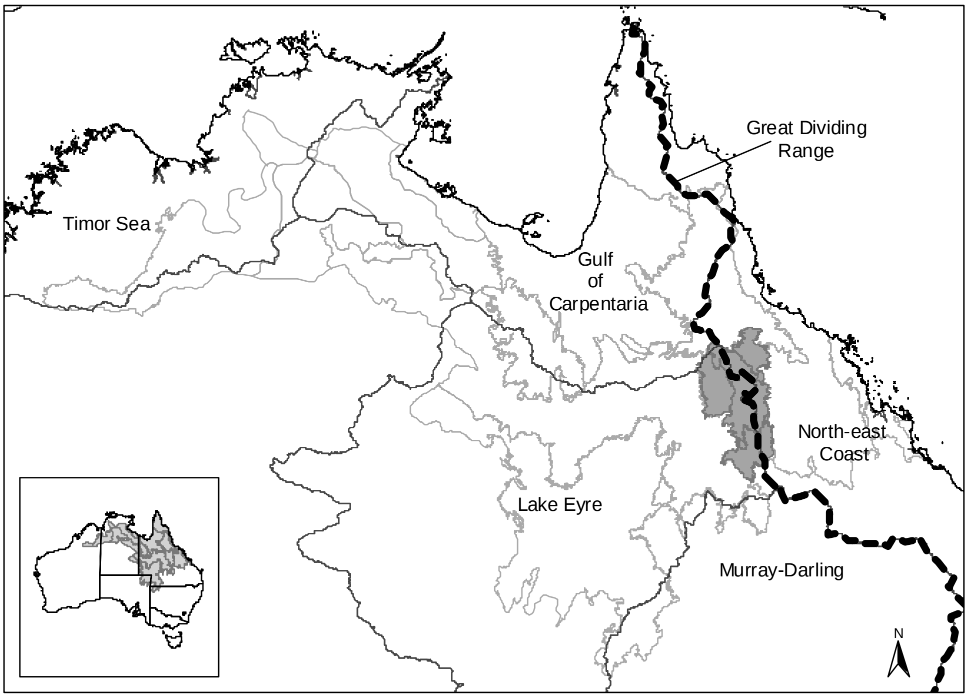


Figure 2.7 Major zoogeographical barriers in the Australian bird fauna as identified by Schodde and Mason (1980). Bioregion boundaries superimposed.

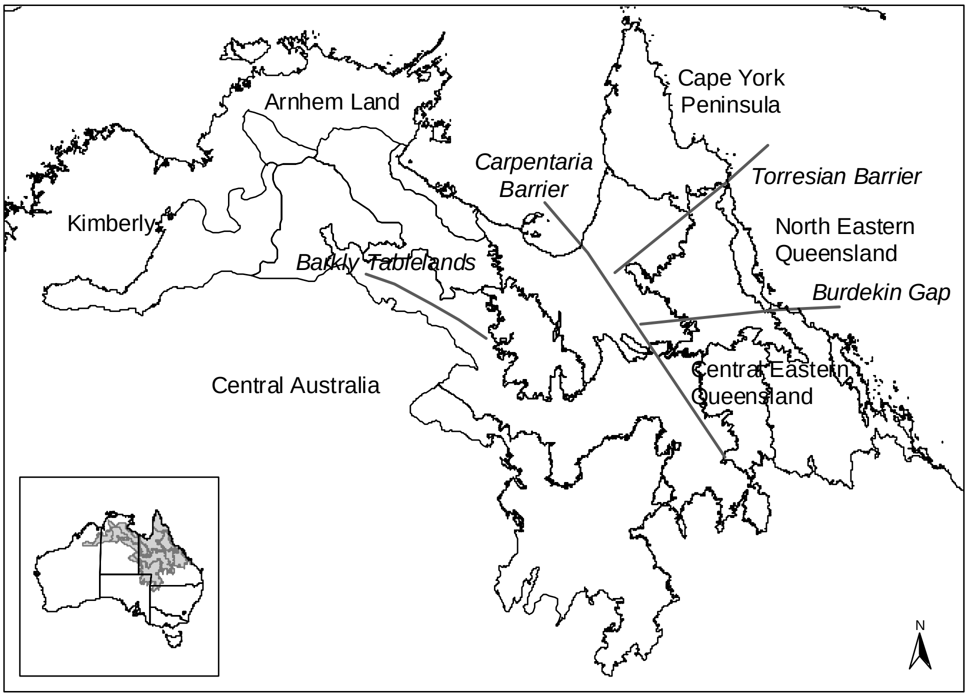
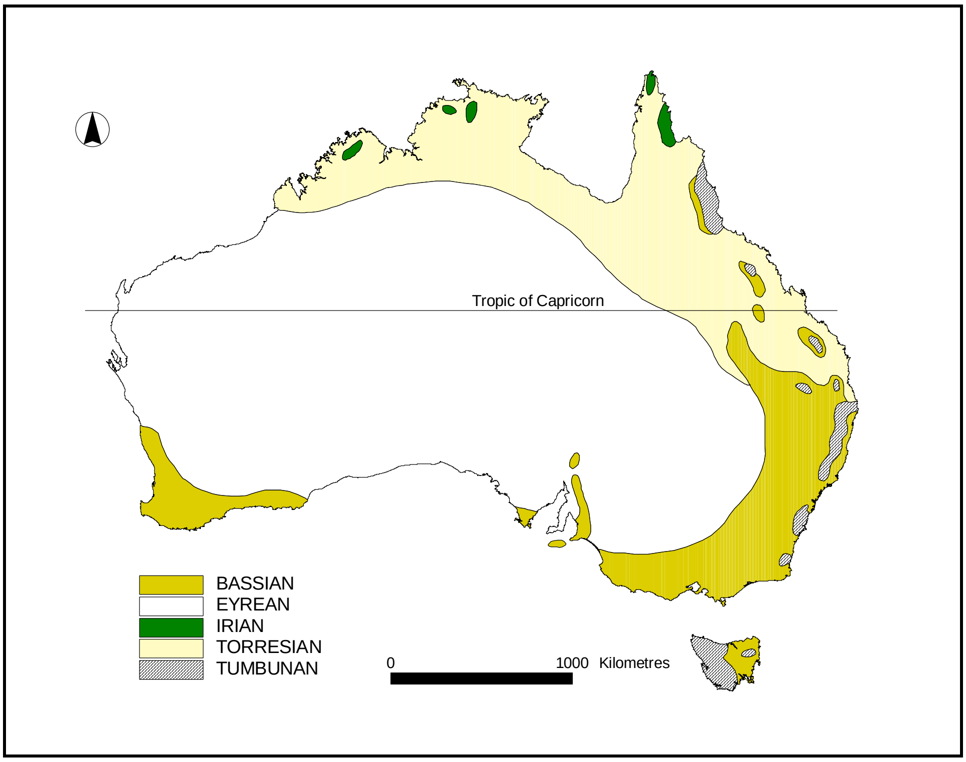


Figure 2.8 Major biotic regions of Australia adapted from Spencer (1896), Serventy and Whittal (1951), Burbidge (1960) and Schodde (1989).



Bioregion species composition

The pattern of composition of assemblages of birds, mammals, reptiles and amphibians across bioregions was examined with ordination on two axes using semi-strong hybrid multi-dimensional scaling (SSHMDS) derived from presence/absence data and modified Bray-Curtis (Czekanowski) association (dissimilarity) indices (Belbin 1991, 1995).

Weighted mean ordination scores were calculated for a sub-set of genera (amphibians, mammals and reptiles) and families (birds) to illustrate which were most influential in the ordination pattern. Weighted mean ordination scores are derived from the species richness of each genus or family in the bioregion multiplied by the ordination axis score for each bioregion, and averaged over the number of bioregions in which they were recorded. These groups are useful indicators of wholesale change in vertebrate composition and speciation, which in turn may reflect historical and biogeographic processes operating at the bioregional scale. For example, genera at the margin of the ordination may influence the location of a bioregion also found in this region of the ordination, as many species in that genera may be found predominantly in that bioregion. Conversely, genera central in the ordination space may be represented by one or a few species widespread in all bioregions, may occur mostly in the central bioregions, or may contain species that demonstrate clear pattern of species representation or replacement across bioregions.

Environmental vectors for bioregions

Principal axis correlation (PCC) was used to examine the relationship between geographic, climate and vegetation measures with the ordination pattern for all four vertebrate taxa. PCC is a multi-linear regression program designed to identify how a set of attributes can be fitted to an ordination space (Belbin 1991, 1995). The resultant output identifies the direction of best fit and a correlation coefficient that is a rough indicator of significance. A Monte Carlo randomisation technique (MCAO) using 500 permutations was undertaken to test the statistical significance of the correlation coefficient of each PCC vector (Belbin 1995). Only vectors significant at $P<0.001$ were listed, and almost exclusively the correlation coefficient was very high ($r>0.8$).

Environmental correlations with richness

Spearman Rank correlations were calculated between bioregion richness of birds, reptiles, mammals and amphibians, and the environmental characteristics of each bioregion identified previously. Landscape and climate features such as rainfall, altitude, area, geographic position, and dominant vegetation types, can influence or reflect historical biogeographic processes operating on a continental scale.

Bioregional species turnover (beta diversity)

Beta-diversity is the turnover of species between two sites, and is generally measured as a change in composition along environmental gradients. Jaccard's coefficient of similarity examines the proportion of species shared between two sites, and these were calculated for all between bioregion comparisons. This index is calculated as:

$$\beta_j = a/(a+b+c)$$

where a is the number of species present in both sites, b is the number present in bioregion 2 but not 1, and c the number present in bioregion 1 but not 2. This index varies from 0 if no species are shared to 1 if all species are shared.

Jaccard similarity indices were calculated for amphibians, birds, mammals and reptiles between all bioregions. Patterns of similarity or difference were examined via constellation diagrams for the four taxa, comparing all other bioregions to the Desert Uplands. By plotting the change between neighbouring bioregions for each taxon, the pattern of species turnover was identified for a series from the coast (Wet Tropics) to the arid inland (Channel Country) of Queensland. Species turnover between the subregions of the Desert Uplands and adjacent bioregions was also examined for all four vertebrate classes, in order to identify whether the geographic position of the subregions influences species composition.

Species replacement

The distribution of some species that illustrate the historical biogeographic processes that may have controlled the extant distribution of vertebrates in the Desert Uplands and across the coastal/inland environmental gradient in Queensland were examined in detail. These species included those either:

- endemic to the Desert Uplands region;
- pairs of closely related species that demonstrate replacement or divergence and the existence of vicariant features centred on the Desert Uplands across a broad Eyrean/Torresian boundary; and
- Eyrean and Torresian species in northern Australia with distributions that are disjunct or reach the edge of their range in the Desert Uplands.

Only species with adequate point locality and distribution data were considered, and only a small set of examples is illustrated. Sources of data included those listed in the methods section.

In regards to bird names in the subsequent chapters results and discussion, only common English names (Christidis and Boles 1994) will be used. This aids clarity and readability as common names are of standard usage for birds, whereas for other taxa, scientific names are more meaningful as agreed and workable common names are not available despite attempts to define these (Stanger *et al.* 1998). Full scientific names for birds are listed in Table 3.11 at the end of this chapter 3.

Results

Bioregion species richness

A total of 883 species (excluding wetland birds, marine mammals, bats and introduced species) were recorded from all bioregions combined, comprising 91 amphibians, 356 birds, 97 mammals and 339 reptiles (Table 2.1). All families and genera, including the number of species recorded in each bioregion for each, are presented in Table 2.5. The number of species unique to each bioregion is also listed. On a bioregion level, the maximum species richness was recorded for the Wet Tropics (WET) at 495 followed closely by the neighbouring Einasleigh Uplands (EIU) at 478 and Northern Brigalow Belt at 442. The reminder have between 250 and 350 species, the Desert Uplands (DEU) and Channel Country (CHC) at the higher end of the scale, and Ord-Victoria Plain (OVP), Gulf Coastal (GUC) and Sturt Plateau (STU) bioregions at the lower end. The Mitchell Grass Downs (MGD) was moderately species rich with 308.

The pattern for each vertebrate class follows a similar path to that for total vertebrate numbers for the bioregions. Some notable features include:

- the high number of amphibians in the near coastal bioregions such as the WET and EIU with a consistently low number in the other bioregions (20-27) except for the MGD and GUC which are especially species poor (19);
- high numbers of reptile species in both the WET and the more arid Queensland bioregions, but a lower tally (<100 spp) in most of the Northern Territory bioregions;
- exceptionally high mammal richness in the WET, EIU and BBN bioregions, easily surpassing a generally low number for all other bioregions (15-30 spp); and
- high bird species richness in coastal Qld bioregions, and a moderate and consistent richness for all other bioregions (150-200 spp) except for the large, but structurally simple MGD (<150 spp).

Table 2.1 Species richness for bioregions in north and central Queensland, running in a series from the coast (Wet Tropics) to the arid inland (Channel Country) incorporating the Desert Uplands, and including a contiguous series of tropical savannas bioregions from the Northern Territory. Data indicates total species richness and in parenthesis the number of species uniquely recorded in that bioregion in comparison with all other bioregions under consideration.

Bioregion	Code	Vertebrates	Amphibians	Birds	Reptiles	Mammals
Brigalow Belt North	BBN	442 (12)	27 (3)	278 (6)	96 (1)	41 (1)
Channel Country	CHC	343 (57)	22 (6)	163 (23)	132 (22)	26 (6)
Daly Basin	DAB	311 (9)	24 (1)	174	94 (6)	19
Desert Uplands	DEU	324 (4)	22	161	111 (4)	30
Einasleigh Uplands	EIU	478 (16)	37 (2)	249 (2)	135 (9)	57 (1)
Gulf Coastal	GUC	260 (5)	19	156 (3)	67 (2)	18
Gulf Fall Uplands	GFU	344 (5)	27 (1)	187 (1)	105 (3)	25
Mitchell Grass Downs	MGD	308 (10)	19 (1)	133	132 (9)	24
Ord-Victoria Plain	OVP	284 (10)	20	154 (1)	89 (6)	21
Sturt Plateau	STU	281 (4)	20	155 (1)	87 (3)	19
Wet Tropics	WET	495 (76)	51 (17)	246 (10)	136 (36)	62 (13)

Correlates of bioregional species richness

Twenty-two geographic, climate and vegetation variables were significantly related to variation in species richness. Many of these variables were highly inter-correlated and climate variables predominated. At a vertebrate class level (refer to Table 2.2):

- amphibian species richness was strongly correlated to presence of coastal communities consisting of rainforest, riparian and tall open forest, high altitude range and high yearly rainfall and high rainfall in the warmer periods;
- bird species richness was correlated with these same variables, except that altitude range was not significant and the area of littoral communities (mangroves, wetlands) was;
- mammal species richness was correlated with presence of east coastal forest communities such as rainforest, tall open forest and sub-humid open woodlands, and associated features of altitude and rainfall range, but also with temperature range and minimum longitude indicating the smaller peak of species diversity in more arid inland areas; and
- reptile richness was most strongly correlated with altitude range, presence of tall open forests and sub-humid tropical woodlands typical of EIU, BBN, WET and DEU bioregions, and with temperature range and heath-land/shrub-land communities, typical features on arid inland bioregions (MGD, CHC). In contrast to the patterns for other vertebrate classes, that for reptiles reflects the greater variety of bioregions with high reptile species numbers, rather than just a peak in wet coastal high altitude and high rainfall rainforest.

Table 2.2 Spearman rank correlation between bioregion species richness for vertebrates, amphibians, birds, mammals and reptiles, and a range of environmental variables representing geographic factors, climate and vegetation. Values in bold are significant at $p<0.05$.

Environmental variable	Code	Vertebrates	Amphibians	Birds	Mammals	Reptiles
Area (log)	area	-0.03	-0.20	-0.15	0.02	0.16
Latitude (max)	lat max	0.01	-0.22	-0.21	0.16	0.31
Latitude (min)	lat min	0.07	-0.14	-0.09	0.25	0.30
Latitude (range)	lat rng	0.19	-0.01	-0.04	0.28	0.40
Longitude (max)	long max	0.43	0.28	0.33	**0.51**	**0.50**
Longitude (min)	long min	0.48	0.37	0.44	**0.57**	0.44
Longitude (range)	long rng	-0.27	-0.41	-0.45	-0.22	-0.03
Altitude (max)	alt max	0.46	0.44	0.33	**0.60**	0.43

Environmental variable	Code	Vertebrates	Amphibians	Birds	Mammals	Reptiles
Altitude (min)	alt min	0.10	0.07	-0.02	0.14	0.22
Altitude (range)	alt rmg	**0.57**	**0.54**	0.45	**0.63**	**0.55**
Distance to coast	coast	**-0.51**	**-0.62**	**-0.67**	-0.42	-0.13
Mean rainfall warmest quarter	mrwq	**0.53**	**0.66**	**0.70**	0.43	0.19
Mean temp. wettest quarter	mtwq	**-0.66**	**-0.71**	**-0.72**	**-0.63**	-0.46
Annual temp. range	temp rng	**0.57**	0.40	0.33	**0.65**	**0.72**
Annual temp. mean	temp m	**-0.57**	-0.41	-0.40	**-0.69**	**-0.62**
Mean temp. driest quarter	mtdq	-0.16	0.04	0.01	-0.31	-0.35
Temp seasonality (CV)	temp cv	-0.43	-0.61	**-0.57**	-0.30	-0.13
Mean rainfall coldest quarter	mrcq	0.46	0.31	0.25	**0.60**	**0.55**
Rainfall range	rain rng	**0.63**	**0.69**	**0.61**	**0.51**	0.42
Rainfall mean	rain m	0.45	**0.62**	**0.63**	0.31	0.10
Rainfall seasonality (CV)	rain cv	-0.27	-0.09	-0.10	-0.37	-0.47
No. of broad vegetation groups	bvg	0.05	-0.02	-0.08	0.19	0.15
Acacia spp woodlands	aw	-0.14	-0.27	-0.18	-0.05	-0.06
Closed-forest communities	rf	**0.63**	**0.61**	**0.67**	**0.70**	0.42
Communities of the littoral zone	litt	0.40	0.42	**0.51**	0.33	0.07
Heathlands and closed shrublands	he/sh	0.47	0.40	0.30	0.47	**0.55**
Hummock grasslands	humm	**-0.54**	**-0.58**	**-0.70**	-0.39	-0.30
Monsoon mixed low woodlands	mlw	-0.37	-0.23	-0.25	-0.45	**-0.51**
Monsoon open woodlands	mow	0.05	0.28	0.24	-0.09	-0.25
Riparian forests and woodlands	ri	0.48	**0.63**	**0.68**	0.33	0.11
Sedge/herb/grasslands, lakes, lagoons	wetland	-0.20	-0.40	**-0.50**	-0.04	0.27
Tall open-forests	tof	**0.74**	**0.71**	**0.70**	**0.81**	**0.59**
Tussock grasslands	tuss	-0.46	**-0.64**	**-0.62**	-0.31	-0.15
Open-woodlands	ow	0.24	0.11	0.16	0.29	0.37
Sub-humid open woodlands	show	**0.58**	0.47	0.45	**0.71**	**0.63**

Assemblage compositions, environmental gradients and species patterns

Though the number of bioregions was moderately low (n=11), the ordination for each taxonomic class indicated some clear patterns in affiliation of species composition and possible biogeographic history (Figure 2.10-2.13). Accompanying environmental vectors identified some gradients of change that were predominantly climatic, and these reiterate those variables identified as significantly associated with species richness for each taxon. Only a subset of each taxon is illustrated (Figure 2.10-2.13) given the large number involved. Those chosen are representative of Australian vertebrates with both restricted and widespread distributions. Three patterns are most common:

- a strong affiliation of some genera to particular bioregions due to associated endemism or a high level of speciation (e.g. rainforest frogs);
- the universal distribution of some genera and their species, often indicated by a position in the centre of the ordination space (e.g. widespread birds); and

- genera that demonstrate species replacement across bioregions, reflecting biogeographic history and environmental association (e.g. *Pseudomys* spp), also often indicated by a position in the centre of the ordination space.

Amphibians

The ordination (stress = 0.14) indicates four broad groups of amphibian composition reflective of geographic position (Figure 2.10a):

- Northern Territory monsoonal tropical savanna group (STU, GFU, DAB, GUC, OVP), characterised by high mean temperatures and high rainfall seasonality;
- arid inland and treeless savannas (MGD, CHC) characterised by large area of *Acacia* woodlands and distance from the coast;
- north-eastern Queensland wet coastal (WET, EIU) characterised by high maximum altitude and high mean annual rainfall; and
- mid-eastern Queensland group (BBN and DEU) characterised by lower mean temperatures, lower rainfall seasonality, and intermediate measures of the other variables such as altitude and distance from coast.

Cophixalus, *Austrochaperina*, *Taudactylus*, *Mixophyes* and *Nyctimystes* are largely restricted to the WET and to a lesser extent the EIU bioregions, all species being endemic to east coastal rainforest areas (Figure 2.10b). Conversely *Cyclorana*, *Neobatrachus* and *Notaden* contribute to the MGD, CHC ordination position, and are most species rich in the central and more arid bioregions. *Cyclorana* is also represented by many species in the STU. *Uperoleia* were generally diverse in wet and near-coastal areas (WET, EIU and GFU), while *Crinia* was most species rich in the monsoon bioregions. The monospecific genus *Megistolotis* was only recorded in OVP, and *Litoria*, though represented by species in all bioregions, are most diverse and therefore most influential on the eastern and northern typically Torresian bioregions. The amphibian fauna of the DEU is only moderately diverse, with low representations of both wetter coastal and inland genera (*Litoria*, *Limnodynastes*, *Uperoleia*, *Pseudophryne*, *Crinia*, *Notaden* and *Cyclorana*).

Birds

In the ordination of bioregions by bird species composition (stress = 0.09) a pattern of four groups is also apparent. Most of the significant environmental gradients run along the first axis of changing altitude, temperature range and area of woodland. Four clusters are apparent (Figure 2.11a):

- Northern Territory monsoonal tropical savanna group (STU, GFU, DAB, GUC, OVP), characterised by high mean temperatures and area of monsoon open woodlands;
- a loose association of arid inland and treeless savannas (MGD, CHC) characterised again by large area of *Acacia* woodlands and distance from the coast, and lower rainfall, temperature and area of woodlands;
- a cluster of north-eastern Queensland coastal groups that this time includes the Brigalow Belt (WET, EIU, BBN) and characterised strongly by high altitude, a high temperature and rainfall range, and large areas of tall open forest and sub-humid woodlands; and
- the DEU, solitary and equidistant from the CHC, the wet east-coast group and the MGD, and characterised by intermediate area of *Acacia* and sub-humid woodland and intermediate rainfall and temperature ranges.

The position in the ordination of the three bird families Cacatuidae, Psittacidae and Meliphagidae was examined (Figure 2.11b-c). The parrots *Pezoporus, Neopsephotus, Northiella, Polytelis*, *Neophema* and honeyeater-allies *Epthianura* and *Ashbyia* are largely restricted to the CHC and to a lesser extent the MGD bioregions, all species predominantly endemic to arid inland areas. Conversely *Cyclopsitta, Glossopsitta, Alisterus* and *Trichoglossus* are most species rich in the WET, EIU and BBN with *Conopophila*, *Certhionyx* and *Psitteuteles* generally occurring in the monsoonal bioregions. There is clear suite of wetter coastal species distributed within the northern and eastern Torresian bioregions (*Platycercus, Philemon* and *Myzomela*), while others, though widespread, are more species-rich in the tall, eastern *Eucalyptus* forests (*Lichenostomus*). Some genera are centrally placed within the ordination due to the widespread distribution of one or two species (e.g. *Nymphicus*, *Calyptorhynchus, Lichmera*) or representation across many bioregions (e.g. *Melithreptus*). The DEU seems very much isolated between the wetter coast and inland bioregion associations, again located closest to the intermediate, widespread species, but influenced by a mix of Torresian and Eyrean birds.

Mammals

The ordination of bioregions by mammal species composition (stress 0.12) was comparable to that of the reptile and amphibian pattern but perhaps best identifies a correspondence to geographic location and sense of gradual species turnover. There is clear distinction between the northeast coast and the monsoon/inland bioregions. Three general clusters are apparent (Figure 2.12a):

- the northeast coast bioregions (WET, EIU, BBN and DEU), characterised by high altitude and annual temperature and rainfall range;
- the arid inland bioregions again (MGD, CHC), characterised by high temperature seasonality and area of *Acacia* woodland; and
- the Northern Territory tropical savanna bioregions, characterised by high mean temperatures, rainfall seasonality and area of monsoon forest.

The positioning in the ordination of two mammal families was examined: Dasyuridae and Muridae (Figure 2.12b-c). Generally dasyurids are more species rich and influential in central and Northern Territory bioregions, whereas the murids are diverse in the Queensland coastal and near-coastal bioregions. There are a few tropical endemic mammals (e.g. *Uromys* and *Pogonomys*) and species in this area associated with tall wet forests east of the Great Dividing Range (e.g. *Phascogale*, *Dasyurus*, *Antechinus*, *Rattus*, *Melomys*). Conversely there are fewer, but quite distinct genera associated with the CHC and MGD bioregions (e.g. *Notomys*, *Dasyuroides* and *Dasycercus*). Species that are central to the ordinations are diverse with similar species spread throughout many bioregions (e.g. *Pseudomys*, *Leggadina*, *Sminthopsis*, *Planigale*) or monotypic and widespread (e.g. *Hydromys*). *Pseudantechinus*, *Ningaui* and *Zyzomys* all strongly affiliate with the Northern Territory bioregions. The Desert Uplands is characterised by association with widespread species such as *Pseudomys*, *Sminthopsis* and *Planigale*.

Reptiles

The ordination of bioregions by reptile composition (stress =0.14) was remarkably similar in pattern to amphibians. Some patterning of groups was apparent (Figure 2.13a):

- two pairs of Queensland bioregions, (WET, EIU and BBN, DEU) the former characterised by high annual rainfall and altitude range, the latter more so by temperature range and area of sub-humid woodlands;
- a group of monsoon savanna bioregions characterised by the area of monsoon tropical forest, high annual and wet season temperatures; and
- the arid inland bioregions again, the distance from coast, area of *Acacia* woodlands and low altitude and rainfall being characteristic.

The positioning in the ordination of three reptile families were examined: Scincidae, Elapidae and Colubridae (Figure 2.13b-c). All families are extremely species rich and diverse, and for both the snake and skink fauna there are a large number of genera that are centrally placed within the ordination due to the widespread distribution of one or two species (e.g. *Boiga*, *Oxyuranus*, *Cryptoblepharus*, *Proablepharus*, *Tiliqua*, *Tropidonophis*, *Pseudechis*). Others are species rich and have species representation across many bioregions (e.g. *Furina*, *Rhinoplocephalus*, *Demansia*, *Menetia* and *Morethia*). *Ctenotus*, *Notechis* and *Pseudonaja* are most diverse in CHC and MGD, whereas *Carlia*, *Saproscincus*, *Lygisaurus*, *Lampropholis* are the most diverse in the WET and EIU). *Myron*, *Fordonia*, *Cerberus* are monospecific reptile genera restricted to the monsoon tropical bioregions, as were *Tropidechis*, *Gnypetoscincus*, *Techmarscincus* and *Calyptotis* to the north-east coast. There is a suite of wetter coastal species distributed within the Torresian bioregions (*Dendrelaphis*, *Stegonotus* and *Glaphyromorphus*) and others with greater inland or Eyrean affiliation (*Simoselaps*, *Suta* and *Egernia*). The DEU is characterised by association with widespread or highly speciated genera, with no relationship to any coastal or inland groups that were endemic. There is however a notable diversity of *Lerista* in the DEU equable to the BBN and MGD.

Figure 2.10 (a) Ordination in two dimensions of all bioregions by species composition for amphibians, indicating the significant environmental vectors (all r >0.7, p <0.001). Variables highly inter-correlated with those on the plot are not shown. Bioregions codes in Table 2.1.

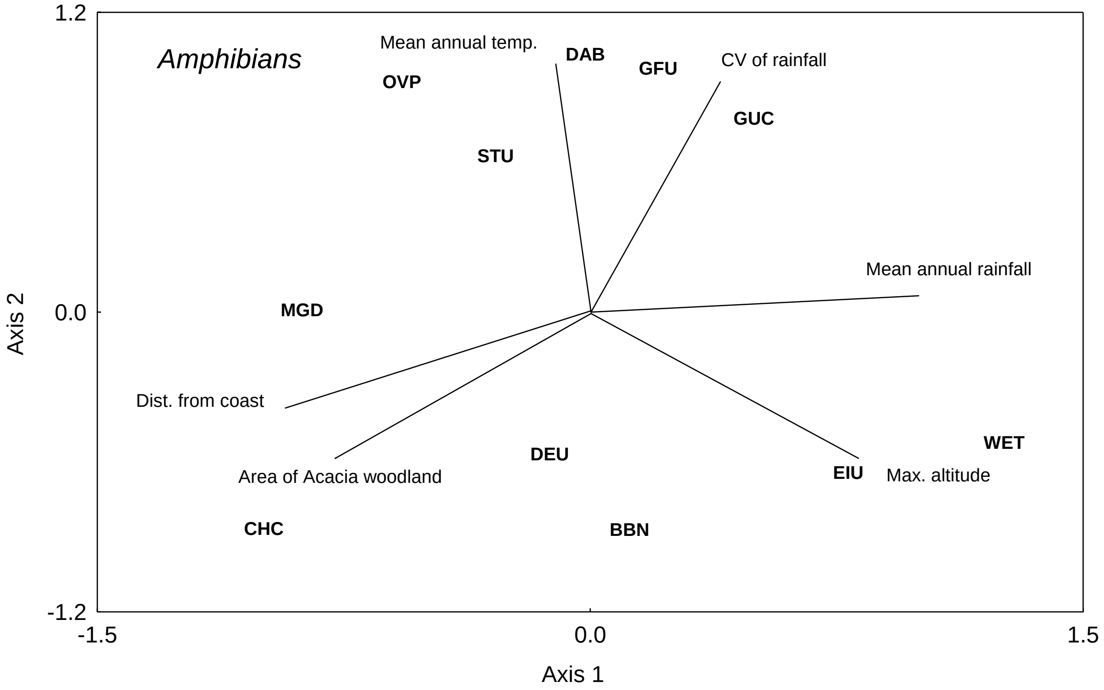


Figure 2.10 (b) Weighted mean ordination score for all amphibian genera. Families, genera and number of species (in parenthesis) include: Hylidae, *Cyclorana* (13), *Litoria* (30), *Nyctimystes* (1), Microhylidae, *Austrochaperina* (3), *Cophixalus* (10), Myobatrachidae, *Crinia* (3), *Limnodynastes* (8), *Megistolotis* (1), *Mixophyes* (1), *Neobatrachus* (2), *Notaden* (3), *Pseudophryne* (3), *Taudactylus* (2), *Uperoleia* (10), Ranidae, *Rana* (1).

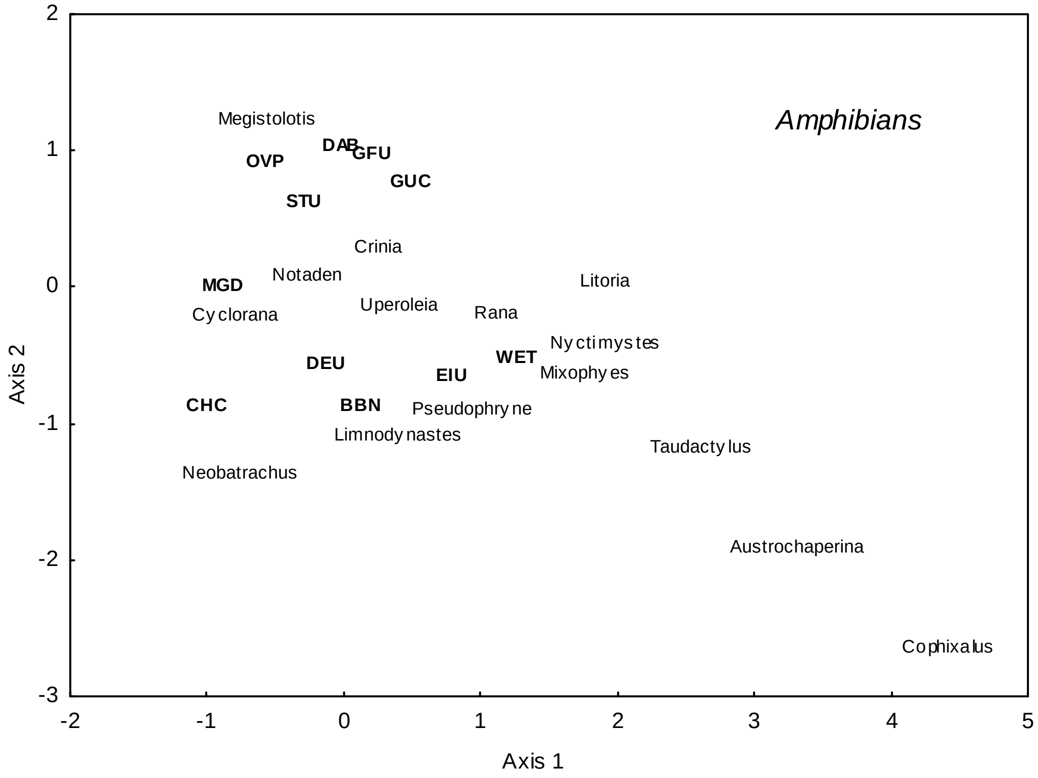


Figure 2.11 (a) Ordination in two dimensions of all bioregions by species composition for birds, indicating the significant environmental vectors (all r >0.7, p <0.001). Variables highly inter-correlated with those on the plot are not shown. Bioregions codes in Table 2.1.

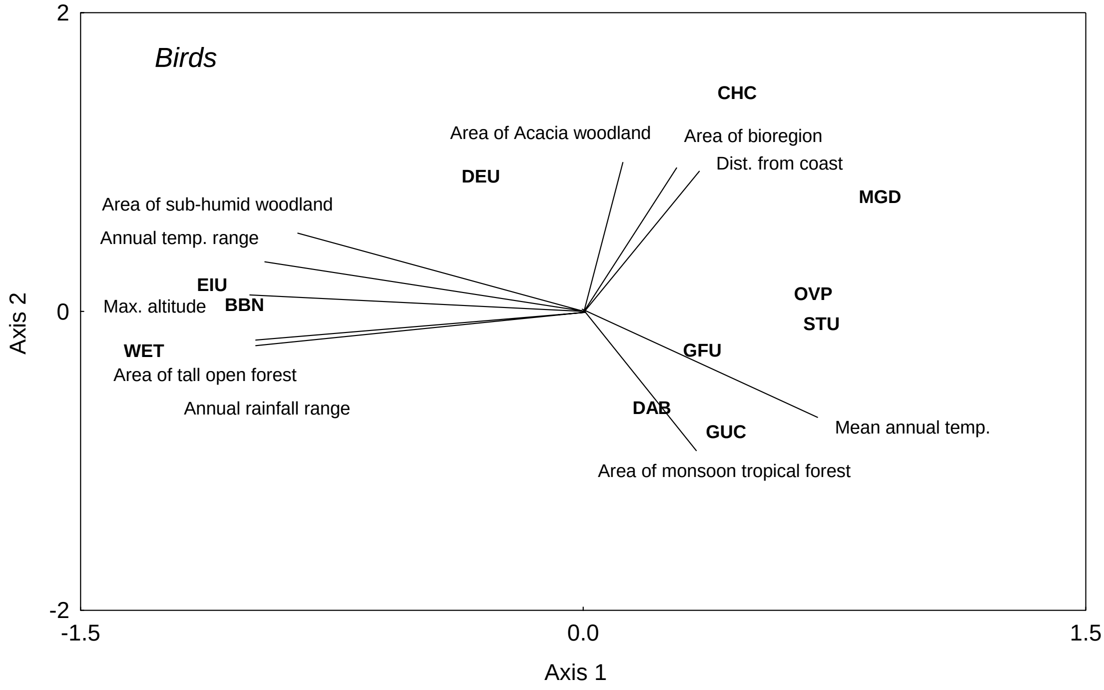


Figure 2.11 (b) Weighted mean ordination score for Cacatuidae and Psittacidae. Families, genera and number of species (in parenthesis) include: Cacatuidae, *Cacatua* (4), *Calyptorhynchus* (2), *Nymphicus* (1), Psittacidae, *Alisterus* (1), *Aprosmictus* (1), *Barnardius* (1), *Cyclopsitta* (1), *Glossopsitta* (1), *Melopsittacus* (1), *Neophema* (2), *Neopsephotus* (1), *Northiella* (1), *Pezoporus* (1), *Platycercus* (3), *Polytelis* (1), *Psephotus* (4), *Psitteuteles* (1), *Trichoglossus* (2).

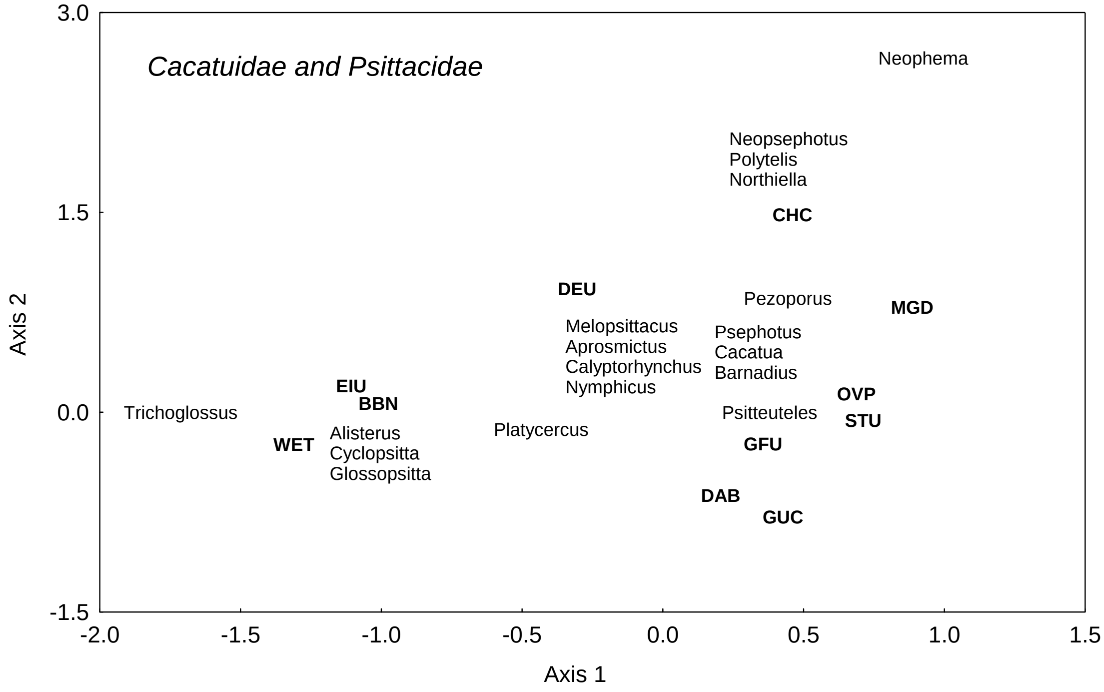


Figure 2.11 (c) Weighted mean ordination score for Meliphagidae. Families, genera and number of species (in parenthesis) include: Meliphagidae, *Acanthagenys* (1), *Acanthorhynchus* (1), *Ashbyia* (1), *Certhionyx* (3), *Conopophila* (3), *Entomyzon* (1), *Epthianura* (4), *Grantiella* (1), *Lichenostomus* (13), *Lichmera* (1), *Manorina* (2), *Meliphaga* (4), *Melithreptus* (4), *Myzomela* (3), *Philemon* (4), *Phylidonyris* (2), *Plectorhyncha* (1), *Plegadis* (1), *Ramsayornis* (2), *Trichodere* (1), *Xanthotis*, (1).

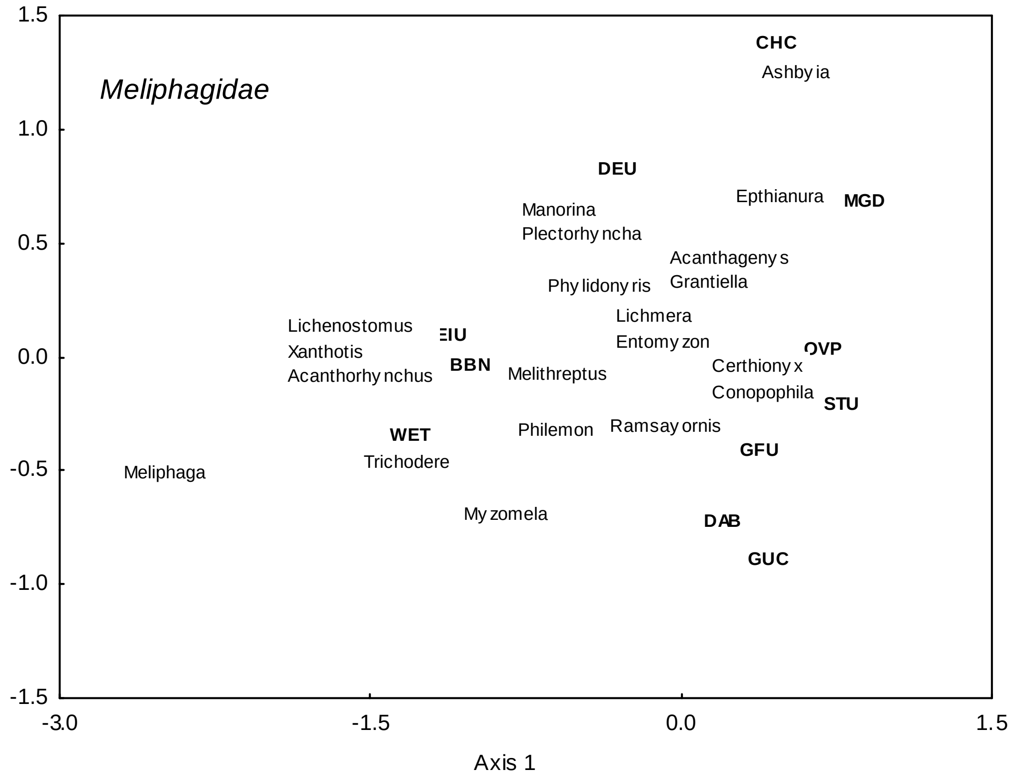


Figure 2.12 (a) Ordination in two dimensions of all bioregions by species composition for mammals, indicating the significant environmental vectors (all r >0.7, p <0.001). Variables highly inter-correlated with those on the plot are not shown. Bioregions codes in Table 2.1.

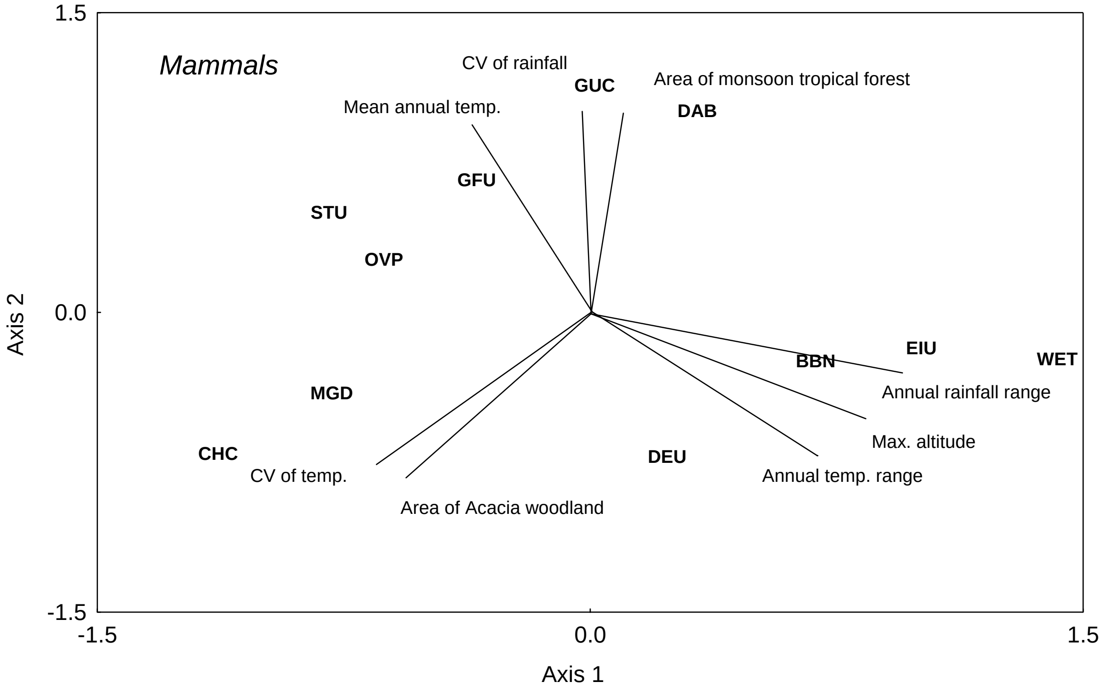


Figure 2.12 (b) Weighted mean ordination score for Dasyuridae. Families, genera and number of species (in parenthesis) include: *Antechinomys* (1), *Antechinus* (3), *Dasycercus* (2), *Dasyuroides* (1), *Dasyurus* (2), *Ningaui* (1), *Phascogale* (1), *Planigale* (4), *Pseudantechinus* (2), *Sminthopsis* (8).

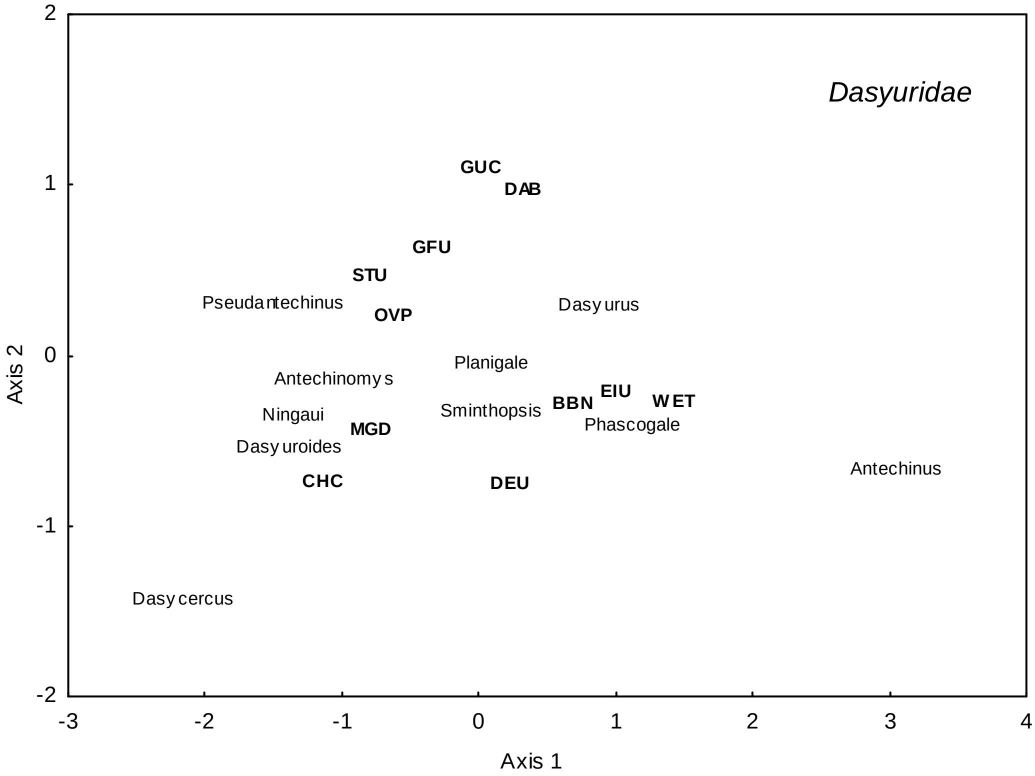


Figure 2.12 (c) Weighted mean ordination score for Muridae. Families, genera and number of species (in parenthesis) include: *Hydromys* (1), *Leggadina* (2), *Melomys* (2), *Mesembriomys* (1), *Notomys* (4), *Pogonomys* (1), *Pseudomys* (7), *Rattus* (8), *Uromys* (1), *Zyzomys* (2).

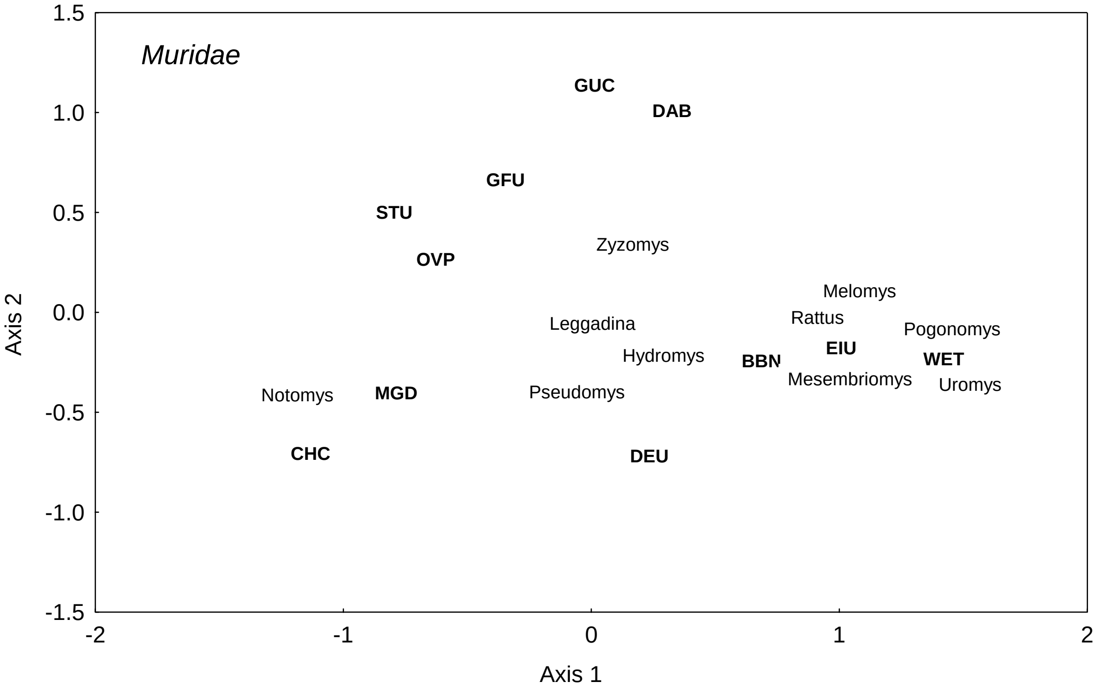


Figure 2.13 (a) Ordination in two dimensions of all bioregions by species composition for reptiles, indicating the significant environmental vectors (all r >0.7, p <0.001). Variables highly inter-correlated with those on the plot are not shown. Bioregions codes in Table 2.1.

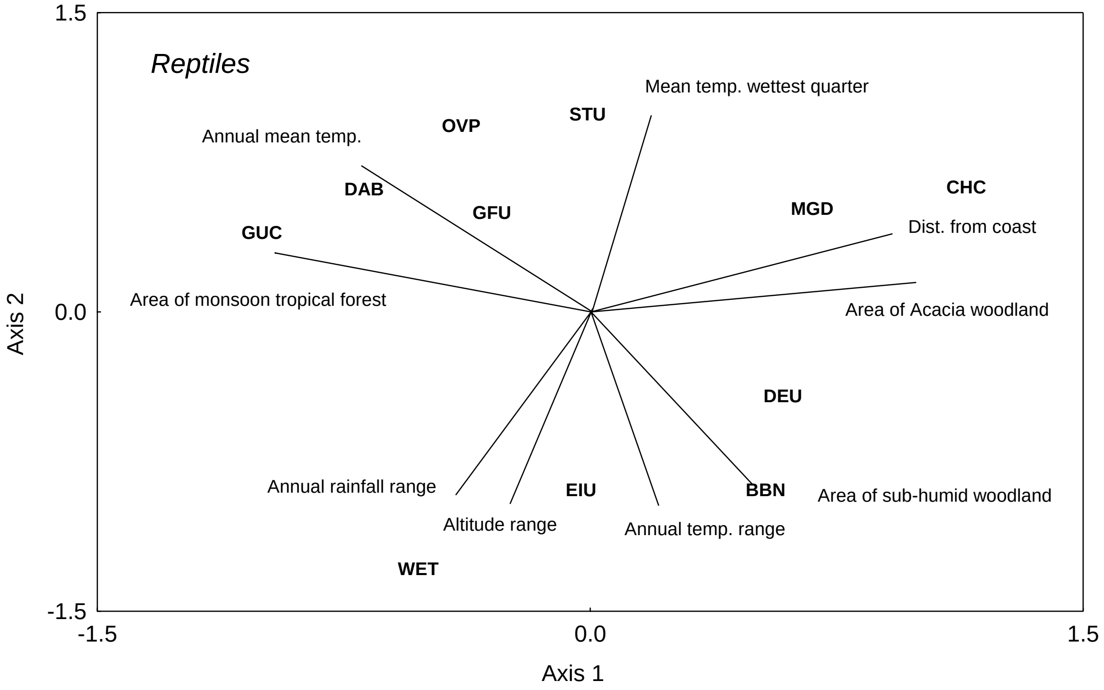


Figure 2.13 (b) Weighted mean ordination score for Scincidae. Families, genera and number of species (in parenthesis) include: *Anomalopus* (1), *Calyptotis* (1), *Carlia* (16), *Coeranoscincus* (1), *Cryptoblepharus* (5), *Ctenotus* (43), *Cyclodomorphus* (3), *Egernia* (6), *Eremiascincus* (2), *Eulamprus* (6), *Glaphyromorphus* (11), *Gnypetoscincus* (1), *Lampropholis* (5), *Lerista* (21), *Lygisaurus* (6), *Menetia* (5), *Morethia* (5), *Notoscincus* (1), *Proablepharus* (2), *Saproscincus* (6), *Techmarscincus* (1), *Tiliqua* (2), *Trachydosaurus* (1).

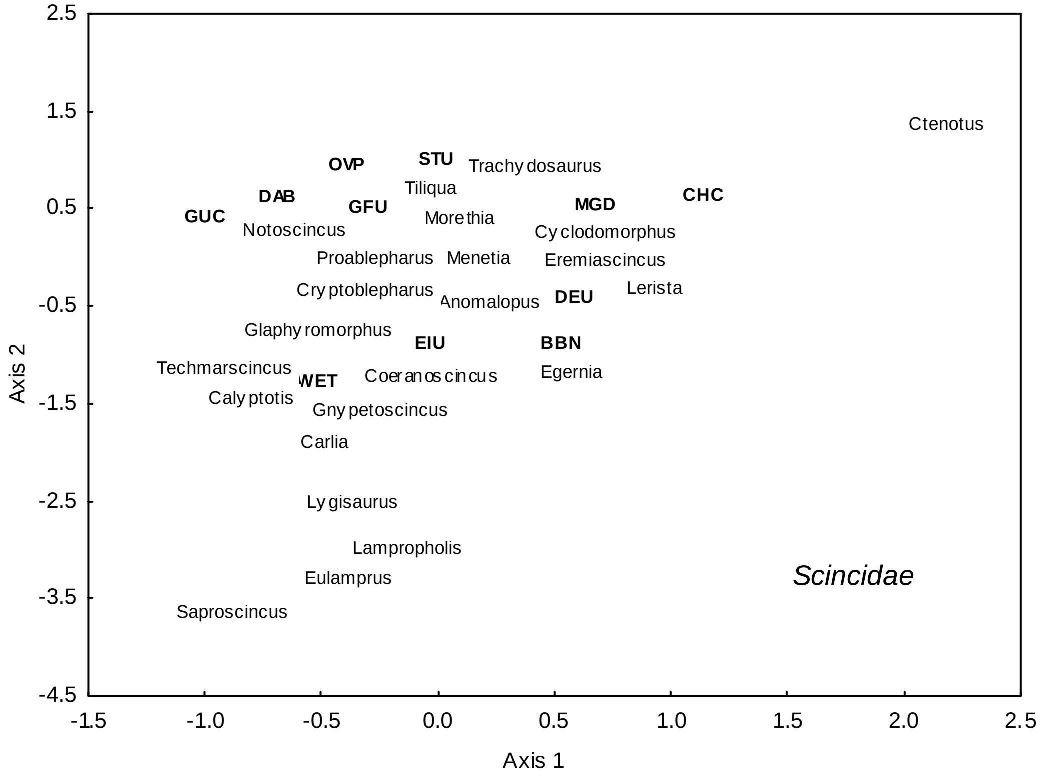


Figure 2.13 (c) Weighted mean ordination score for Colubridae and Elapidae. Families, genera and number of species (in parenthesis) include: Colubridae, *Boiga* (1), *Cerberus* (1), *Dendrelaphis* (2), *Myron* (1), *Stegonotus* (1), *Tropidonophis* (3), Elapidae, *Acanthophis* (3), *Cacophis* (2), *Demansia* (6), *Denisonia* (2), *Fordonia* (1), *Furina* (4), *Hemiaspis* (2), *Hoplocephalus* (1), *Notechis* (1), *Oxyuranus* (2), *Pseudechis* (3), *Pseudonaja* (5), *Rhinoplocephalus* (4), *Simoselaps* (6), *Suta* (3), *Tropidechis* (1), *Vermicella* (2).

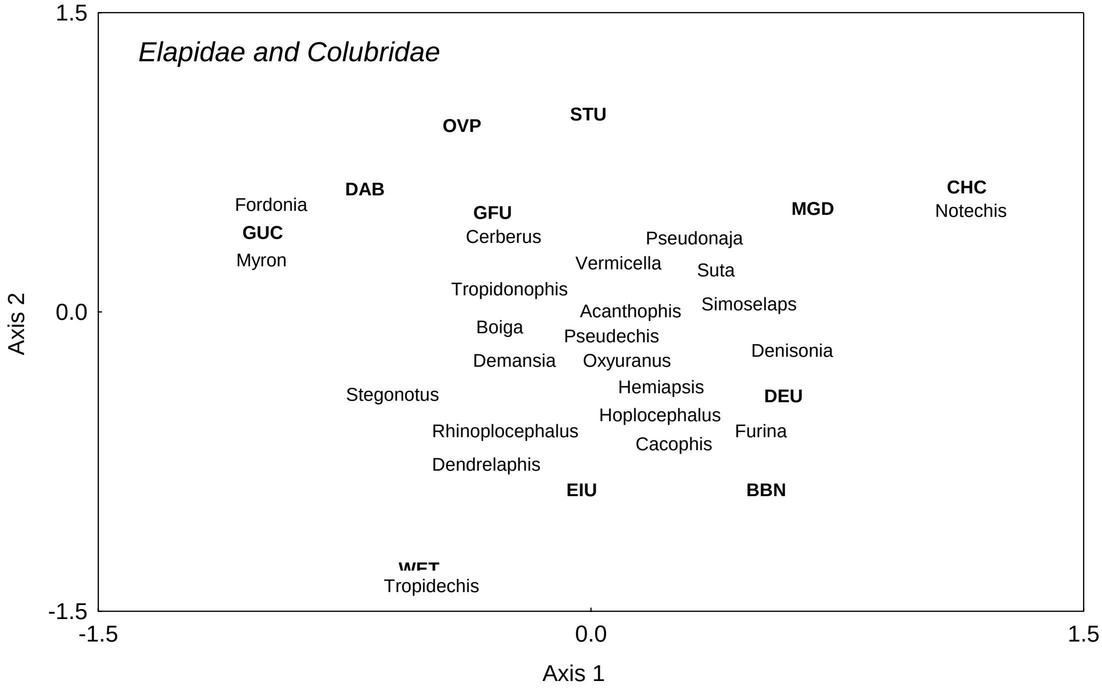


Table 2.3 Average scores for all significantly correlated environmental variables identified in the ordinations (Figures 2.5-2.8). Definition of codes for vectors in Table 2.2. Data in bold are the maximum values and those underlined are the minimum values.

Bioregion	alt rng	alt max	area	coast	tof	show	aw	mow
BBN	750	800	11.8	143	3.5	48.8	24.8	0.4
CHC	210	260	25.6	**783**	0	1.3	**30.2**	0
DAB	300	300	1.8	156	0	0	0	14.3
DEU	550	750	6.9	304	0.1	**74.4**	15.9	2.6
EIU	950	1200	10.1	141	3.4	68.4	2.3	1.5
GFU	200	200	9.5	150	0	0	3.3	**63.4**
GUC	200	200	2.2	38	0	0	0	13
MGD	250	360	**29.1**	459	0	0.4	19.3	2.2
OVP	500	500	6	210	0	0	0.3	48.9
STU	200	400	8.3	276	0	0	23.8	41.3
WET	**1550**	**1600**	1.7	22	**20.1**	5.2	0	0
Bioregion	rain m	rain cv	rain rng	temp m	temp cv	temp rng	mtwq	
BBN	674	69.8	1710	21.9	1.5	6.7	26.7	
CHC	227	65.8	294	22.6	**2.1**	3.6	29.4	
DAB	1023	114.9	547	**26.4**	1	1.6	28.4	
DEU	521	75.1	294	22.5	1.6	3.4	27.5	
EIU	761	108	1894	22.6	1.2	9.1	25.9	
GFU	689	117	623	25.9	1.3	3.4	29.1	
GUC	832	**122.3**	325	26.1	1.2	2.5	28.9	
MGD	370	86.5	467	23.8	1.8	6.8	29.3	
OVP	578	115.7	481	26.1	1.4	2.7	**29.5**	
STU	625	118.7	462	26	1.3	2.1	29.4	
WET	**2135**	89.2	**6554**	22.2	1	**9.3**	24.9	

Bioregional species turnover

The pattern of species turnover across bioregions was examined using Jaccard indices. Comparisons of the DEU with all other bioregions are illustrated with constellation diagrams (Figure 2.14 a-d). The most notable features of the DEU fauna relative to that of other bioregions for each of the four major taxonomic groups were:

- amphibian composition was least similar to the WET and EIU (<0.4), and most similar to the BBN and the arc of northern tropical savanna bioregions (>0.7). There was intermediate similarity with the MGD and CHC both approximately 0.5;
- bird composition remained remarkably stable across all comparisons, never declining below 0.62 (GUC) or increasing beyond 0.73 (EIU);
- mammal composition was most clearly similar to the EIU (0.8), WET (0.64) and BBN (0.68), and unlike the remaining bioregions (all <0.45); and
- reptile composition, as with birds, was also extraordinarily stable, the best comparisons between the EIU and BBN (both 0.75), but never less than 0.63 (WET).

As a further examination of the pattern of species turnover, two series of Queensland bioregions were graphed (Figure 2.15) representing the change in composition as one moves away further from the coast (WET to CHC) or further from the arid inland (CHC to WET). The progressive magnitude of change for each indicates there is a rapid turnover, particularly as the sequence passes through the DEU. For the WET sequence, bird and reptile composition is similar in the neighbouring EIU and BBN bioregions, with a marked decline through the DEU. The comparisons are moderately high and stable with the inland bioregions (SI~0.5, CHC, MGD). Conversely amphibian and mammal composition declines consistently and rapidly the further one moves from the wet tropical coast. For the CHC sequence, the pattern is similar though reversed, though the similarity between nearest neighbours declines more rapidly (CHC-MDG-DEU), and differences in amphibian composition between the CHC and the DEU, MGD and BBN consistent. In both cases what is most notable is the general stability in the reptile and bird composition (SI~0.5) from one end of the gradient to the other, and that the turnover along each axis is greatest for mammals and amphibians.

Figure 2.14 Constellation diagrams indicating similarity of the native fauna of the Desert Uplands bioregion to adjacent Queensland bioregions, and bioregions in the semi-arid tropical savannas in the Northern Territory. Similarity values are represented by the thickness of the connecting lines, the font size being proportional to the similarity (i.e. 0.3 = 3 point).

Figure 2.14 (a) Constellation diagram for amphibians.

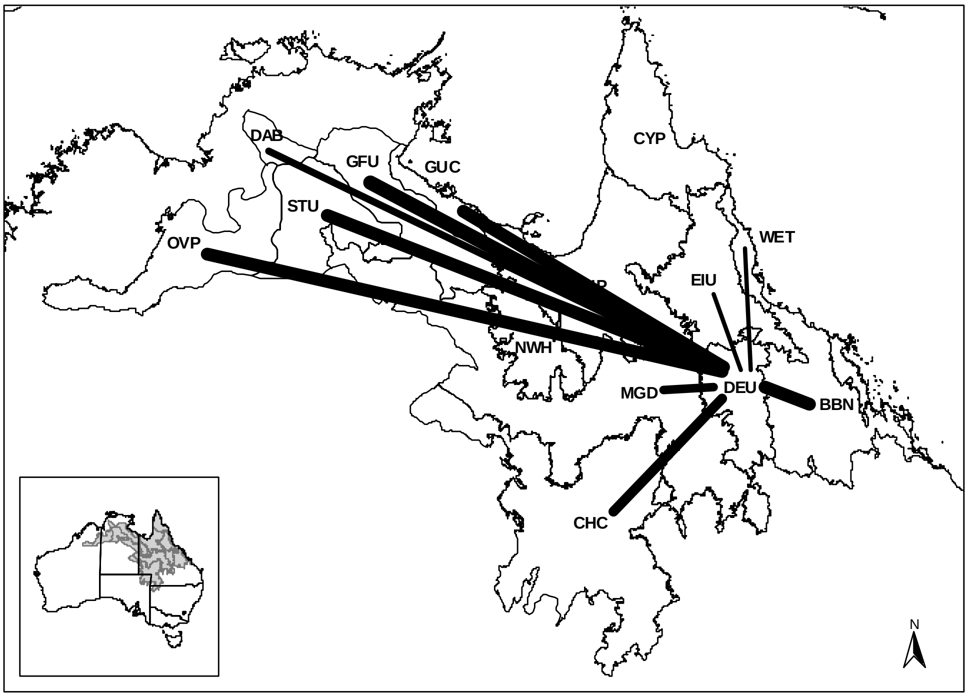


Figure 2.14 (b) Constellation diagram for birds.

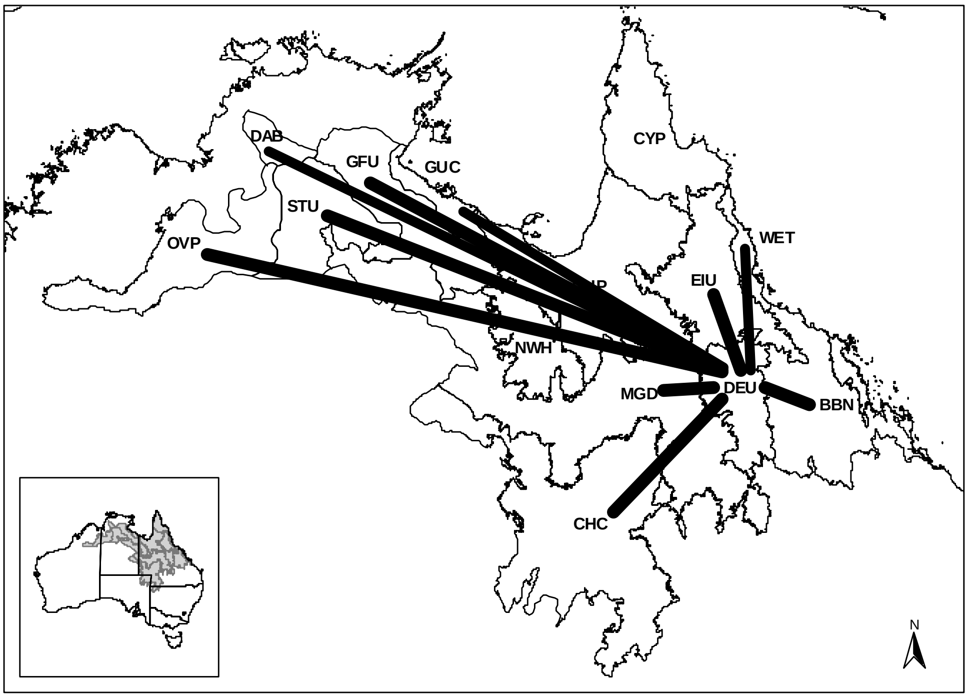


Figure 2.14 (c) Constellation diagram for mammals.

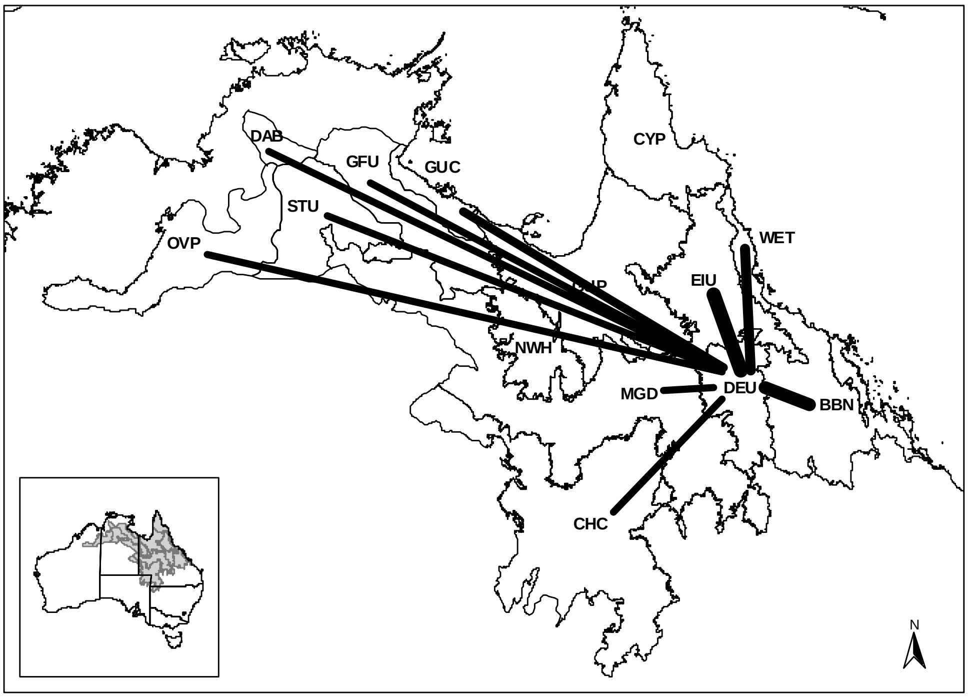


Figure 2.14 (d) Constellation diagram for reptiles.

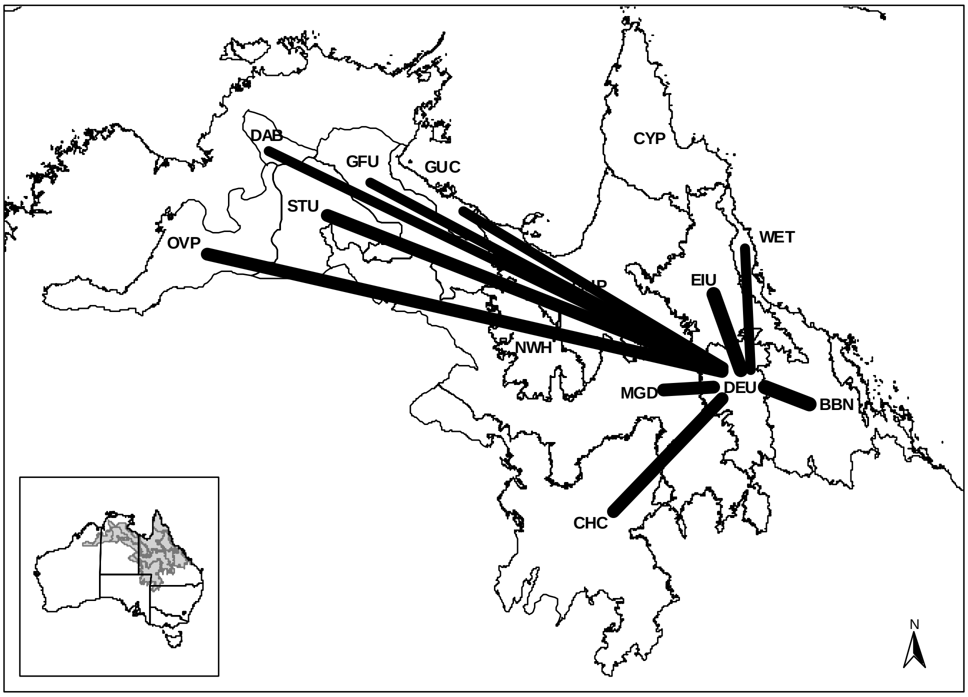
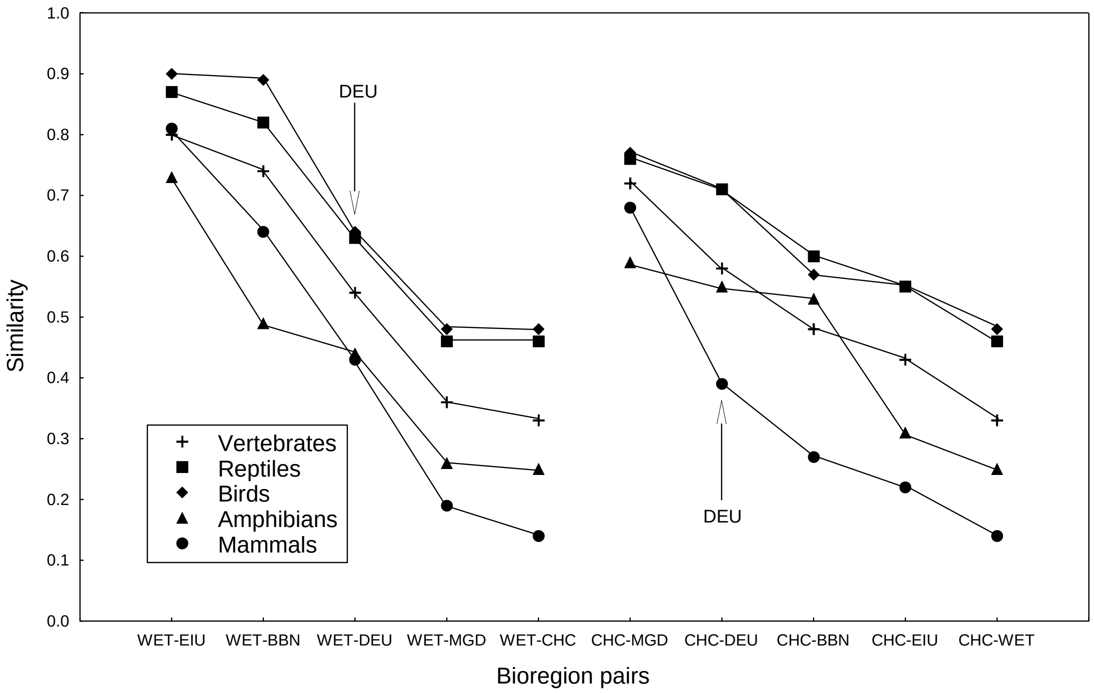


Figure 2.15 Comparisons of species turnover in a sequence of the Queensland coast (WET) to the inland (CHC), examining the magnitude of change, progressively from the coast to inland and visa versa. Patterns for vertebrates, amphibians, birds, mammals and reptiles considered.



Relationships of Desert Uplands, sub-regions and neighbouring bioregions

Patterns of compositional similarity between the Desert Uplands, its subregions and neighbouring bioregions were examined. As may be expected, the highest degree of similarity was between the Desert Uplands and the Subregions themselves, implying a reasonable level of internal consistency within the Desert Uplands (Table 2.4):

- for birds the similarity indices were high (>0.79), regardless of whether the sub-regions were adjacent or not;
- a like pattern was identified for reptiles (all > 0.77);
- mammal correspondence was less consistent, with Subregion 2 and Subregion 3 being most similar (>0.8) indicating that these two subregions reflect the majority of mammal richness in the bioregion. For the other pairs of subregional comparisons SIs were all <0.75, regardless of position; and
- SIs for amphibians were all <0.8, except for the entire Desert Uplands bioregion and Subregion 2 (0.9) suggesting that the amphibian composition varied somewhat

across the bioregion and that the subregion Subregion 2 composition accounted for the majority of the frog species for the bioregion.

Comparisons with neighbouring bioregions indicated moderate to low similarity with all scores for all taxa (SI<0.72). This shows that there is generally cohesiveness within the subregions of the Desert Uplands - each being more similar to each other, than they are to adjacent bioregions.

Table 2.4 Jaccard coefficient of similarity for species composition for comparisons between Desert Uplands bioregion (DEU), subregion (DEU1-4) and directly adjacent bioregions, the Brigalow Belt North (BBN), the Einasleigh Uplands (EIU) and the Mitchell Grass Downs (MGD). Bold indicates a similarity of >0.8, normal number indicate a similarity of 0.6-0.8 and italic numbers indicate a similarity of <0.6. Grey cells identify bioregions and sub-regions that share a boundary.

Table 2.4 (a) Amphibians (bottom left) and birds (top right).

	BBN	DEU	DEU1	DEU2	DEU3	DEU4	EIU	MGD
BBN		0.72	*0.59*	0.65	0.65	*0.55*	**0.93**	*0.57*
DEU	0.73		**0.84**	**0.93**	**0.91**	**0.80**	0.73	0.71
DEU1	*0.47*	0.67		**0.88**	**0.87**	**0.82**	0.62	0.70
DEU2	0.67	**0.90**	0.78		**0.86**	0.79	0.68	0.72
DEU3	0.60	0.74	0.76	0.71		**0.81**	0.70	0.70
DEU4	0.62	0.71	0.74	0.60	0.72		*0.58*	0.61
EIU	0.63	0.64	*0.53*	*0.58*	0.64	*0.41*		*0.56*
MGD	*0.43*	*0.59*	0.63	*0.59*	*0.55*	*0.45*	*0.36*	

Table 2.4 (b) Reptiles (bottom left) and mammals (top right).

(b)	BBN	DEU	DEU1	DEU2	DEU3	DEU4	EIU	MGD
BBN		0.68	*0.48*	0.63	0.65	*0.48*	**0.80**	*0.40*
DEU	0.75		0.72	**0.87**	**0.82**	0.60	0.60	*0.52*
DEU1	0.60	**0.82**		0.60	0.68	0.73	*0.38*	0.68
DEU2	0.69	**0.93**	**0.85**		**0.82**	0.67	*0.55*	*0.38*
DEU3	0.68	**0.90**	**0.84**	**0.86**		0.65	*0.54*	*0.44*
DEU4	*0.59*	0.79	**0.80**	0.77	**0.80**		*0.37*	*0.49*
EIU	**0.89**	0.75	0.61	0.70	0.71	*0.58*		*0.32*
MGD	*0.58*	0.69	0.71	0.71	0.69	*0.58*	*0.56*	

Species patterns

Examination of the Queensland-wide distribution of species recorded in the Desert Uplands bioregion indicates that there are a number of distribution patterns that reflect the zoogeographic features in this broad area. A similar pattern of turnover or distribution may occur in the western Einasleigh Uplands, Gulf Plains and Northwest Highlands, however adequate locality data were not available for these bioregions and they were not the focus of this study. Species-pairs generally include a more typically coastal Torresian/Bassian species and a more typically Eyrean species, that overlap in distribution (turnover) either in or near the Desert Uplands Bioregion. A large number of cases exist, however only a few representative examples are listed and illustrated.

Species-pairs whose distribution data suggests a degree of replacement of one species by another within the DEU : *Uperoleia lithomoda* and *U. littlejohni* (Figure 2.16), *Malurus leucopterus* and *M. melanocephalus*, *Diplodactylus ciliaris* and *D. williamsi* (Figure 2.18), *Gehyra dubia* and *G. variegata* (Figure 2.19), *Antaresia stimsoni* and *A. maculosa* (Figure 2.20), Narrow-nosed Planigale *Planigale tenuirostris,* Long-tailed Planigale *Planigale ingrami*, Common Planigale *Planigale maculata* (Figure 2.21), Forrest's Mouse *Leggadina forresti* and Lakeland Downs Mouse *L. lakedownensis* (Figure 2.22), Delicate Mouse *P. delicatulus* and Sandy Inland Mouse *P. hermannsburgensis* (Figure 2.23) and the Canefield Rat *Rattus sordidus* and Long-haired Rat *R. villosissimus* (Figure 2.24).

Eyrean species represented in the Desert Uplands by a disjunct population, or who reach the edge of their mesic geographic range in the Desert Uplands: *Tympanocryptis cephalus* and *T. lineata* (Figure 2.25), *Tiliqua multifasciata* and *Varanus mertensi* (Figure 2.27), Spinifexbird *Eremiornis carteri* (Figure 2.30), Julia Creek Dunnart *Sminthopsis douglasi* (Figure 2.32) and Desert Mouse *Pseudomys desertor* (2.33).

Torresian/Bassian species whose distribution within the Desert Upland is disjunct or on the xeric edge of their geographic range: *Oedura castelnaui* and *Diplodactylus vittatus* (Figure 2.26), *Paradelma orientalis* and *Simoselaps warro* (Figure 2.28), White throated Honeyeater *Melithreptus albogularis* and White-eared Honeyeater *Lichenostomus leucotis* (Figure 2.29), Squirrel Glider *Petaurus norfolcensis* and Greater Glider *Petauroides volans* (Figure 2.31) and Common Dunnart *Sminthopsis murina* (Figure 2.32).

Species endemic to the Desert Uplands: *Ctenotus rosarium* (Couper *et al.* 2002; Appendix 1, Figure 2.34 including distribution of the closely related *C. strauchii*) and *Lerista* sp nov (Figure 2.35), both species discovered in this study.

Figure 2.16 Three species of *Uperoleia* (Myobatrachidae) indicating a degree of replacement through the Desert Uplands bioregion.

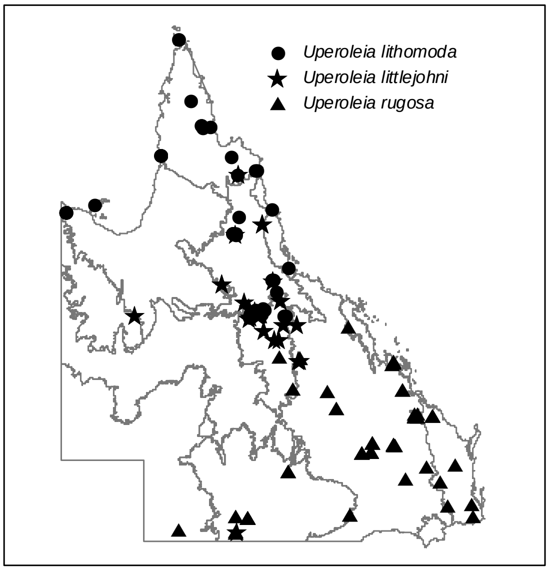


Figure 2.17 Two species of *Malurus* (Maluridae) indicating a degree of replacement through the Desert Uplands bioregion.

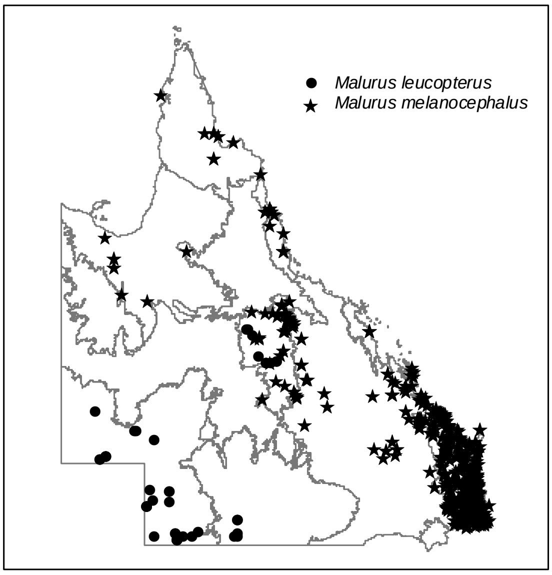


Figure 2.18 A pair of *Diplodactylus* (Gekkonidae) species indicating a degree of replacement through the Desert Uplands bioregion.

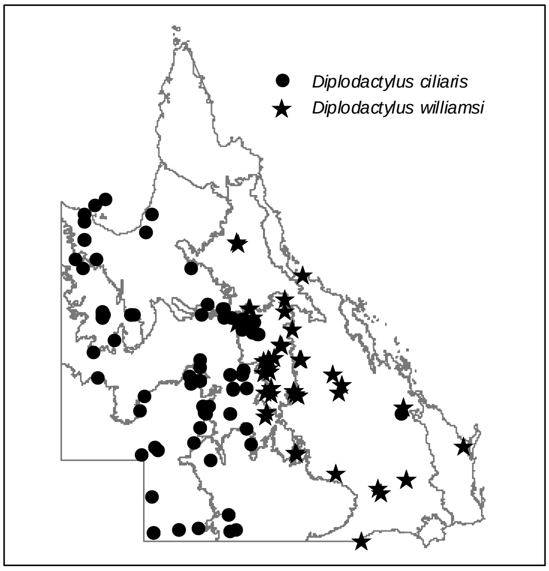


Figure 2.19 A pair of *Gehyra* (Gekkonidae) species indicating a degree of replacement through the Desert Uplands bioregion.

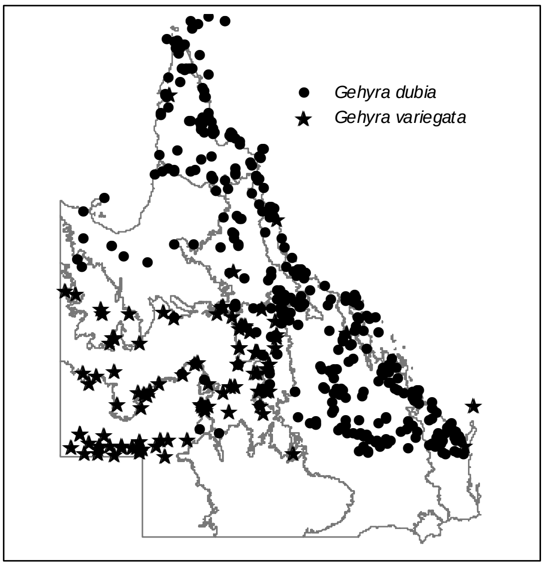


Figure 2.20 A pair of *Antaresia* (Boidae) species indicating a degree of replacement through the Desert Uplands bioregion.

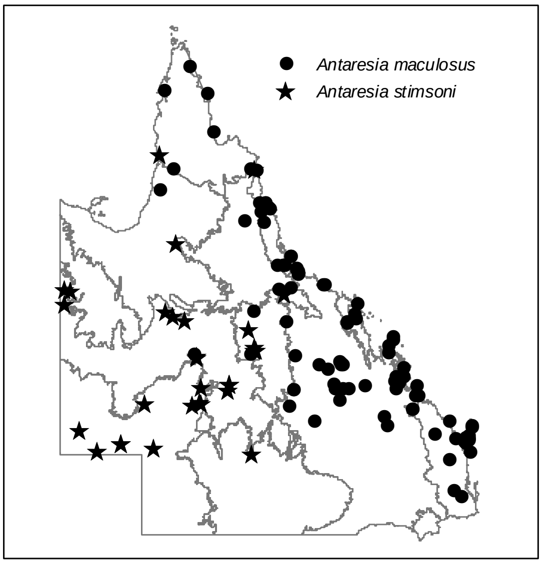


Figure 2.21 Three species of *Planigale* (Dasyuridae) indicating a degree of replacement through the Desert Uplands bioregion.

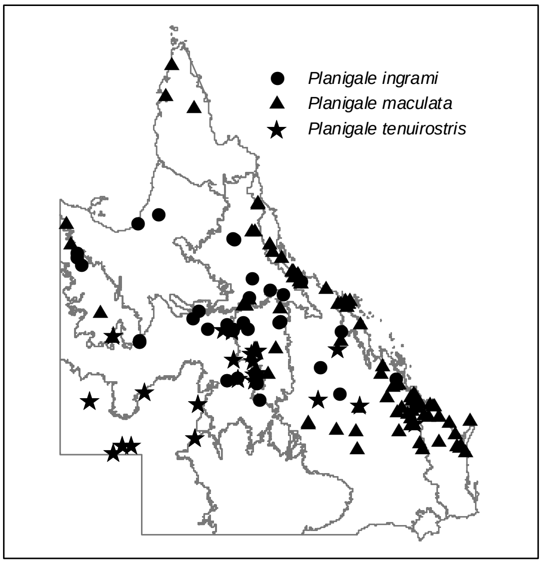


Figure 2.22 Two species of *Leggadina* (Muridae) indicating a degree of replacement through the Desert Uplands bioregion.

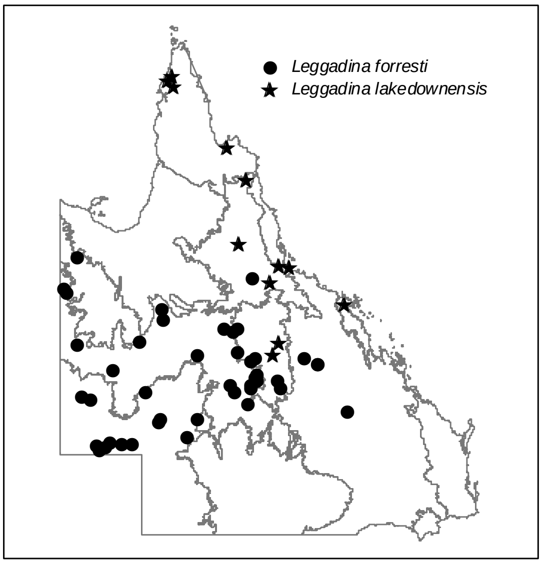


Figure 2.23 Two species of *Pseudomys* (Muridae) indicating a degree of replacement through the Desert Uplands bioregion.

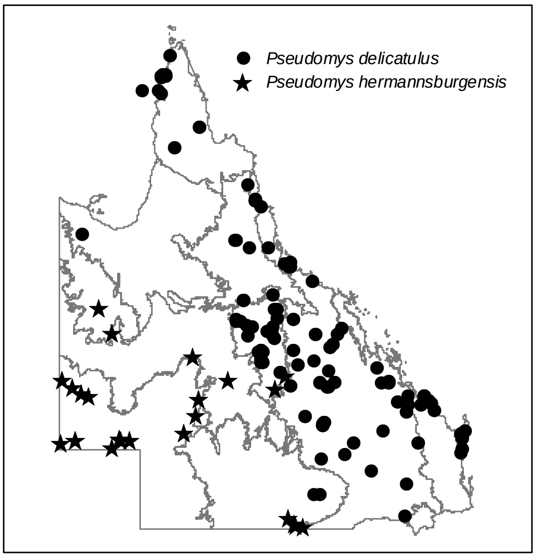


Figure 2.24 Two species of *Rattus* (Muridae) indicating a degree of replacement through the Desert Uplands bioregion.

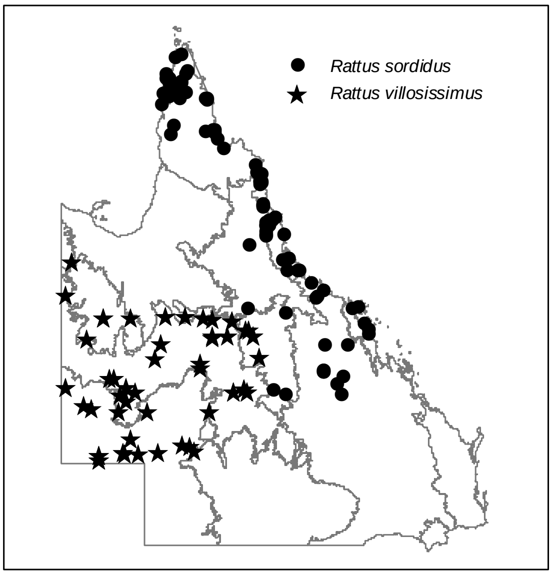


Figure 2.25 Two species of *Tympanocryptis* (Agamidae) typically distributed in arid central Australia, whose eastern distribution extends into the Desert Uplands bioregion.

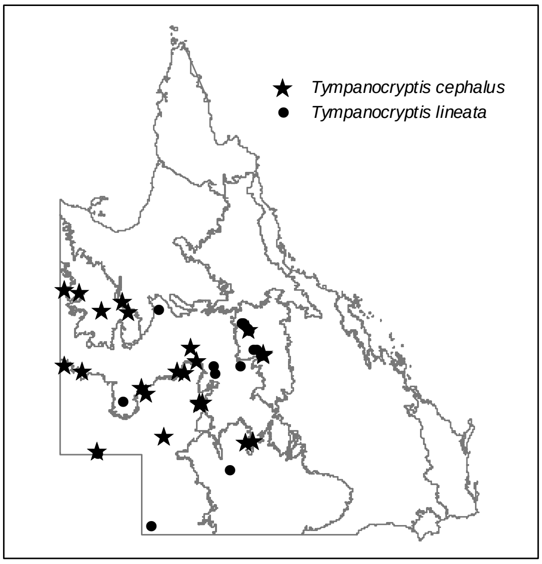


Figure 2.26 One species of *Diplodactylus* and *Oedura* (Gekkonidae) typically distributed in wetter coastal Australia, whose western distribution extends into the Desert Uplands bioregion.

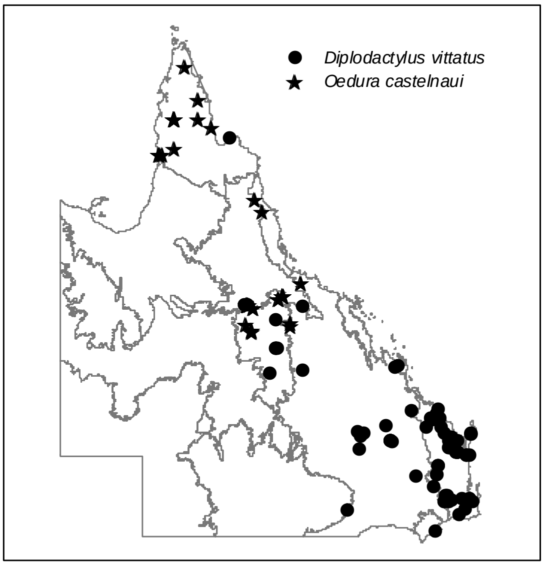


Figure 2.27 One species of *Tiliqua* (Scincidae) and one *Varanus* (Varanidae), the former typically distributed in arid central Australia, the latter in the western Gulf and Northern Territory, whose distributions extends into the Desert Uplands bioregion.

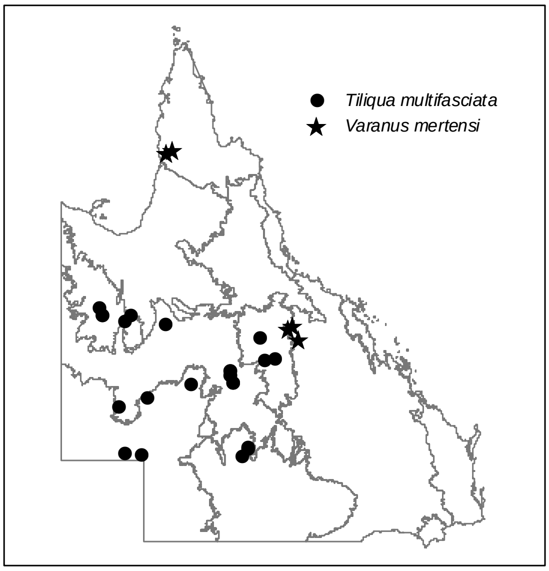


Figure 2.28 Two rare reptile species, *Paradelma orientalis* (Pygopodidae) and *Simoselaps warro* (Elapidae), the former typically distributed in south-eastern Queensland and the latter in north-eastern Queensland, whose western distributions extends into the Desert Uplands bioregion.

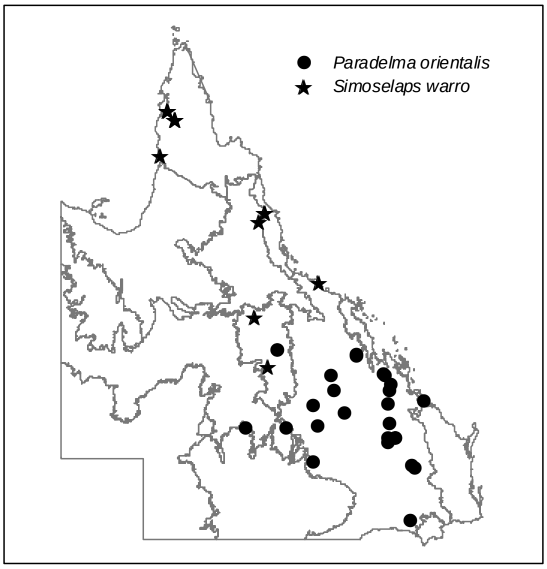


Figure 2.29 Two honeyeater species (Meliphagidae) typically distributed in wetter coastal Australia, whose western distribution extends into the Desert Uplands bioregion.

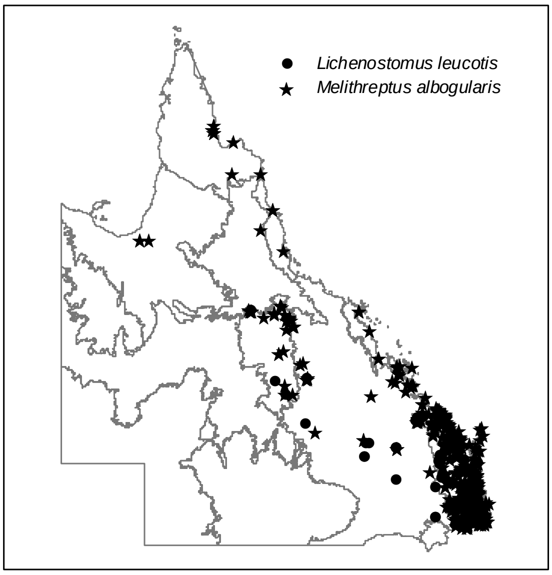


Figure 2.30 Distribution of the Spinifexbird (Sylviidae) typically distributed throughout arid central Australia, with a clearly disjunct eastern distribution extending into the Desert Uplands bioregion.

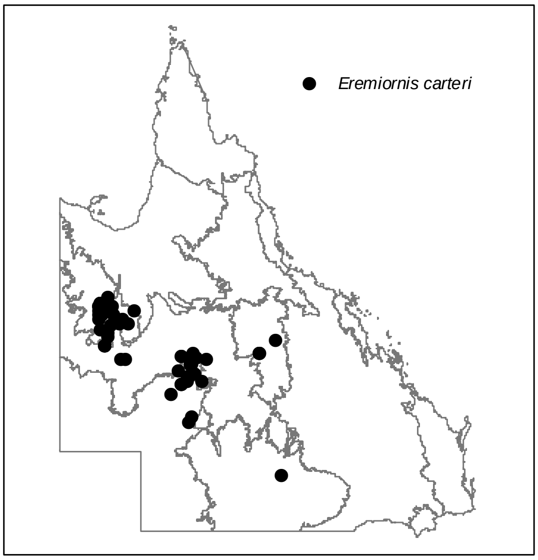


Figure 2.31 Two gliding possum species (Petauridae) typically distributed in wetter coastal Australia, whose western distribution extends into the Desert Uplands bioregion.

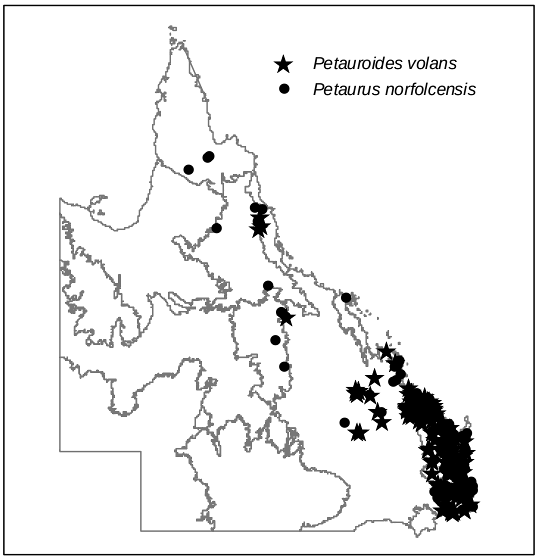


Figure 2.32 Two *Sminthopsis* species (Dasyuridae), one restricted to the a small region of the north-western Mitchell Grass Downs and the other a common wet coastal inhabitant, both of which have their distributional limits occurring the Desert Uplands bioregion.

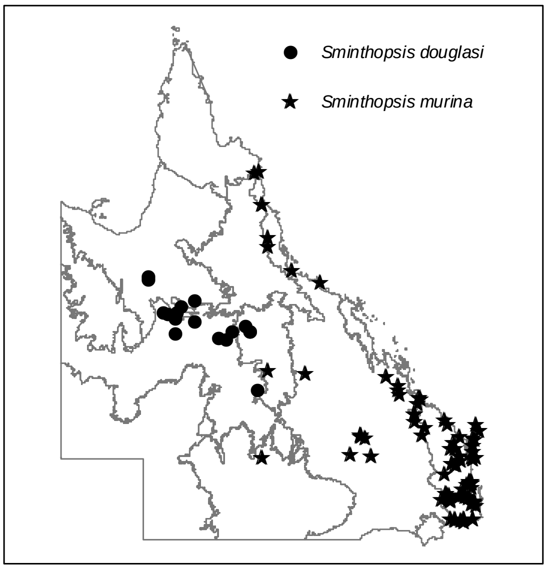


Figure 2.33 Distribution of *Pseudomys desertor* (Muridae) typically distributed throughout arid central Australia, but recorded in high abundances throughout the Desert Uplands bioregion, clearly extending its distributional range to the east.

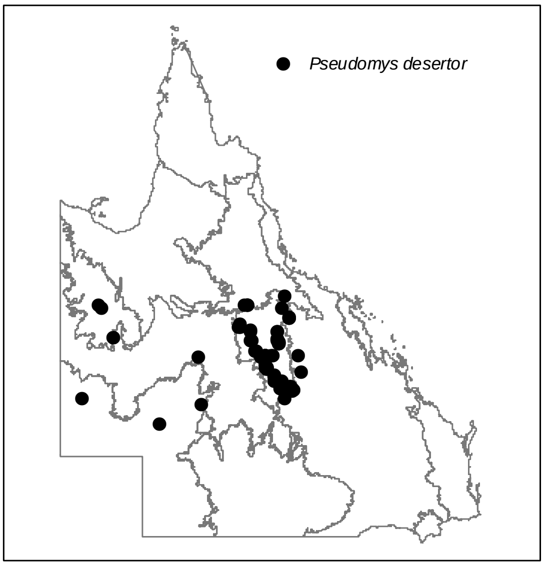


Figure 2.34 Distribution of *Ctenotus rosarium* (Scincidae) a species recently described and seemingly restricted to the Alice Tablelands in Desert Uplands bioregion. The distribution of the closely related *Ctenotus strauchii* is also indicated.

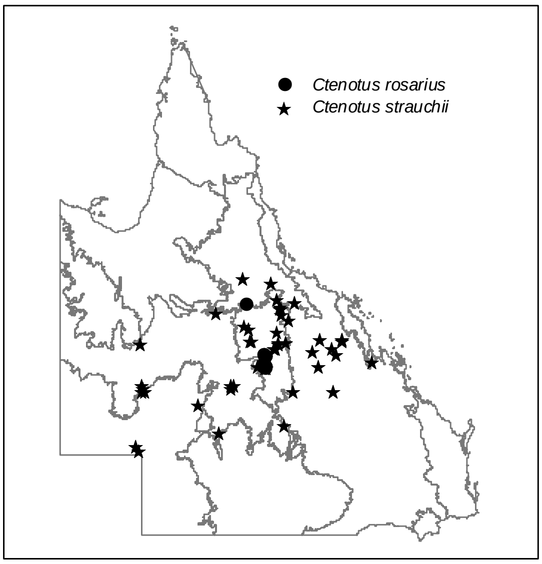
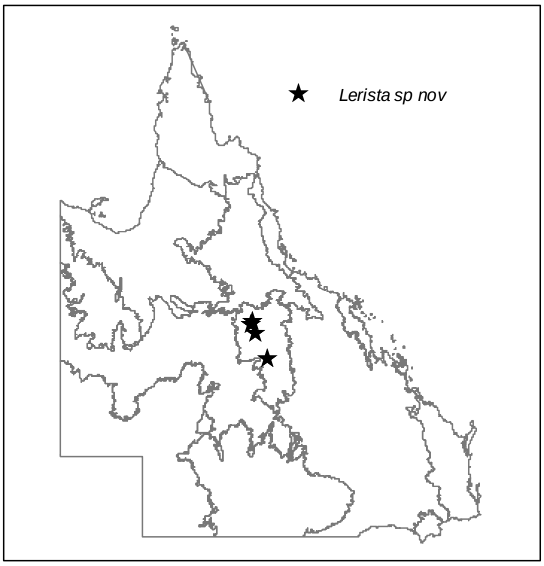


Figure 2.35 Distribution of *Lerista* sp nov (Scincidae), potentially another taxonomically distinct species currently only known from localities within the Desert Uplands bioregion.



Discussion

Bioregional species richness

The broad overview of bioregional patterns of vertebrate species assemblages presented here reinforces the existing understanding of northern Australian zoogeography (Schodde 1982; Heatwole 1987; Bowman *et al.* 1988; Crisp *et al.* 1999; Fisher 2001a). The detailed review of the composition and distribution in the Desert Uplands fauna identifies this bioregion as one both typical of semi-arid regions at the interzone of core zoogeographic regions, and one that currently supports a fauna of intergradation and replacement, with both inland and coastal elements apparent.

The biogeography of tropical savannas has been best studied in the Northern Territory. Obvious latitudinal bands of biota exist which have been linked to steep climatic gradients and relatively uniform topography (Whitehead *et al.* 1992). Confounding this pattern slightly is the influence of soil type (e.g. clay content), which differentially affects the structure and composition of the flora and fauna, depending on location and rainfall (Williams *et al.* 1996b; Woinarski *et al.* 1999b; Fisher 2001a). In northern Queensland the landscapes are more complex. North-south climate gradients do exist, but are interrupted by the Great Dividing Range that runs down the east coast of Australia. This topographic feature creates a distinctive east-west barrier and provides high altitude refugia (Nix and Switzer 1991). Coupled with periods of land bridge connection with New Guinea, the interplay of climate change with species invasion and isolation has greatly influenced the extant Queensland fauna (Schodde and Calaby 1972; Ford 1986; Heatwole 1987; Williams and Pearson 1997; Moritz *et al.* 1997). Of the tropical savanna regions, only the Mitchell Grass Downs region has received any detailed biogeographic consideration in Queensland. In this broad, featureless landscape, climate (namely temperature, rainfall seasonality) is identified as the primary control on floristic variation (Fensham *et al.* 2000).

The species richness of the bioregions reflects these determinants of the diversification of Australia’s fauna. The east coastal (WET, EIU) and arid inland regions (CHC) are particularly rich in species with many endemics, and include genera from all classes that are restricted to, or extremely diverse within these bioregions (e.g. *Cophixalus*, *Meliphaga*, *Saproscincus* and *Uromys* in the WET and *Neobatrachus*, *Neophema*, *Ctenotus* and *Notomys* in the CHC). Though operating at different scales processes such as isolation via geographic barriers, dispersal, stranding within refugia, and subsequent habitat adaptation, are considered the primary cause for such speciation (Schodde 1982; Ford 1987; Williams and Pearson 1997; Winter 1997). Furthermore the high species richness within the Wet Tropics is not only a function of montane isolation, but also of productivity, latitude, habitat heterogeneity and invasions of northern tropical and southern temperate species during periods of favourable climate (Schmida and Wilson 1985; Tilman and Pacala 1993; Southwood 1996; Winter 1997). The significant environmental correlates of fauna species richness with bioregions reported in this study simply re-emphasise this history and geography and correspond to previous studies that identify these factors as deterministic: altitude range (Williams and Pearson 1997; Williams and Hero 2001); vegetation patterns (Kikkawa and Pease 1969; Cody 1993); climatic gradients (Nix 1982; Whitehead *et al.* 1992), cycles of widespread aridity (Jones and Bowler 1980; Schodde 1982; Pianka 1986; Morton 1993); the existence of refugia and barriers such as the Great Dividing Range (Schodde 1982; Ford 1986); and linkage via dispersal corridors and land bridges (Schodde and Calaby 1972; Winter 1997).

The semi-arid bioregions including the Desert Uplands have intermediate species richness, reflecting their transitional location. The shift in climate to greater aridity or cooler temperatures is associated with a decline in species richness (Bowman *et al.* 1993; Bowman 1996; Williams *et al.* 1996b; Woinarski *et al.* 1999b; Fensham *et al.* 2000), though this is confounded by substrate variation (Woinarski *et al.* 1999b; Fisher 2001a). Historically these regions were ones where the frontier of climate and vegetation change oscillated (Jones and Bowler 1980; Frakes *et al.* 1987). The lack of topography meant there were few refuges or barriers causing isolation and diversification of species, unlike central and coastal Australia. Therefore the patterns of species richness for the semi-arid belt of tropical savanna bioregions are reasonably equable. Minor refuges exist in the form of monsoon and dry vine thickets (Menkhorst and Woinarski 1992; Bowman and Woinarski 1994) and in the case of the Desert Uplands, the existence of endemic and disjunct plant and animal species restricted to the central Alice Tableland indicate some recent isolation and speciation has occurred (see further discussion below). There are clear regional differences in species composition but there is also widespread landscape and ecological connectivity in the tropical savannas bioregions of northern Australia (Woinarski 1999b).

Bioregion species composition and environmental correlates

The composition of the vertebrate fauna of each bioregion reflects their geographic alliance. Simple rules of autocorrelation would suggest regions in closer geographic proximity have a fauna assemblage more similar to those distant (Legendre 1993), and generally this seems to be the case. For the most part, the monsoon savanna bioregions group together for each taxon, as do the more arid inland CHC and MGD bioregions. The pattern for the eastern Queensland bioregions is more variable with the Desert Uplands either grouping with the BBN (amphibians and reptiles), the WET, EIU and BBN (mammals) or being moderately isolated (birds). As one of the postulated major points of entry to Australia for vertebrates is in the north-east (Cogger and Heatwole 1981) and the major impediment to fauna exchange is the Eyrean barrier (Schodde 1982), this bioregional grouping is understandable. For example, despite the existence of rainforest in the Northern Territory, non-volant mammals typical of eastern Australia are lacking due to Pleistocene aridity and divergence coupled with the small size of remnant rainforest areas (Bowman and Woinarski 1994). Similarly, reptiles have diversified enormously in central Australia due in part to long-term isolation and extensive suitable habitat (Cogger and Heatwole 1981; Pianka 1989; Morton 1993). In comparison such autochthonous evolution has not extended to the avifauna due to the lack of adequate refugia to withstand the exigencies of climate change (Schodde 1982). Mobility and expansion via mesic corridors across these biogeographic zones has muddied the patterns of distribution (Schodde 1982), and bird communities in tropical savanna woodlands are renowned for their transient, widespread and at times indefinable distribution (Woinarski *et al.* 1988).

The patterns of composition similarity between the Desert Uplands and other bioregions further reflect on its twin east coast and northern Australian allegiance. Amphibian composition was most similar to the arc of northern tropical savanna bioregions, and comprises mainly widespread species of Gondwanan origin (Hylidae, *Litoria* and Myobatrachidae, *Limnodynastes*, *Crinia* and *Uperoleia*) (Roberts and Watson 1993). Conversely there is only a small suite of arid adapted species (*Cyclorana* and *Neobatrachus*). In contrast the Desert Uplands mammal assemblage was poorly related to other tropical savanna bioregions, due to the presence of a range of tropical and sub-tropical mammals more common to east coast woodlands and forests in the BBN and EIU bioregions (e.g. *Aepyprymnus rufescens*, *Phascolarctos cinereus*, *Trichosurus vulpecula*, *Petaurus norfolcensis*, *Petauroides volans*, *Rattus sordidus*, *Pseudomys gracilicaudatus*, *Leggadina lakedownensis*). Monsoon areas lack the diverse non-volant fauna of north-east Queensland (Winter *et al.* 1991; Bowman and Woinarski 1994) and arid Australian bioregions (CHC) have a large company of endemic dasyurid and murid species. Comparisons between Queensland bioregions also indicated a high turnover for mammals and amphibians in successive bioregions from the coast.

There was limited variation in bird and reptile composition in all comparisons between the DEU and other bioregions, and this was also a notable feature across Queensland bioregions from the WET to the CHC. Tropical woodlands have high generic diversity (varanids, elapid, skinks), sourced from older and recently invaded and diversified groups (e.g. *Gehyra*, *Carlia/Lygisaurus*) (Cogger and Heatwole 1981). The broad band of Torresian woodland also supports a suite of reptiles with catholic habitat preferences (e.g. *Tiliqua*, *Morethia*, *Carlia*, *Cryptoblepharus*, *Proablepharus*, *Pseudechis*, *Demansia*, *Simoselaps*, *Suta*). This, coupled with the ability for large numbers of reptile species to coexist (Pianka 1986), suggests that small terrestrial exotherms are possibly more resilient to long-term climatic vagaries and associated habitat variability. In the case of avifauna, the high mobility and dispersal ability of birds have created assemblage uniformity within broad structurally similar regions such as the tropical savannas. As the major direction of speciation is via Bassian and Torresian routes to arid areas (Schodde 1982), tropical savanna woodlands also lie closer to the source rather than the destination.

Within the Subregions of the Desert Uplands there is a general cohesiveness of vertebrate composition, each being more similar to each other than it is to other adjacent bioregions. Though the composition is influenced by, and is an amalgam of, portions of all surrounding bioregions, in itself it is characterised as a discrete and unique fauna composition and assemblage. This also hints at the significance of the Alice Tableland (Subregion 2) as an area of species turnover, with the fauna assemblage being strongly associated to bioregions to its east (BBN, EIU) and west (MGD) for different taxa.

Species patterns

A number of vertebrate genera were used to illustrate the patterns of speciation and endemism within the bioregions. In essence endemic or species-rich groups are associated with coastal (e.g. *Austrochaperina*, *Cyclopsitta, Meliphaga, Antechinus, Rattus, Tropidechis, Saproscincus*) and inland bioregions (e.g. *Neobatrachus, Neophema, Ashbyia, Dasycercus, Notomys, Notechis, Ctenotus*). This pattern is a reflection of the lack of long term climate stability (arid or wet) coupled with inadequate refugia to permit the derivation of diverse locally endemic fauna. Semi-arid tropical savannas such as the Desert Uplands are characterised by widespread generalists (e.g. *Limnodynastes, Uperoleia, Nymphicus, Cacatua, Entomyzon, Hydromys, Menetia, Oxyuranus*) or representatives of related species from a single genus (e.g. *Manorina, Pseudomys, Planigale, Sminthopsis, Menetia, Pseudechis*). The biota is predominantly an invasive assemblage from both Torresian and Eyrean origin. Though there are many complementary species between the Queensland and the monsoon bioregions, there are particular regional patterns and species in the Northern Territory that reflect separate historical Asian connections, vicariant species from Cape York Peninsula and or species derived from sandstone refugia such as the Kimberley or the Arnhem Plateau (e.g. *Megistolotis*, *Psitteuteles*, *Myzomela*, *Pseudantechinus*, *Notoscincus*, *Fordonia*, *Myron*, *Cerberus*, Woinarski 1992). Some specific examples of species recorded in the Desert Uplands and their wider Queensland distribution illustrate and complement the broad patterns discussed above (Figs. 2.16-2.35).

Amphibians

A traditional pattern of biogeographic zonation for anurans has been rejected in preference to delineation of nine areas of high diversity principally determined by climate (Tyler *et al.* 1981). The presence of some more arid adapted genera and species

(*Neobatrachus* spp) and widespread, but climate limited species (*Litoria* spp) indicate multiple historical causes of amphibian diversification in Australia (Roberts and Watson 1993). In the Wet Tropics climate and topography were significant predictors of frog species richness, suggesting that both localised extinction and re-colonisation, and refugial isolation, have both determined amphibian composition (Williams and Hero 2001).

The amphibian fauna of the Desert Uplands was of moderately low diversity dominated by widespread species (*Litoria* spp, *Limnodynastes* spp), and some coastal (e.g. *Pseudophryne*) and inland (e.g. *Notaden*) incursions at the edge of their range. Very few amphibians identified a clear pattern of turnover for related species (*Litoria latopalmata L. pallida*; *Cyclorana australis C. novaehollandiae*) and even these were confounded by rainfall gradients. The three *Uperoleia* illustrated hint at some influence of localised speciation, with overlap of all three in the Desert Uplands, though the distribution of the three is typically in wetter coastal forests. This supports the contention that amphibian distribution is partly influenced by current climate and habitat. Bioregions such as the Desert Uplands may be the distributional limit for many amphibian species, the Great Dividing Range being a defining barrier. Beyond this, only a small suite of arid adapted burrowing species such as *Cyclorana* and *Neobatrachus* proliferate, coupled with more recent expansion of widespread riparian and wetland generalists (*Limnodynastes* and *Litoria*). Vicariant diversification in central Australia simply failed due to aridity (Roberts and Watson 1983).

Birds

The biogeographic, taxonomic and distribution patterns for avifauna in Australia have been extensively studied (Keast 1961; Kikkawa and Pearse 1969; Schodde and Calaby 1972; Keast 1981; Schodde and Mason 1980; Schodde 1982; Ford 1986; Ford 1987; Cody 1993; Schodde and Mason 1999). Throughout the cycles of Tertiary and Quaternary climate change, there is considered to have been a continuous adaptive flow between xeric and mesic environments as suggested by the large number of vicarious species and genera (Schodde 1982). These patterns have been muddied by the high mobility and dispersal ability of birds, and some contemporary patterns illustrate this:

mesic species invade drier habitat via riparian systems; translocation of species such as Laughing Kookaburra *Dacelo novaeguineae* in Western Australia and Tasmania; and habitat modification advantaging increaser species such as Crested Pigeon *Ocyphaps lophotes* (Schodde 1982).

Major features like the Great Dividing Range are still influential barriers, as well as smaller landscape features (e.g. Burdekin-Lynd barrier, Ford 1986). Though the data is not presented here, the abundance of the southern ultrataxa of Squatter Pigeon *Geophaps scripta scripta* and Black-throated Finch *Poephila cincta cincta* at their north and western extremity of the Desert Uplands support this biogeographic regionalisation. Similarly the location of the Spinifexbird *Eremiornis carteri* was a surprising disjunct population, given it is a species widely distributed across central Australia. Two populations were recorded in the Desert Uplands, possibly as a result of current land management patterns, nomadism and historical factors, and this case is discussed in detail in Kutt (2003b, Appendix 3). Other examples of typical nomadic Eyrean avifauna that are sparsely distributed in the Desert Uplands are the Crimson Chat *Epthianura tricolor* and Painted Finch *Emblema pictum*, and more sedentary species such as the Crested Bellbird *Oreoica gutturalis* which was abundant in many habitats in the Desert Uplands, but predominantly in western and central subregions.

In contrast there are a number of coastally distributed species all of clear Torresian origin and restricted to environments on and east of the Great Dividing Range (e.g. Figbird *Sphecotheres viridis*, White-bellied Cuckoo-shrike *Coracina papuensis*, Masked Owl *Tyto novaehollandiae*) (Keast 1961; Schodde and Mason 1999). These species have specific resource requirements (tall forests, fruiting trees, hollow-bearing trees) that decline in availability further west from their core distribution. Refugial habitat with these elements would have been lacking from inland areas during periods of aridity (Schodde 1982). These species are Austro-Papuan in origin with extra-limital distribution through parts of south-east Asia, suggesting the ability to spread quickly across landscape barriers into appropriate habitat.

The presence of a number of well-established pairs of vicariant species (*Gerygone* spp, *Manorina* spp and *Chlamydera* spp) indicated a degree of replacement across the Great

Dividing Range through the Desert Uplands (Schodde 1982; Ford 1986). The patterns for *Gerygone* and *Manorina* are confounded by recent changes in distribution, namely the passage of *Gerygone* species through riparian and other corridors beyond its core biogeographic distribution (Schodde 1982), and the expansion of *Manorina* species due to habitat disturbance (Reid 1999). The illustrated example of the White-winged Fairy-wren *Malurus leucopterus* and Red-backed Fairy-wren *Malurus melanocephalus* is a particularly well-defined recent example of division. Recent electrophoretic analysis indicated that these two species are most closely related belonging to the bicoloured *leucopterus* group, and have split via Pleistocene divergence (Christidis and Schodde 1997). Their distribution in the Desert Uplands indicates the approximate position of this partition in eastern Australia.

Mammals

The distribution of mammals presents some of the most clear biogeographic patterns in Australia. Two distinct lineages exist: the clear suite of Gondwana (marsupial) species and recently invaded murid and bat faunas (Archer 1984). The rodents consist of two groups, one more ancient lineage (Conilurini) and one more recent consisting only of the genus *Rattus* (Baverstock 1984). More recently areas such as Cape York Peninsula have formed significant land bridges with New Guinea allowing invasion of more arboreal and terrestrial species into the wet tropical uplands and tall forests on the eastern seaboard (Kikkawa *et al.* 1981; Heatwole 1987).

Recent mammal invasions, coupled with periods of climatic fluctuation (notably Pleistocene aridity), have created some moderately lucid patterns of divergence such as a series of closely related inland and wet coastal rodents (Baverstock *et al.* 1981; Baverstock 1982). In the Desert Uplands there was a large number of Conilurini and Murinae rodent species-pairs demonstrating species turnover and allopatry (*Leggadina forresti* and *L. lakedownensis, P. delicatulus* and *P. hermannsburgensis*, *Rattus sordidus* and *R. villosissimus*). This broad geographic band is coincident with the Great Dividing Range in Queensland, and a similar zone of intergradation is apparent in the semi-arid tropical savannas of the Northern Territory (Coles and Woinarski 2002). The significance of allopatric rodents in the Desert Uplands, and the distribution of *P.*

desertor, a typically Eyrean species captured in large numbers in the Desert Uplands, are discussed further in Kutt *et al.* (2003c, 2003 in press, Appendix 5, 6).

Due to a more ancient continental history, Dasyurid patterns are less distinct. For example, recent evaluation of the genus *Planigale* indicated a much higher level of genetic divergence than previously thought, including great heterogeneity in widespread species *Planigale maculata* and possibly two new cryptic species (Blacket *et al.* 2000). The data suggest some broad distribution parallels to biogeographic zones, but more subtle variations that follow drainage basins, refugia and discontinuities. The pattern of distribution records in Queensland and the Desert Uplands for *Planigale tenuirostris*; *P. ingrami* and *P. maculata* indicate a great complexity and overlap in distribution patterns, though this could also be a function of poor taxonomy (Blacket *et al.* 2000).

Two other dasyurids recorded were unusual range extensions for more typically Eyrean and widespread south-eastern species. Firstly *Sminthopsis murina* was recorded in some rocky escarpments on the Alice Tableland. This creates a discontinuous distribution from south-eastern Queensland, via a series of central sandstone ranges (including Carnarvon) through to the Wet Tropics, where it is considered an isolated sub-species (*S. murina tatei*). However the Desert Uplands and Einasleigh Uplands may form a link between the north and south populations for this species. The taxonomy of *Sminthopsis* in Queensland is poorly known and the distribution and taxonomic status of the *S. murina* complex needs revision. Secondly *Sminthopsis douglasi* was previously considered restricted to a small region of the Queensland Mitchell Grass Downs (Woolley 1992), though a disjunct population in the Desert Uplands suggests a greater distribution south and east. The significance of the *S. douglasi* records in the Desert Uplands is discussed in more detail in Kutt (2003a) (Appendix 2).

Large arboreal marsupials are almost exclusively restricted to northern and eastern Australia, their distribution almost wholly determined by appropriate vegetation (Winter *et al.* 1991). Similar to amphibians, the process of wet-dry vicariance had little influence in creating a distinct arid inland assemblage, simply due to the lack of sufficient refugial habitat (Bowman and Woinarski 1994). Arboreal mammals have two distinct origins: an ancient sclerophyll forest adapted suite and a more recent rainforest suite, that invaded from New Guinea and subsequently diversified during periods of wet tropical isolation (Winter 1997). All are Austro-Papuan in origin (Schodde and Calaby 1972; Winter 1997). Two large gliding possums were recorded in the Desert Uplands, the Squirrel Glider *Petaurus norfolcensis* and Greater Glider *Petauroides volans*, both older sclerophyll adapted species. Their Queensland distribution identifies an association with taller coastal forests on the east of the Great Dividing Range. Other more generalist species (*Trichosurus vulpecula, P. breviceps*) were more widespread, but in the western Desert Uplands Sub-region, restricted to predominantly riparian ribbons in open woodlands and grassland mosaics.

Reptiles

The herpetofauna, and in particular skinks, are exceptionally species-rich in Australia (Cogger and Heatwole 1981). Consistent patterns occur in most reptile families, with centres of species richness and diversity for different genera occurring variably in central and western Australia, south-east Queensland and monsoon regions (Cogger and Heatwole 1981). Generic richness for reptiles is highest in south-eastern Queensland (Hutchinson and Donellan 1993).

As with other vertebrates, there are broad speculative explanations for the rate of evolution, vicariant events and dispersal routes for the squamates, using geological history and current patterns of diversity and environment (Cogger and Heatwole 1981). In general, with the exception of the recently dispersed Colubridae (Austro-Papuan origin and distribution), most reptile families have diversified in Australia since the Tertiary (Hutchinson and Donellan 1987). Relationships for Australian taxa are generally Asian, and some groups are considered to have derived and diversified *in situ* (e.g. diplodactyline geckos, *Pygopodidae*, *Egernia*, *Varanus*, *Ramphotyphlops*, Hutchinson and Donellan 1987). However Greer (1989) provides a pungent critique of past zoogeographic thought regarding reptiles, in particular the propensity of zoogeographers to ignore phylogenetics. This is possibly easy criticism in an era now where burgeoning electrophoretic techniques can debunk past notions based purely on morphology and geography. For example Stuart-Fox *et al.* (2002) examined electrophoretically the Austro-Papuan radiation of lizards in the genus *Carlia*, and reincorporated *Lygisaurus* to *Carlia*, a genus previously split by morphology. Furthermore paraphyletic (divergent) lineages were found within some widely distributed species, indicating periods of rapid divergence among some lineages (Stuart-Fox *et al.* 2002). The message is that quite valid broad zoogeographic explanations will be refined through ongoing detailed genetic studies (Hutchinson and Donellan 1993).

In the Desert Uplands, the reptile fauna is moderately species rich, and predominantly influenced by northern Australian species. Examples described for other vertebrate taxa and here for reptiles, serve simply to identify the context for the Desert Upland herpetofauna within well-established geological and phylogenetic patterns. Illustrated examples of species pairs represent two primitive (*Diplodactylus ciliaris* and *D. williamsi*; *Antaresia stimsoni* and *A. maculosa*) and a recent Asian (*Gehyra dubia* and *G. variegata*) lineage that are phylogenetically related (Greer 1989; 1997). These indicate that speciation has occurred via climatic or other environmental factors, with the centre of the Desert Uplands acting as the vicariant barrier.

The Desert Uplands records of *Varanus mertensi*, a predominantly aquatic monitor, represent an unusually disjunct population from its normal Gulf and north-western Australian range. It occurs in the Cape River, part of the large Burdekin catchment that flows in to the Pacific Ocean. There have been periods where parts of the upper Burdekin catchment flowed westward into the Gulf via the Gilbert River, which was later diverted back east via Miocene lava flows (Pusey *et al.* 1998). This breach must have allowed the invasion of *V. mertensi* into this catchment. The presence of other disjunct species (*Tiliqua multifasciata*, *Tympanocryptis cephalus* and *T. lineata*, *Oedura castelnaui* and *Simoselaps warro, Diplodactylus vittatus* and *Paradelma orientalis*) identifies the climatic and habitat affinity of the western, northern and eastern Desert Uplands Subregions with proximity with Eyrean and Torresian/Bassian regions (for further discussion of *P. orientalis* see Kutt *et al.* 2003d, Appendix 4). Species at the edge of their range echo this past climatic shadow, though current environmental gradients and limitations also control extant distribution patterns.

Possibly three reptile species are endemic to the Desert Uplands. *Ctenotus rosarium* (closely related to *C. strauchii*) discovered and described in the current study (Couper *et al.* 2002, Appendix 1), *C. capricorni* (closely related to *Ctenotus robustus*) which occurs in the southern section of the Alice Tableland, and *Lerista* sp nov, was discovered in this study, and is considered a new species (Andrew Amey, pers. comm. 2001, Queensland Museum). The presence of these species reflects both *in situ* speciation and resource and habitat partitioning independent of larger biogeographic forces, evidence that during periods of Pleistocene climatic fluctuation, the environment (possibly refugia) of the Alice Tableland has been conducive to diversification. Current studies examining the ecological and taxonomic electrophoretic relationships of this diverse group are still few (Greer 1989; Greer 1997; Storr *et al.* 1999).

Plants

Though vertebrates are the major focus of this study, a number of plant species identify smaller scale patterns of speciation within parts of the Desert Uplands Bioregion. Five species of plants found exclusively in the Alice Tableland (Sub-region 2) have clearly disjunct populations from their typical range: the tree fern *Cyathea rebeccae*; the spinifex *Triodia triaristata*; the shrub *Triplarina paludosa*; the eucalypt *Eucalyptus eucentrica*; and the forb *Dysphania plantaginella* (Morgan *et al.* 2002). A further 10 plants are also considered endemic to the bioregion, again all restricted to regional ecosystems of the Alice Tableland. Three are restricted to the closed catchment of Lake Buchanan, *Lawrencia buchananensis*, *Calotis* sp (Yarrowmere J. Kemp+ 3365H) and *Dactyloctenium* sp (Yarrowmere J. Kemp+ 3384H), a wetland perched on the watershed of the Flinders and Burdekin River catchments. On current distributional information, these represent species that have become isolated in refuges in the central Desert Uplands on the Great Dividing Range.

Conclusions

The broad overview of distribution patterns of vertebrate species identifies the Desert Uplands bioregion as one both typical of semi-arid regions at the interface of core zoogeographic regions and one that currently supports a fauna of intergradation and replacement, with both inland and coastal elements apparent. It lies on a number of major landscape boundaries, most notably the Great Dividing Range, which also coincide with the broad boundary of Torresian and Eyrean zoogeographic zones. Historically, the frontier of climate change would have oscillated across this feature, and the distribution of many vertebrate fauna examples suggests the Desert Uplands Bioregion is central to some vicariant speciation. The fauna composition indicates a distinct alliance with neighbouring coastal bioregions, yet there is also affinity to the wider arc of tropical savanna bioregions across northern Australia.

The key question is whether the Desert Uplands Bioregion adequately demarcates a fauna assemblage that is a discrete and unique entity. From a geomorphologic and geological point of view, there is strong evidence for this regionalisation (Sattler and Williams 1999; Morgan *et al.* 2002), while the local pastoral community consider the Alice Tableland colloquially as the “desert country”, having a vegetation, productivity and carrying capacity distinct from surrounding bioregions. However the similarity of composition between many bioregions across northern Australia, including those considered particularly unique (e.g. WET versus BBN, or EIU versus MGD) suggests there are a continuous turnover of species and never a neat partitioning of assemblages between bioregions. Regardless, this first examination of the Desert Uplands fauna indicates a level of variation of the fauna assemblages between it and other bioregions. This indicates a degree of cohesion within the fauna composition. From the perspective of biogeographic history, its position as a point of replacement and hybridisation suggests it as a landscape that helped mould the biotic patterns of north-eastern Australia. Furthermore the Alice Tableland alone has both a distinctive geological character and including endemic plant and animal species, which identify it as a unique entity. Having set a biogeographical context for the study area, in the next three chapters I examine in detail the regional and local scale patterns of assemblage and environmental gradients within the Desert Uplands Bioregion.

Table 2.5 List of all families and genera recorded in the bioregions examined in this study, including the number of species recorded for each within each bioregion. n = the total number of species within that genera within the area considered here.

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Amphibians																	
Hylidae	*Cyclorana*	13	3	6	5	4	3	3	3	3	4	5	1	7	3	6	2
Hylidae	*Litoria*	30	10	5	13	7	5	6	5	4	14	12	10	7	9	8	20
Hylidae	*Nyctimystes*	1									1						1
Microhylidae	*Austrochaperina*	3									3						3
Microhylidae	*Cophixalus*	10	1								3						9
Myobatrachidae	*Crinia*	3	1	1	1	1	1	1			1	3	3	1	2	1	2
Myobatrachidae	*Limnodynastes*	8	6	4	2	5	1	3	3	3	5	1	2	1	3	2	5
Myobatrachidae	*Megistolotis*	1													1		
Myobatrachidae	*Mixophyes*	1									1						1
Myobatrachidae	*Neobatrachus*	2	1	2													
Myobatrachidae	*Notaden*	3	1	2	1	1	1	1		1		2	1	2		1	
Myobatrachidae	*Pseudophryne*	3	1			1		1			1						1
Myobatrachidae	*Taudactylus*	2															2
Myobatrachidae	*Uperoleia*	10	3	2	2	3		3	2	1	4	4	2	1	3	2	4
Ranidae	*Rana*	1															1
Birds																	
Accipitridae	*Accipiter*	3	3	2	3	2	2	2	2		3	3	2	2	2	3	3
Accipitridae	*Aquila*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Accipitridae	*Aviceda*	1	1		1	1			1	1	1	1	1				1
Accipitridae	*Circus*	2	2	2	2	2	1	1	2		2	1	2	2	1	2	2
Accipitridae	*Elanus*	2	2	2	2	1	1	1	1	1	2	1	1	2	2	1	1
Accipitridae	*Erythrotriorchis*	1	1								1	1					1
Accipitridae	*Haliaeetus*	1	1	1	1	1		1	1		1	1	1	1	1	1	1
Accipitridae	*Haliastur*	2	2	1	2	1	1	1	1	1	1	2	2	1	1	1	2
Accipitridae	*Hamirostra*	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1
Accipitridae	*Hieraaetus*	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1
Accipitridae	*Lophoictinia*	1	1	1	1	1		1	1		1	1	1	1	1	1	1
Accipitridae	*Milvus*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Accipitridae	*Pandion*	1	1		1						1	1	1				1
Aegothelidae	*Aegotheles*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Alaudidae	*Mirafra*	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Alcedinidae	*Alcedo*	2	2		2						2	2	2		1	1	2
Apodidae	*Apus*	2	1	1	1	1		1	1		1	1		1		1	2
Apodidae	*Collocalia*	2	1								1						2
Apodidae	*Hirundapus*	1	1	1		1			1		1						1
Artamidae	*Artamus*	6	6	5	5	6	4	4	4	5	6	5	5	5	5	5	6
Artamidae	*Cracticus*	5	3	2	3	2	2	2	2	2	2	3	2	1	2	2	3
Artamidae	*Gymnorhina*	1	1	1		1	1	1	1	1	1						1
Artamidae	*Strepera*	1	1			1		1		1	1						1
Burhinidae	*Burhinus*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Burhinidae	*Esacus*	1															1
Cacatuidae	*Cacatua*	4	3	4	3	3	2	3	2	2	3	3	3	4	4	4	2
Cacatuidae	*Calyptorhynchus*	2	1	1	1	2	1	1	2	1	2	1	1	1	1	1	1
Cacatuidae	*Nymphicus*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Campephagidae	*Coracina*	5	5	2	4	4	2	3	4	4	5	3	3	3	3	3	4
Campephagidae	*Lalage*	2	2	1	2	1	1	1	1	1	2	2	2	1	2	2	2
Caprimulgidae	*Caprimulgus*	1	1		1						1	1	1				1
Caprimulgidae	*Eurostopodus*	2	2	1	1	2	1	2	1		2	1	1	1	1	1	2
Casuariidae	*Casuarius*	1	1								1						1
Casuariidae	*Dromaius*	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1
Centropodidae	*Centropus*	1	1		1	1	1	1	1		1	1	1	1	1	1	1
Cinclosomatidae	*Cinclosoma*	1		1													
Cinclosomatidae	*Psophodes*	3	1	2							1					1	1
Climacteridae	*Climacteris*	3	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Climacteridae	*Cormobates*	1	1								1						1
Columbidae	*Chalcophaps*	1	1		1						1		1				1
Columbidae	*Columba*	1	1								1						1
Columbidae	*Ducula*	1	1		1						1	1	1	1		1	1
Columbidae	*Geopelia*	3	3	2	3	3	2	3	3	2	3	3	3	3	3	3	3
Columbidae	*Geophaps*	3	2	1	1	1	1	1	1		1	2	1	2	1	1	1
Columbidae	*Lopholaimus*	1	1								1						1
Columbidae	*Macropygia*	1	1								1						1
Columbidae	*Ocyphaps*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Columbidae	*Phaps*	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	2
Columbidae	*Ptilinopus*	3	3		1						3		1				3
Coraciidae	*Eurystomus*	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Corcoracidae	*Corcorax*	1	1	1		1	1	1	1		1						1
Corcoracidae	*Struthidea*	1	1	1	1	1	1	1	1	1	1	1		1	1	1	
Corvidae	*Corvus*	3	3	3	1	2	2	2	2	2	2	3	3	3	2	3	2
Cuculidae	*Cacomantis*	3	2	1	1	2	1	2	1	1	2	1	1		1	1	3
Cuculidae	*Chrysococcyx*	5	5	2	3	3	3	3	2	2	5	3	2	1	1	2	5
Cuculidae	*Cuculus*	2	2	1	2	1	1	1	1	1	2	2	2	1	1	2	2
Cuculidae	*Eudynamys*	1	1		1	1		1	1		1	1	1		1	1	1
Cuculidae	*Scythrops*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dicaeidae	*Dicaeum*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dicruridae	*Monarcha*	1	1			1				1	1						1
Dicruridae	*Arses*	1	1								1						1
Dicruridae	*Dicrurus*	1	1		1	1		1			1						1
Dicruridae	*Grallina*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dicruridae	*Machaerirhynchus*	1	1								1						1
Dicruridae	*Monarcha*	2	2								2						2
Dicruridae	*Myiagra*	5	4	1	4	2	2	2	2	2	3	4	4	1	3	3	5
Dicruridae	*Rhipidura*	5	4	2	4	3	2	2	3	2	4	4	5	1	3	3	4
Falconidae	*Falco*	6	5	6	6	5	3	5	5	2	6	6	3	6	6	6	6
Halcyonidae	*Dacelo*	2	2		1	2	2	2	2	1	2	1	1		1	1	2
Halcyonidae	*Tanysiptera*	1	1								1						1
Halcyonidae	*Todiramphus*	4	4	2	4	3	3	3	3	3	3	3	4	2	3	3	4
Hirundinidae	*Cheramoeca*	1	1	1											1		
Hirundinidae	*Hirundo*	4	3	3	2	2	2	2	2	2	3	2	2	3	2	2	4
Maluridae	*Amytornis*	5		4								1					
Maluridae	*Malurus*	8	4	3	3	3	3	3	2	2	2	3	3	3	4	4	3
Maluridae	*Stipiturus*	1		1													
Megapodiidae	*Alectura*	1	1			1			1		1						1
Megapodiidae	*Megapodius*	1	1		1						1						1
Meliphagidae	*Acanthagenys*	1	1	1		1	1	1	1	1	1	1		1	1	1	
Meliphagidae	*Acanthorhynchus*	1	1								1						1
Meliphagidae	*Ashbyia*	1		1													
Meliphagidae	*Certhionyx*	3	2	2	2	1		1	1		1	3	1		2	1	1
Meliphagidae	*Conopophila*	3	1		2	1	1	1	1		1	2	1	1	1	2	
Meliphagidae	*Entomyzon*	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1
Meliphagidae	*Epthianura*	4	3	4		1		1				3		3	3	1	

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Meliphagidae	*Grantiella*	1	1	1								1		1			
Meliphagidae	*Lichenostomus*	13	12	5	5	5	3	4	4	4	9	6	4	5	6	6	6
Meliphagidae	*Lichmera*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Meliphagidae	*Manorina*	2	1	1		1	1	2	1	2	1						
Meliphagidae	*Meliphaga*	4	3		1						3						3
Meliphagidae	*Melithreptus*	4	4	1	2	3		2	2	2	3	2	2	1	2	2	3
Meliphagidae	*Myzomela*	3	2		1						2	2	2				2
Meliphagidae	*Philemon*	4	4	1	3	2	2	2	2	2	4	2	2	1	3	2	4
Meliphagidae	*Phylidonyris*	2	1	1							1			1			1
Meliphagidae	*Plectorhyncha*	1	1	1		1	1	1	1	1	1						
Meliphagidae	*Plegadis*	1		1	1							1	1	1	1	1	
Meliphagidae	*Ramsayornis*	2	2		1						2	1	1	1	1	1	1
Meliphagidae	*Trichodere*	1															1
Meliphagidae	*Xanthotis*	1	1								1						1
Meropidae	*Merops*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Motacillidae	*Anthus*	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1
Muscicapidae	*Zoothera*	2	2								1						1
Nectariniidae	*Nectarinia*	1	1														1
Neosittidae	*Daphoenositta*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Oriolidae	*Oriolus*	2	2	1	2	1	1	1	1	1	1	2	1		2	2	2
Oriolidae	*Sphecotheres*	2	1		1	1		1		1	1	1				1	1
Orthonychidae	*Orthonyx*	1	1								1						1
Otididae	*Ardeotis*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pachycephalidae	*Colluricincla*	4	3	1	3	1	1	1	1	1	3	3	3	1	2	2	3
Pachycephalidae	*Falcunculus*	1	1		1						1	1			1	1	1
Pachycephalidae	*Oreoica*	1	1	1		1	1	1	1	1	1	1		1	1	1	
Pachycephalidae	*Pachycephala*	5	3	1	3	1	1	1	1	1	3	1	3	1	1	1	3
Paradisaeidae	*Ptiloris*	1	1								1						1
Pardalotidae	*Acanthiza*	8	6	4		6	5	4	4	3	5	1		1	1		3
Pardalotidae	*Aphelocephala*	2		2													
Pardalotidae	*Chthonicola*	1	1			1				1							
Pardalotidae	*Gerygone*	7	6	1	4	2	1	2	1	2	4	4	4	1	2	3	5
Pardalotidae	*Oreoscopus*	1	1								1						1
Pardalotidae	*Pardalotus*	3	3	2	1	2	2	2	2	2	3	2	2	2	2	2	3
Pardalotidae	*Pyrrholaemus*	1		1													

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Pardalotidae	*Sericornis*	5	3								3						5
Pardalotidae	*Smicrornis*	1	1	1		1	1	1	1	1	1						1
Passeridae	*Emblema*	1	1	1		1		1				1		1	1		
Passeridae	*Erythrura*	2			1	1		1			1	1			1	1	1
Passeridae	*Heteromunia*	1	1		1							1	1	1	1	1	
Passeridae	*Lonchura*	3	2		2						2	2	1		2	1	2
Passeridae	*Neochmia*	4	4	1	1	2	1	2	1		4	2	1		2	1	4
Passeridae	*Poephila*	3	1		2	1	1	1	1		1	2	2	1	2	2	1
Passeridae	*Taeniopygia*	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Pedionomidae	*Pedionomus*	1		1										1			
Petroicidae	*Eopsaltria*	2	2								1	1	1				2
Petroicidae	*Heteromyias*	1	1								1						1
Petroicidae	*Melanodryas*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Petroicidae	*Microeca*	2	2	1	2	1	1	1	1	1	2	2	2	1	2	2	2
Petroicidae	*Petroica*	1	1	1		1	1	1	1	1	1			1			
Petroicidae	*Petrophassa*	2			1										1	1	
Petroicidae	*Petropseudes*	1			1							1	1				
Petroicidae	*Poecilodryas*	1	1		1						1	1	1		1	1	1
Petroicidae	*Tregellasia*	1	1								1						1
Phasianidae	*Coturnix*	3	3	1	2	2	1	1	2	2	3	1	2	2	2	1	3
Pittidae	*Pitta*	2	1		1						1						1
Podargidae	*Podargus*	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2
Pomatostomidae	*Pomatostomus*	4	1	4	1	1	1	1	1	1	1	1	1	3	1	1	1
Psittacidae	*Alisterus*	1	1								1						1
Psittacidae	*Aprosmictus*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Psittacidae	*Barnardius*	1	1	1		1		1				1		1	1	1	
Psittacidae	*Cyclopsitta*	1	1								1						1
Psittacidae	*Glossopsitta*	1	1								1						1
Psittacidae	*Melopsittacus*	1	1	1	1	1	1	1		1	1	1	1	1	1	1	
Psittacidae	*Neophema*	2		2													
Psittacidae	*Neopsephotus*	1		1													
Psittacidae	*Northiella*	1		1													
Psittacidae	*Pezoporus*	1		1										1			
Psittacidae	*Platycercus*	3	2	1	1	1	1	1	1	1	2	1	1		1	1	2
Psittacidae	*Polytelis*	1		1													

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Psittacidae	*Psephotus*	4		2	1						1	1				1	
Psittacidae	*Psitteuteles*	1	1		1	1	1	1				1	1	1	1	1	
Psittacidae	*Trichoglossus*	2	2			1	1	1	1	1	2						2
Ptilonorhynchidae	*Ailuroedus*	1	1								1						1
Ptilonorhynchidae	*Chlamydera*	2	2	1	1	2	1	1	2	1	2	1	1	1	1	1	1
Ptilonorhynchidae	*Prionodura*	1	1								1						1
Ptilonorhynchidae	*Ptilonorhynchus*	1	1								1						1
Ptilonorhynchidae	*Scenopoeetes*	1	1								1						1
Strigidae	*Ninox*	3	3	2	3	1	1	1	1	1	3	3	3	1	2	1	3
Sturnidae	*Aplonis*	1	1								1						1
Sylviidae	*Acrocephalus*	1	1	1	1						1	1	1	1			1
Sylviidae	*Cincloramphus*	2	2	2	1	2	2	2	1	1	2	2		2	2	2	2
Sylviidae	*Cisticola*	2	2		2	1	1		1		2	2	2	1	1	1	1
Sylviidae	*Eremiornis*	1		1		1		1				1		1		1	
Sylviidae	*Megalurus*	2	2	2	1						1	2	1				2
Turnicidae	*Turnix*	6	4	2	3	4	3	3	4	1	5	4	3	2	3	4	4
Tytonidae	*Tyto*	4	4	1	1	2	1	2	2	1	4	2	1	2	1	1	4
Zosteropidae	*Zosterops*	3	3			1			1	1	1	1	1				1
Mammals																	
Acrobatidae	*Acrobates*	1									1						1
Burramyidae	*Cercartetus*	1									1						1
Dasyuridae	*Antechinomys*	1		1								1		1	1		
Dasyuridae	*Antechinus*	3									2						3
Dasyuridae	*Dasycercus*	2		2													
Dasyuridae	*Dasyuroides*	1		1										1			
Dasyuridae	*Dasyurus*	2	1		1						2	1				1	2
Dasyuridae	*Ningaui*	1		1												1	
Dasyuridae	*Phascogale*	1									1						1
Dasyuridae	*Planigale*	4	2	2	1	3	2	1	2		2	2	1	2	2	1	1
Dasyuridae	*Pseudantechinus*	2		1								1	1	1			
Dasyuridae	*Sminthopsis*	8	2	3	2	3	2	2	1	1	3	3		4	1	2	4
Macropodidae	*Dendrolagus*	2															2
Macropodidae	*Lagorchestes*	1	1		1	1	1	1	1		1	1	1	1	1	1	
Macropodidae	*Macropus*	7	6	3	3	4	3	4	4	3	7	4	4	3	4	4	4
Macropodidae	*Petrogale*	7	2		1	1		1	1		4	1	1		1	1	4

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Macropodidae	*Thylogale*	1	1								1						1
Macropodidae	*Wallabia*	1	1			1		1	1		1						1
Muridae	*Hydromys*	1	1	1	1	1			1		1				1		1
Muridae	*Leggadina*	2	1	1	1	2	1	1		1	1	1		1	1	1	1
Muridae	*Melomys*	2	2		1						2	1	1				2
Muridae	*Mesembriomys*	1									1						1
Muridae	*Notomys*	4		4								1		1	1	1	
Muridae	*Pogonomys*	1															1
Muridae	*Pseudomys*	7	3	4	1	4	2	4	2	3	4	3	1	4	4	3	3
Muridae	*Rattus*	8	4	1	2	2	1	1	1		4	2	4	2	1		5
Muridae	*Uromys*	2	1								1						2
Muridae	*Zyzomys*	2	1		1	1		1			1	2	2		1	1	1
Ornithorhynchidae	*Ornithorhynchus*	1	1								1						1
Peramelidae	*Isoodon*	2	1		1						2		1				1
Peramelidae	*Macrotis*	1		1										1	1	1	
Peramelidae	*Perameles*	1	1								1						1
Petauridae	*Dactylopsila*	1	1								1						1
Petauridae	*Petaurus*	4	2		1	2	1	2	2	1	3	1	1				4
Petauridae	*Pseudochirops*	1									1						1
Phalangeridae	*Trichosurus*	1	1			1	1	1	1	1	1			1			1
Phascolarctidae	*Phascolarctos*	1	1			1	1	1	1	1	1			1			1
Potoroidae	*Aepyprymnus*	1	1			1	1	1	1	1	1						1
Potoroidae	*Bettongia*	1									1						1
Potoroidae	*Hypsiprymnodon*	1															1
Pseudocheiridae	*Hemibelideus*	1															1
Pseudocheiridae	*Petauroides*	1	1			1			1		1						1
Pseudocheiridae	*Pseudocheirus*	1	1								1						1
Pseudocheiridae	*Pseudochirulus*	2															2
Tachyglossidae	*Tachyglossus*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Reptiles																	
Agamidae	*Amphibolurus*	4	1	2	2	3	3	3	1	2	2	1	1	2	1	2	1
Agamidae	*Chelosania*	1			1								1			1	
Agamidae	*Chlamydosaurus*	1	1		1	1		1	1		1	1	1		1	1	1
Agamidae	*Cryptagama*	1												1			
Agamidae	*Ctenophorus*	5	1	5		1	1	1	1	1		3	1	4	2	3	

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Agamidae	*Diporiphora*	7	1	2	4	3	2	2	2	1	2	5	4	3	4	5	2
Agamidae	*Hypsilurus*	1									1						1
Agamidae	*Moloch*	1		1										1			
Agamidae	*Physignathus*	1									1						1
Agamidae	*Pogona*	3	1	2		3	3	1	1	1	2	1		2			
Agamidae	*Tympanocryptis*	5		4		2	2	2					1	4	2	1	
Boidae	*Antaresia*	3	1	2	1	1	1				2	2	1	1	1	1	1
Boidae	*Aspidites*	2	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1
Boidae	*Liasis*	3	1		2						1	2	1	1	2	1	1
Boidae	*Morelia*	3	1	1							2	1					3
Colubridae	*Boiga*	1	1		1	1		1		1	1	1	1		1	1	1
Colubridae	*Cerberus*	1										1					
Colubridae	*Dendrelaphis*	2	1		1	2		2	1		2	1	1				2
Colubridae	*Myron*	1											1				
Colubridae	*Stegonotus*	1			1												1
Colubridae	*Tropidonophis*	1	1		1	1		1	1		1	1	1	1	1	1	1
Elapidae	*Acanthophis*	3	1	2	1	2		2		1	1	1	1	2	2		2
Elapidae	*Cacophis*	2		1							1						1
Elapidae	*Demansia*	6	4	2	4	3	1	3	2	2	4	5	4	4	3	2	4
Elapidae	*Denisonia*	2	1	1		1	1	1			1			1			
Elapidae	*Fordonia*	1											1				
Elapidae	*Furina*	4	2	2	1	2	1	2	1	1	3	1		2	1	1	4
Elapidae	*Hemiaspis*	2		1													1
Elapidae	*Hoplocephalus*	1	1			1		1	1	1	1			1			1
Elapidae	*Notechis*	1		1													
Elapidae	*Oxyuranus*	2	1	1							1		1	1			1
Elapidae	*Pseudechis*	3	1	1	1	2	1			2	2	1	1	2	1	1	2
Elapidae	*Pseudonaja*	5	1	5	3	3	2	3	2		2	3	2	5	3	1	2
Elapidae	*Rhinoplocephalus*	4	1		1	1	1	1	1	1	3			1	1		2
Elapidae	*Simoselaps*	6	1	3	2	2	1	2	1	1	3	1	1	2		2	1
Elapidae	*Suta*	3	2	3	1	2	1	1		2	1	2		2	2	2	1
Elapidae	*Tropidechis*	1															1
Elapidae	*Vermicella*	2	1	1	2	1				1	1	1		1		1	1
Gekkonidae	*Carphodactylus*	1															1
Gekkonidae	*Crenadactylus*	1		1								1			1		

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Gekkonidae	*Cyrtodactylus*	1									1						1
Gekkonidae	*Diplodactylus*	10	4	5	3	4	3	3	2	2	2	5	1	9	3	4	1
Gekkonidae	*Gehyra*	10	4	4	3	3	3	3	2	2	4	6	3	5	5	4	3
Gekkonidae	*Hemidactylus*	1			1											1	1
Gekkonidae	*Heteronotia*	2	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1
Gekkonidae	*Lepidodactylus*	1															1
Gekkonidae	*Lucasium*	1		1													
Gekkonidae	*Nactus*	2									1						2
Gekkonidae	*Nephrurus*	5	1	4	1	1		1	1	1	1	1		2	1	1	
Gekkonidae	*Oedura*	6	3	2	2	4	2	4	2	1	5	2	2	2	2	2	5
Gekkonidae	*Onychogalea*	1			1							1	1	1	1	1	
Gekkonidae	*Rhynchoedura*	1	1	1	1	1	1	1		1		1	1	1	1	1	
Gekkonidae	*Rostratula*	1										1				1	
Gekkonidae	*Saltuarius*	1									1						1
Gekkonidae	*Strophurus*	4	2	2		2	1	2	1	1	1			2			2
Pygopodidae	*Delma*	7		3	2	1	1		1		2	3	2	2	4	3	3
Pygopodidae	*Lialis*	1	1	1	1	1	1	1			1	1	1	1	1	1	1
Pygopodidae	*Paradelma*	1	1			1		1									
Pygopodidae	*Pygopus*	2	2	1	1	1	1	1	1		1	1	1	1	1	1	1
Scincidae	*Anomalopus*	1				1			1		1						
Scincidae	*Calyptotis*	1															1
Scincidae	*Carlia*	16	7		5	4	1	3	4	1	10	4	2	4	4	3	11
Scincidae	*Coeranoscincus*	1	1								1						1
Scincidae	*Cryptoblepharus*	5	3	2	3	3	2	3	3	2	3	3	3	2	3	1	3
Scincidae	*Ctenotus*	43	6	24	10	11	5	9	5	6	11	9	5	20	10	11	6
Scincidae	*Cyclodomorphus*	3	1	2							1			1			1
Scincidae	*Egernia*	6	3	2		3	2	1	2	2	4	1	1	2			2
Scincidae	*Eremiascincus*	2	1	2		2				2	2	2		2	1	1	
Scincidae	*Eulamprus*	6	1			2		2	2		3						6
Scincidae	*Glaphyromorphus*	11	1		2	1		1			3	1	1	2		2	7
Scincidae	*Gnypetoscincus*	1															1
Scincidae	*Lampropholis*	5	3								1						4
Scincidae	*Lerista*	21	4	5	2	7	3	7		3	8	1	2	7	1	5	1
Scincidae	*Lygisaurus*	6	1			1		1	1	1	2						5
Scincidae	*Menetia*	5	3	2	2	3	2	3	2	3	3	2	1	3	2	2	1

Family	Genus	n	BBN	CHC	DAB	DEU	DEU1	DEU2	DEU3	DEU4	EIU	GFU	GUC	MGD	OVP	STU	WET
Scincidae	*Morethia*	5	2	4	2	2	2	2	2	1	2	2	2	3	1	2	1
Scincidae	*Notoscincus*	1		1	1						1	1	1		1	1	
Scincidae	*Proablepharus*	2	1	1	1	1	1	1	1		1	2	1	2	1		1
Scincidae	*Saproscincus*	6	1								2						6
Scincidae	*Techmarscincus*	1															1
Scincidae	*Tiliqua*	2	1	1	1	2	2	2	1	1	1	2	2	2	2	2	1
Scincidae	*Trachydosaurus*	1		1										1			
Typhlopidae	*Ramphotyphlops*	14	4	4	5	3	1	2	2	2	4	3	1	4	4	3	4
Varanidae	*Varanus*	19	3	9	10	6	2	4	5	2	7	13	6	6	9	5	7

Chapter 3. Vertebrate fauna composition patterns and environmental gradients.

"The Cape River, another tributary of the Burdekin, led right into the unknown country, hilly and rough. Red streaks appeared where desert sandstone overlay plutonic rock. In ghastly contrast to the red conglomerate, sparse white spinifex grass grew in wiry tussocks. The country became frightfully rough. The creeks could be counted on only for a few miles, and when they reached the open, were lost in swamps. He followed up the rocky gullies, and inaccessible ridges barred advance………through an opening in the sparse forest Christison caught a glimpse of a plain - the Forty Mile Plain - and knew that he had come out onto the western watershed. The character of the country changed. The forest gathered into belts of timber of various kinds that intersected plains of Mitchell grass. The air was lighter and drier - an eager, hungry air of diamond brightness."

(pp. 49-50. Account of Robert Christison's first traverse of the Desert Uplands from Cape River, across the Alice Tableland, and into Prairie-Torrens Creek Sub-region, Bennett 1928).

Introduction

Two contrasting landscape processes influence the tropical savannas of northern Australia: a strong climatic seasonality and gradual environmental variation over large geographic areas (Williams *et al.* 1996b; Ludwig *et al.* 1999b; Woinarski 1999b; Woinarski *et al.* 1999b; Cook and Heerdegen 2001). The annual climatic fluctuation - a short intense wet season followed by a long period of very dry conditions - creates a corresponding resource pulse and decline (Woinarski 1999b; Cook and Heerdegen 2001). The tropical savanna biota responds to these conditions using a variety of strategies. These include nomadism and resource tracking or the use of heterogenous home ranges and resource switching (Woinarski *et al*. 1992c; Woinarski and Tidemann 1992; Franklin 1999; Woinarski *et al.* 2000a, b). Sometimes species contract to refugia, become dormant or locally extinct, only to subsequently irrupt when conditions become favourable (Carstairs 1974; Dickman *et al.* 1999; Fensham and Holman 1999). These patterns can be exacerbated by climatic extremes (Fensham and Holman 1999) or inappropriate fire regimes (Londsdale and Braithwate 1991; Bowman and Panton 1993; Franklin 1999; Russell-Smith *et al.* 2002), which can override the annual cycle causing wholesale change.

The gradual environmental variation provides widespread ecological connectivity within tropical savannas (Woinarski 1999b). In some areas small discontinuities and refuges may punctuate the landscape. However, local and regional variability of topography, moisture and soils generally control the local and regional diversity patterns of plants (Bowman *et al.* 1993; Bowman 1996) and animals (Whitehead *et al.* 1992; Woinarski and Gambold 1992; Woinarski *et al.* 1999b). Coupled with a pattern of traditional patchy burning and localised storms early in the wet season, this creates a complex but fluid mosaic of habitat (Russell-Smith *et al.* 1998; Yibarbuk *et al.* 2001). The consequences for biotic assemblages are twofold: species are mobile, dispersed and widespread; and changes in prevailing conditions or management can affect species and environments over large areas (Woinarski 1990; Franklin 1999; Bowman 2001). Therefore a conservation management framework proposed for tropical savannas is one that recognises a transient biota reliant on a geographically variable and widespread resource base that requires regional maintenance, understanding and protection (Woinarski 1999b). This is in contrast with a vision for both arid Australia and the coastal wet tropical rainforests, where protection of significant refugia and pockets of high fertility and diversity, is a priority (Keto and Scott 1986; Stafford Smith and Morton 1990). Maintenance of the tropical savanna landscape variation is in conflict with pastoral management which seeks to homogenise the landscape via tree-clearing, promotion of a monoculture of introduced pasture, addition of multiple water points and removal of regular mosaic burning, to create consistent productive environment for livestock (Ash *et al.* 1997), an attitude that is not necessarily successful for grazing of livestock (Winter 1990) or wildlife diversity (Landsberg *et al.* 1997).

In the Northern Territory there has been recent recognition in the value of examining the underlying regional and biogeographic biotic and abiotic patterns in tropical savannas, and the significance of this data to adequately inform conservation planning (Woinarski and Braithwaite 1990; Whitehead *et al.* 1992). One impetus has been the acknowledgement that these northern landscapes are currently intact and diverse, and despite a long history of pastoralism, less modified than contemporary agricultural areas in south-eastern Australia (Woinarski and Braithwaite 1990). An opportunity exists to plan carefully for future biodiversity protection (Woinarski 1999b). Consequently there has been a subtle evolution from surveys that produced biological inventories of areas perceived to be of high conservation value (Gibson 1986; Woinarski 1992; Woinarski *et* *al.* 1992a, b), to targeted landscape and bioregional surveys that examine not only the distribution and abundance, but environmental determinants of finer-scale local and regional species patterns such as climate, landscape, soils, fragmentation, fire and grazing (Woinarski *et al.* 1988; Woinarski 1990; Woinarski and Gambold 1992; Menkhorst and Woinarski 1992; Woinarski and Fisher 1995a, b; Williams *et al.* 1996b; Ludwig *et al.* 1999a, b; Price *et al.* 1999; Woinarski *et al.* 1999a, b; Woinarski *et al.* 2000a, b; Woinarski *et al.* 2001b). These have also incorporated specific identification of bioregional conservation priorities (Price *et al.* 1995; Price *et al.* 2000; Woinarski 1998; Fisher 2001a). Underpinning these were primary overviews of biogeographic patterns and conservation foci that formed the basis of this research (Bowman *et al.* 1988; Woinarski 1992; Woinarski and Braithwaite 1992; Whitehead *et al.* 1992).

In contrast to the Northern Territory, the biological patterns and processes of the tropical savannas of northern Queensland are surprisingly poorly known and inadequately surveyed, despite the value of regional fauna surveys for conservation planning being historically recognised and undertaken in the state between 1964 and 1975 (for review see Kirkpatrick and Lavery 1979), and continued into the early 1980's (Crossman and Reimer 1986; McGreevy 1987; Blackman unpubl. data; Gordon unpubl. data, Queensland Parks and Wildlife Service). Though the intent of the work was to provide a baseline to monitor long term change (Kirkpatrick and Lavery 1979), the opportunistic and descriptive nature of the surveys, essentially the derivation of qualitative species lists with no quantification of abundance or environmental pattern, and the already fragmented and disturbed nature of the landscapes being surveyed (Crossman and Reimer 1986; McGreevy 1987), suggest this aim was partly ambitious. There was also an inherent bias in the sampling to cultivated landscapes and habitats of production potential. For example Kirkpatrick and Lavery (1979) state “heath is a recognisable type frequently identified on the coastal lowlands of southern Queensland but of doubtful special significance to the vertebrate fauna” and as such did not sample or recognise this vegetation type in discussion. However heath in this region is highly significant for restricted and threatened species, such as the Ground Parrot *Pezoporus wallicus* (MacFarland 1991). Most of the completed surveys also focussed on Queensland's fertile coastal belt, the biological significance and variation of the broader tropical savannas seemingly dismissed - “while it is imperative that the whole fauna of the State be assessed, much of the country, particularly inland situations is uniform over large areas." (p. 186, Kirkpatrick and Lavery 1979). However, some significant surveys in the broad monsoonal zone were completed, albeit near-coastal: the Townsville and Burdekin areas in the Northern Brigalow Belt bioregion (Lavery 1968; Lavery and Johnson 1968; Lavery and Johnson 1974; Lavery and Seton 1974); the Dalrymple Shire in the 1970's and 1980's which includes parts of the Desert Uplands and Einasleigh Uplands (Blackman *et al.* 1987; Blackman unpubl. data, QPWS); the Emerald Shire in the Northern Brigalow Belt (G. Gordon unpubl. data, QPWS) in the 1970's and 1980's; and parts of Cape York Peninsula in the 1980's (Winter and Atherton 1985).

A bias against inventory and survey in the broad savannas may stem from consistent presumptions that the impacts on fauna by pastoralism are perhaps benign or very localised (Kirkpatrick and Lavery 1979; McKenzie 1981; Curry and Hacker 1990; Read 2002), despite firm evidence to the contrary (Krefft 1866; Lunney 2001). Instead research effort in tropical savannas has focussed on maintenance of ecosystem well being for grazing (Burrows *et al.* 1990; Landsberg *et al.* 1998; Ash *et al.* 1997), the expectation perhaps that what is a sustainable landscape for cattle *ipso facto* has neutral biodiversity impacts (Curry and Hacker 1990). In Queensland there is perhaps still a disparity between vertebrate fauna studies concentrating on the extensive savanna rangelands (see reviews in Sattler and Williams 1999; Woinarski *et al.* 2001a) and those areas perceived to have higher intrinsic biodiversity significance and nature conservation value (e.g Cape York Peninsula, Abrahams *et al.* 1995; Wet Topics, Williams *et al.* 1996c; Channel Country McFarland 1991; southeast Queensland forests, Queensland Government 1997). However there is burgeoning effort on studies examining the interaction of rangeland biota (predominantly flora), their environmental determinants and the impacts of current land management regimes (Ash *et al.* 1997; Thurgate 1997; Crowley and Garnett 1998; Fensham 1998a, b; McIvor 1998; Fensham and Holman 1999; Fensham and Skull 1999; Fensham *et al.* 2000; Fairfax and Fensham 2000; Ludwig *et al.* 2000; Hannah and Thurgate 2001; Fisher 2001a; Woinarski and Ash 2002; Woinarski *et al.* 2002). Bioregional or smaller-scale surveys are still rare (Sattler and Williams 1999), and generally descriptive or review-based (MacFarland 1991; Johnson 1997; Fisher 1999; Sattler and Williams 1999).

Regardless of the perception of the merits for study of various biological systems, species or regions over one another, determination of processes that control biotic assemblage structure and diversity is fundamental to the conservation and management of any ecosystem (Ricklefs and Schluter 1993; Brown 1995; Gaston and Blackman 2001). There is an hierarchal range of processes which mould extant species assemblages (Ricklefs and Schluter 1993), ranging from local competition, predation and other intraspecific interactions (Williams *et al.* 2002), metapopulation and patch dynamics (Hanski and Gilpin 1991; Cody 1994), landscape habitat heterogeneity and selection (Woinarski *et al.* 1990; Williams and Hero 2001), regional biogeographic effects (Moritz *et al.* 1997; Williams 1997), and continental and global-scale evolutionary episodes (Schodde 1982; Ford 1987; Winter 1997). There is debate regarding the relative influence of each (Ricklefs and Schluter 1993), though it is clear that all will affect the species assemblage in some capacity (Williams *et al.* 2002). The scale of examination of any system will naturally influence the perception of which process is controlling the pattern (Weins 1989).

Recent studies in the Wet Tropics Bioregion have highlighted the significant influence of vicariant biogeographic history and climate variation on regional patterns of vertebrates (Moritz *et al.* 1997; Williams and Pearson 1997; Winter 1997; Williams and Hero 2001), and local habitat complexity and spatial heterogeneity on mammal assemblage composition (Williams *et al.* 2002). More pertinent examples from Australian tropical savannas have indicated similarly the historical evolution of assemblages in refugia (Woinarski *et al.* 1992a, b), broad biogeographic patterns of biota due to clear climatic and environmental gradients (Woinarski 1990; Woinarski *et al.* 1992a; Williams *et al.* 1996b; Fensham *et al.* 2000) and local species variation due to finer-scale habitat variation and heterogeneity in birds, reptiles and mammals (Woinarski and Tideman 1992; Woinarski and Gambold 1992; Woinarski *et al.* 1999b).

However as alluded to earlier, there is seemingly an important disparity in the scale of effect between tropical savanna and wet tropical environments, which has implications for vertebrate fauna assemblage patterns and distribution in each. In the wet tropics spatial and habitat variation is discrete due to sharp altitudinal, climatic and vegetation changes, as influenced by regional biogeographic history and topography. Consequently the fauna is diverse, endemic-rich and strongly patterned (Williams and Pearson 1997; Williams *et al.* 2002). In contrast, the tropical savannas are characterised by broad environmental inter-connectivity and gradual climatic and altitudinal variation, resulting in widespread landscape heterogeneity, moulded by continental-scale biogeographic events (Bowman 1996; Woinarski 1999b). The result is a more subtle mosaic of fauna distribution, broadly patterned, with perhaps less well defined local habitat relationships (Woinarski and Gambold 1992; Woinarski 1993). There are still pockets of species-rich refugia, characterised by strong habitat association (e.g. sandstone ranges: Woinarski *et al.* 1992a, b), but pattern among the generally prevalent biota is more diffuse, particularly in the predominant *Eucalyptus* woodlands (Woinarski and Fisher 1995b; Woinarski *et al.* 1999b).

This suggests two important facets of tropical savanna assemblage structure. Firstly, there is generally a core recognisable species assemblage coupled with a more transitory peripatetic community (Woinarski 1990; Cody 1994). Fauna are contingent on a more fluid and constantly changing patch dynamic, with a regional and local species richness being highly interdependent. Secondly, tropical savanna communities may be at non-equilibrium, being composed of a composite of species structured according to the periodical continuum of available resources, and local ecological interactions that vary in response to these conditions (Weins 1984; Cody 1994; Walker 1997). As such these fauna assemblages may consist of large numbers of functionally redundant, opportunistic and loose patterns of species, susceptible to large stochastic events and constantly changing in proportion due to prevailing environmental conditions (Weins 1984; Walker 1997). In other words tropical savanna biota are much more mutable, resource and climate-driven entities, rather than constrained by a strong local habitat association (e.g. rainforest). These characteristics have been suggested as a possible foundation for calamitous species loss and decline in northern Australia for specific functional groups. Though the communities are adapted to unstable environmental conditions, widespread change that imposes an unnatural state of resource limitation or homogenisation, such as those associated with pastoral and fire management, create a regulation of resources (e.g. loss of seasonal seed spread) which affect specialised groups (e.g. granivorous birds). The ecosystem has a capacity to deal with environmental fluctuations, which declines progressively as species are gradually lost (Doherty *et al.* 2000). Eventually these changes pass a threshold and then, due to the inherent connectivity resonate across entire landscapes and swamp complete functional groups (Burbidge and McKenzie 1989; Franklin 1999; Woinarski 1999b).

The Desert Uplands Bioregion has been very poorly surveyed for vertebrate fauna, despite recognition of the region as a zone of high biogeographic interest and significance (Ford 1986). A number of early explorers traversed the area (Smith 1994), though there are few observations of the biota save descriptions of landscapes, waterways and pastures (Landsborough 1862; Bennett 1928; Buchanan 1933; Mitchell 1969). Early museum collectors passed through the northern reaches (Le Soeuf 1920; Wilkins 1929; Hall 1974), with little data available except for discursive travelogues and species lists. More recently the Cape-Campaspe sub-region was included in a detailed survey of the Dalrymple Shire (Blackman *et al.* 1987), and though the results were included in the biogeographic analysis (Chapter 2), no formal publication or analysis of the results have ever been completed for review. Munks (1993) examined the distribution of arboreal fauna in the Prairie-Torrens Creek sub-region, reporting mainly on the distribution and feeding ecology of Koala *Phascolarctos cinereus*, Brush-tailed Possums *Trichosurus vulpecula* and Sugar Gliders *Petaurus breviceps*, and some areas of the Desert Uplands were included in a review of Pebble-mound Mouse *Pseudomys patrius* records and distribution (Van Dyck and Birch 1996).

This study represents the first concerted examination of the patterns of composition and distribution in the vertebrate fauna of the Desert Uplands bioregion. In chapter 2, I reviewed the composition of the entire suite of vertebrate fauna species recorded for the Desert Uplands in the context of the known zoogeography of northern Australia. Both data from this current survey, and a range of secondary sources was utilised. The character of the extant fauna assemblage was clearly a function of its geographical position, and the distribution of many sibling and taxonomically related species, demonstrated turnover, sympatry and parapatry within the Desert Uplands. Neighbouring Queensland bioregions influence the nature of the fauna and environment of the Desert Uplands, but there are also discrete similarities in the larger arc of semi-arid tropical savannas spread across northern Australia.

In this chapter I describe the results of a systematic quadrat-based vertebrate fauna survey of the Desert Uplands. In particular I examine the patterns of distribution, composition and abundance of species recorded within the bioregion, and the environmental factors that determine the distribution and relationships of assemblages within the regional ecosystems sampled. I consider whether these assemblages vary in a predictable fashion with environmental gradients. The similarities and differences in relation to patterning in other semi-arid savanna vertebrate communities are examined. I also test possible predictors of local species richness across the range of quadrats sampled. More specifically the questions asked are:

- is local species richness best explained by geographic factors or by productivity? Area and shape of regional ecosystems sampled were assessed as a measure of geographic influence, as was a range of factors considered surrogates of point productivity (basal area, ground cover or strata complexity), and measures of productivity itself (landscape characteristics based directly on soil nutrient, moisture and pastoral capability);
- is there any seasonal variation in the pattern of species recorded? Though it is recognised that vertebrate fauna can express cycles of great temporal and spatial variability, and a relatively short term study such as this has only limited ability to describe cycles that course over tens and hundreds of years, some broad seasonal effects can be expected;
- what are the broad patterns of species assemblage and what environmental and habitat variables control or predict this assemblage or spatial variation?; and
- what environmental factors may be controlling the distribution and abundance of species and guilds, and do these factors correspond to known biology of the species?

Methods

Study sites

The sampling sites were all within the Desert Uplands bioregion (see chapter 1 for general environment and location). Quadrats were stratified to sample the range of regional ecosystems (see chapter 1 for definition, Sattler and Williams 1999). Initially the characteristics, distribution and variation in the Desert Uplands landscapes and regional ecosystems were reviewed by reference remote sensed satellite imagery, expert advice (Gethin Morgan, QEPA, pers. comm.) and extensive reconnaissance trips. As such, quadrats were located to sample the geographical extent and environmental variation in the major regional ecosystems of the Desert Uplands and in proportion to their area, skewed to allow increased sampling of regional ecosystems of limited extent, and widespread regional ecosystems. In widespread regional ecosystems, sites were chosen to sample climatic and geographic extremes, whereas in restricted regional ecosystems, sampling was naturally localised. Regional ecosystems that were too small to map, could not be identified due to poor definition or were outliers from other bioregions were not considered for sampling. Sites were located on properties that represented a variety of regional ecosystems, were logistically accessible and were managed by landholders sympathetic to the survey.

Vertebrate sampling

The standardised quadrat was a nested trap and search array, modified from Woinarski and Fisher (1995a). The base quadrat area was a 50 x 50m square demarcated by twenty Elliott traps placed 10 m apart along the perimeter and two cage traps placed at opposing corners. Four pitfalls arranged in a ‘T’ configuration (30 and 20 m of drift fence) were placed along one edge of this array, with the stem of the ‘T’ projecting into the quadrat. Elliott and cage traps were baited with peanut butter, honey and oats, and alternatively with pet biscuits. Traps were checked in the morning and afternoon and opened for a 96-hour period. Trapping was supplemented by timed searches: four instantaneous morning bird counts within a 1 ha area, centred on the 50x50 m quadrat, and two diurnal and two nocturnal searches each of 30 minute duration conducted within the trapping square. Nocturnal and diurnal counts included active (log rolling, litter raking) and passive (looking for eye-shine, listening for nocturnal birds) searches.

Where possible, quadrats were positioned more than 500 m from the nearest unit edge, more than 200 m from fence-lines or tracks, and between 3-5 km from water-points. All quadrats were located at least 500 m from another quadrat, and in most cases the minimum distance apart among quadrats at any site was over 2 km. A total of 158 quadrats was sampled, 105 sampled in both the wet (October-March) and dry season (April-September), and an additional 53 in the wet season only. This represented 28 regional ecosystem types, and these were sampled across 14 properties.

All data collected were entered into a larger Desert Uplands bioregional database that included primary survey data and all secondary data records. Only data accurately geocoded and from verifiable sources were included. From this data set, species presence, abundance and distribution could be summarised and used for later analysis. Quadrat abundance (the relative abundances of all species records for one discrete sampling period) or total abundance (the relative abundances of all species records for a matched wet and dry sample) was generally used in subsequent analyses.

Environment and habitat sampling

A range of environmental and habitat variables was recorded for each quadrat. These were:

- unique quadrat identifier and season; date; property name; sub-region, regional ecosystem; altitude; landzone; latitude and longitude using a GPS; written description of location;
- landform element (hilltop, hill-slope, ridge/scarp, dune, flat/plain, drainage line, lake/swamp); landscape position (on, off, mid, flat); slope (flat, gentle, steep);
- nearest edge (<1 km, 1-3 km, 3-5 km, >5 km); patch size (<10 ha, 10-100 ha, 100-1,000 ha, 1,000-10,000 ha, >10,000 ha);
- distance to permanent water (<1 km, 1-3 km, 3-5 km, >5 km); distance to ephemeral water (<1 km, 1-3 km, 3-5 km, >5 km);
- fire impact, weed impact, cattle damage, tree death (categories 0= no visible impact to 5 = recent major impact affecting all of quadrat);
- rock cover of pebbles <0.6 cm diameter, small stones 0.6-2 cm, stones 2-6 cm, small rocks 6-20 cm, rocks 20-60 cm, big rocks 60 cm-2 m, boulders >2 m, continuous outcrop (categories 0=none, 1=<2%, 2=2-10%, 3=10-20%, 4=20-50%, 5=50-90%, 6=>90%);
- ground cover of bare, rock, hummock grass, tussock grass, sedges, forbs, litter, ferns (total = 100%);
- rock type (basalt, sandstone, laterite, limestone, alluvial, other); soil colour (white, yellow, red, orange, brown, grey, black); dominant soil type (sand, sand-loam, sand-clay, loam, clay-loam, clay, cracking clay, peat, rock);
- number of logs >10 cm diameter around perimeter; number of standing dead trees >10 cm diameter; number of fallen trees, trunks >10 cm diameter;
- number of soil cracks along one 50m edge; modal size of cracks;
- number of termite mounds; modal height of termite mounds;
- average canopy height; canopy richness; canopy crown cover percent;
- total basal area (m^2/ha) derived from average of five Bitterlich sweeps, one from each corner and one central; dead basal area; live basal area;
- average ground-stratum height; ground-stratum richness; ground-stratum crown cover percent;
- foliage profile cover score for strata >10m, 5-10m, 3-5m, 1-3m, 0.5-1m; <0.5m (categories 0=0, 1=0.1-5%, 2=5-10%, 3=10-25%, 4=25-50%, 5=50-75%, 6=>75%).

Habitat variables were measured only once for each quadrat except for items that varies with season (e.g. ground cover), which were measured twice.

Plant sampling

For each 50x50 m quadrat, floristic data were recorded each time it was sampled for fauna. Only plants with at least 2% cover were identified. Data collected included species name (or collection if needing further examination); average height; foliage projective cover (categories, 1=2-5%, 2=5-10%, 3=10-25%, 4=25-50%, 5=50-75%, 6=>75%); level of fruiting or flowering (categories 1=few on scattered plants, 2=abundant on few plants or moderate on most, 3=abundant on most plants); basal area for canopy species (using a Bitterlich gauge), the average scored from four corners and one central sweep. Any plant species that could not be identified was collected and pressed, and identified at a later date using keys and other reference material, or by staff at the Queensland Herbarium.

Vertebrate species composition and groups

The composition of vertebrate species in the quadrats was examined with ordination using semi-strong hybrid multi-dimensional scaling (SSHMDS) derived from Bray-Curtis association (dissimilarity) indices (Belbin 1991, 1995). Ordinations used range transformed vertebrate abundance data, and only species recorded in more than one quadrat were used. Hierarchical agglomerative clustering was undertaken using the flexible UPGMA routine in PATN (Belbin 1995) and the Bray-Curtis association measures. Characteristic or typical fauna of each group was identified using the SIMPER routine in PRIMER (Clarke and Gorley 2001) and the Bray-Curtis dissimilarity measures. SIMPER (similarity percentages) compares the average dissimilarity between all pairs of intra-group samples, and then identifies the separate percentage contribution from each species. This routine distinguishes species that are generally found at consistently high abundances within samples and can be used as possible discriminators between groups, particularly in the case where groups have been defined based on species abundances and compositions of samples. Total species richness and mean sample richness for taxa in each group were calculated, as well as mean abundance per quadrat for species in each group. Characteristic vegetation was also defined by identifying the regional ecosystems that were represented by the quadrats in each group.

Environmental gradients

Principal axis correlation (PCC) was used to examine the correlation between environmental and habitat measures with the ordination pattern. PCC is a multi-linear regression program designed to identify how a set of attributes can best be fitted to an ordination space (Belbin 1995). The resultant output identifies the direction of best fit and a correlation coefficient. A Monte Carlo randomisation technique (MCAO) using 500 permutations was undertaken to test the statistical significance of the correlation coefficient of each PCC vector (Belbin 1995). Mean scores for each significant vector were calculated for each group and the vectors were presented on the ordination to indicate direction of effect.

Plant species composition and correlation to fauna

The composition of plants in the quadrats was examined with ordination also using SSHMDS and Bray-Curtis dissimilarity (Belbin 1995). Ordinations used cover abundance scores, and only species recorded in more than one quadrat were used. The ordination was labelled with the fauna groups (n=13) in order to examine how well the distribution of quadrats due to plant composition corresponded to the fauna.

Analysis of similarity (ANOSIM) (Clarke 1993) was used to examine how well the imposed fauna group categories account for plants composition. ANOSIM is an approximate analogue to standard univariate 1-way ANOVA tests, and allows the examination of assemblage differences between groups of samples specified by *a priori* treatments (Clarke 1993). The test is built on a simple non-parametric permutation procedure applied to the (rank) similarity matrix underlying the ordination (Clark and Green 1988). The resultant statistic (Global R) generally lies between 0 and 1, and tends toward 1 when replicates within sites are more similar to each other than are replicates from different sites, and towards 0 when the null hypothesis is true (Clark and Warwick 1994). In this case the relationship between fauna groups (13 classes) was examined for a range of plant dissimilarity matrices, derived from quadrat by species arrays scored by cover abundance, basal area of the species and height of species, and subsets of composition by cover abundance for the canopy, mid-storey and ground strata. In the case of quadrats lacking an abundance or score for a particular measure (e.g. basal area, mid-storey trees, canopy trees), an additional column was added (e.g. no basal area, no canopy) and that quadrat here was given a score of 1 and other quadrats a score of 0.

The correlation between plant and fauna composition was examined via Mantel type permutations tests (RELATE in PRIMER, Clarke and Gorley 2001). This test calculates rank correlation coefficient (Rho) between all respective elements of the dissimilarity matrices. Standardised Bray-Curtis dissimilarity matrices derived from abundance data were used, and a permutation test (n=999) was applied to the matching coefficients to identify significance of the coefficient (number of permuted statistics greater than or equal to Rho, where Rho=1 indicates a perfect match) (Clarke and Gorley 2001). Comparisons were made between all vertebrates, birds, mammals and reptiles, and the plant dissimilarity matrices derived for the ANOSIM as described above.

Vertebrate guilds, family and species response to environment

Generalised linear modelling was used to examine the variation in abundance of a range of species and composite vertebrate groups (bird guilds, mammal and reptile families) in each quadrat (Crawley 1993). Bird species were assigned to guilds after Woinarski and Tidemann (1991) and Fisher (2001a). However given the large number of species recorded (n=227) and the large range of environmental variables measured for each quadrat (>35), it was decided to refine the process of modelling to identify a more meaningful set of patterns and responses. Models over-populated with explanatory terms are unwieldy to interpret and, although they may be reflective of moderately complex ecological systems they generally fail to identify key determinants of species abundance. Therefore a subset of factors was derived from the larger list. Initially the set of 10 most significant environmental gradients identified in the PCC were utilised (see Results: *Environmental gradients* and Table 3.3), as these were considered key determinants of the assemblage patterns reported. However preliminary investigation resulted in models with up to eight estimates, so a subset of six variables was chosen (basal area, foliage projective cover between 1-3 m, hummock grass cover, tussock grass cover, bare ground cover and soil type). Though this choice seems arbitrary, they were chosen as being: the most common and significant terms consistently being identified in the preliminary, exploratory modelling, as being the most reflective of broad and different habitat resources, and representing the key and most divergent environmental vectors on the ordination. Given the potential for model complexity, I eschewed consideration of interaction terms. In addition only species recorded in ten or more quadrats were used.

These six factors were then used to derive minimum adequate models for species and guilds, using a backwards-stepwise elimination and a Poisson (log-link) error distribution, as this provides the best fit to count data that contain many zero values (Crawley 1993). Initially I examined the distribution of the response and explanatory variables, and found that none needed transformations. Percentage variance explained by the final model is derived via the difference in goodness of fit in a model with no terms and the final model. The pattern of response was examined by illustrating the predicted distribution against abundance groups of species or guilds sharing significant variables.

Influences of area, habitat heterogeneity and productivity species richness

The relationships between quadrat species richness, productivity and areal characteristics of the regional ecosystem sampled were examined using generalised linear modelling. For each quadrat, total richness for all vertebrates, birds, reptiles and mammals was calculated, as were eight higher order factors:

- the area of the regional ecosystem in which the quadrat was located (equivalent to the mapped polygon size);
- the shape index (si = perimeter/2$(\pi\text{*area})^{0.5}$) of the regional ecosystem sampled. A high shape index equates to a long thin, or convoluted polygon unit (e.g riparian units, SI=5.0) and a low shape index to a smooth-edged round polygon (e.g. uniform sand plain, SI= 1.5);

- the total area of that regional ecosystem in the entire bioregion (i.e. the sum of all polygons of that unit); and
- the average shape of the regional ecosystem throughout the bioregion;
- canopy tree basal area of the quadrat;
- total vegetation ground cover of the quadrat;
- landzone rank. As each regional ecosystem occurs in a particular land zone based on underlying geology (Chapter 1), these can be ranked according to known soil nutrient, soil structure, moisture and carrying capacity characteristics (Dr M. Lorimer pers. comm., Environment Protection Agency). Six categories were identified (1 = low to 6 = high productivity), and Table 3.7 indicates which regional ecosystems belong to which category. There is little relationship between vegetation structure and landzone productivity; and
- structure classes. Structure simply reflects the complexity of the vegetation strata, and each quadrat was assigned using one of five broad categories that reflect the increasing complexity of the vertical strata: grassland (no tree cover); heath (shrub or very low tree cover); *Acacia* woodland (intermediate canopy height, but uniform structure with little mid-storey or ground cover complexity); *Eucalyptus* woodland (well formed woodlands with a range of mid-storey and ground cover structural diversity); and riparian woodland (tall tree cover, complex mid-storey and ground cover). Vegetation structure and biomass is considered an adequate surrogate measure of productivity (Southwood 1996).

Examination of the distribution of the richness data again indicated that the use of a normal (log-linear) error distribution was necessary. Initially the variation in species richness in each quadrat was tested independently to examine the relative effect of each term (significance and deviance explained). All model terms were then used to derive a minimal adequate model, using backward stepwise elimination (Crawley 1993). The final model represents the lowest number of terms that represents the highest percentage deviance explained.

Results

A total of 227 species comprising 119 birds, 22 mammals, 75 reptiles and 11 amphibians were recorded from the 158 wet season samples. Of these only 36 species were recorded in a single quadrat. Within the 105 composite seasonal samples, 228 species were recorded comprising 121 birds, 24 mammals, 71 reptiles and 12 amphibians.

Initially both the 105 paired quadrat samples and the 158 wet season samples were analysed by ordination and classification, and for higher-order effects on richness using generalised linear modelling. There was no pronounced difference in patterns between the two data sets and only minor difference in the total species richness and abundance. Therefore the 158-quadrat set was used, giving a slightly wider spread of sites and regional ecosystems. Seasonal differences were considered in other analyses, using the paired quadrats. For the initial analyses examining species composition and its relationship to environmental and geographic factors, all frog species were excluded, because their occurrence in the data sets was highly influenced by rainfall events around the time of sampling. Introduced species (House Mouse *Mus musculus*, Black Rat *Rattus rattus*, Feral Pig *Sus scrofa* and Cane Toad *Bufo marinus*) were excluded from analysis as they were sporadically encountered and the rationale of the survey was the examination of patterns in native species.

Seasonal variation of vertebrates

There was a significant seasonal difference in the abundance of 36 species (comprising 22 birds and 14 reptiles) based on matched-pairs analysis of the 105 quadrats, which were repeat-sampled (Table 3.1). There was no significant seasonal difference for the remaining 160 species recorded from at least two quadrats. Of the 14 reptiles with significant seasonal variation, 13 were more abundant in the wet season; only the small fossorial skink *Menetia maini* was more abundant in the dry season. Of the birds, 12 were more abundant in the dry season and 10 in the wet season. Eleven of the birds are known seasonal migrants (Blakers *et al.* 1984), Australian Bustard, Brown Songlark, Black-faced Cuckoo-shrike, Pallid Cuckoo, Dollarbird, Olive-backed Oriole, Red-capped Robin, Grey Fantail, Red-backed Kingfisher, Sacred Kingfisher, Red-chested Button-quail, while the remainder are either locally nomadic tracking water, nectar and seed resources, or exhibit behavioural characteristics (e.g. more vocalisations) which made them more detectable in one season.

Table 3.1 Seasonal differences in abundance for species. Data indicates mean abundance per quadrat across 105 repeated samples. z = the Wilcoxon matched pairs test statistic. Higher values are denoted in bold. Only significant species tabulated. Probability levels are *p<0.05, **p<0.01, ***p<0.001.

Species	Common name	Dry	Wet	z	p
Birds					
Acanthiza reguloides	Buff-rumped Thornbill	0.07	**0.12**	1.80	*
Ardeotis australis	Australian Bustard	**1.51**	1.11	2.02	**
Cacatua galerita	Sulphur-crested Cockatoo	0.70	**1.01**	1.81	*
Chlamydera maculata	Spotted Bowerbird	**0.12**	0	1.88	*
Cincloramphus cruralis	Brown Songlark	**1.03**	0.57	1.83	*
Climacteris picumnus	Brown Treecreeper	**0.72**	0.27	2.05	**
Coracina novaehollandiae	Black-faced Cuckoo-shrike	0	**0.10**	2.45	**
Cuculus pallidus	Pallid Cuckoo	0.21	**0.43**	3.03	***
Dromaius novaehollandiae	Emu	**0.35**	0.03	1.86	*
Eurystomus orientalis	Dollarbird	**1.46**	1.10	2.02	**
Geopelia striata	Peaceful Dove	0.08	**0.23**	1.70	*
Gymnorhina tibicen	Australian Magpie	**0.72**	0.34	2.36	**
Lichenostomus virescens	Singing Honeyeater	**0.47**	0.18	2.25	**
Microeca fascinans	Jacky Winter	0.71	**1.11**	1.82	*
Oriolus sagittatus	Olive-backed Oriole	0.01	**0.20**	2.01	**
Petroica goodenovii	Red-capped Robin	**0.12**	0	1.83	*
Platycercus adscitus	Pale-headed Rosella	**0.37**	0.15	2.27	**
Rhipidura fuliginosa	Grey Fantail	0.03	**0.31**	3.08	***
Smicrornis brevirostris	Weebill	**1.27**	0.89	1.71	*
Todiramphus pyrrhopygia	Red-backed Kingfisher	0.07	**0.22**	2.87	***
Todiramphus sanctus	Sacred Kingfisher	**0.34**	0.12	2.86	***
Turnix pyrrhothorax	Red-chested Button-Quail	**2.46**	1.94	2.35	**
Reptiles					
Amphibolurus nobbi	Nobbi Lizard	0.10	**0.30**	2.32	**
Ctenotus capricorni	Capricorn Ctenotus	0.06	**0.22**	2.67	***
Ctenotus hebetior	skink	0.24	**1.52**	4.43	***
Ctenotus pantherinus	Leopard Ctenotus	0.21	**0.50**	2.72	***
Diplodactylus conspicillatus	Fat-tailed Diplodactylus	0.12	**0.41**	1.99	**
Diplodactylus steindachneri	Box-patterned gecko	0.19	**0.62**	2.74	***
Diporiphora australis	Eastern Two-line Dragon	0.01	**0.10**	2.20	**
Egernia striolata	Tree Skink	0.25	**0.37**	1.69	*
Gehyra catenata	Chain-backed Dtella	0.50	**0.98**	2.96	***
Pogona barbata	Bearded Dragon	0.09	**0.31**	3.18	***
Proablepharus tenuis	Northern Soil-crevice Skink	0.15	**0.32**	2.08	**
Suta suta	Myall/Curl Snake	0.02	**0.09**	1.96	*
Varanus tristis	Black-tailed Monitor	0.07	**0.25**	2.75	***

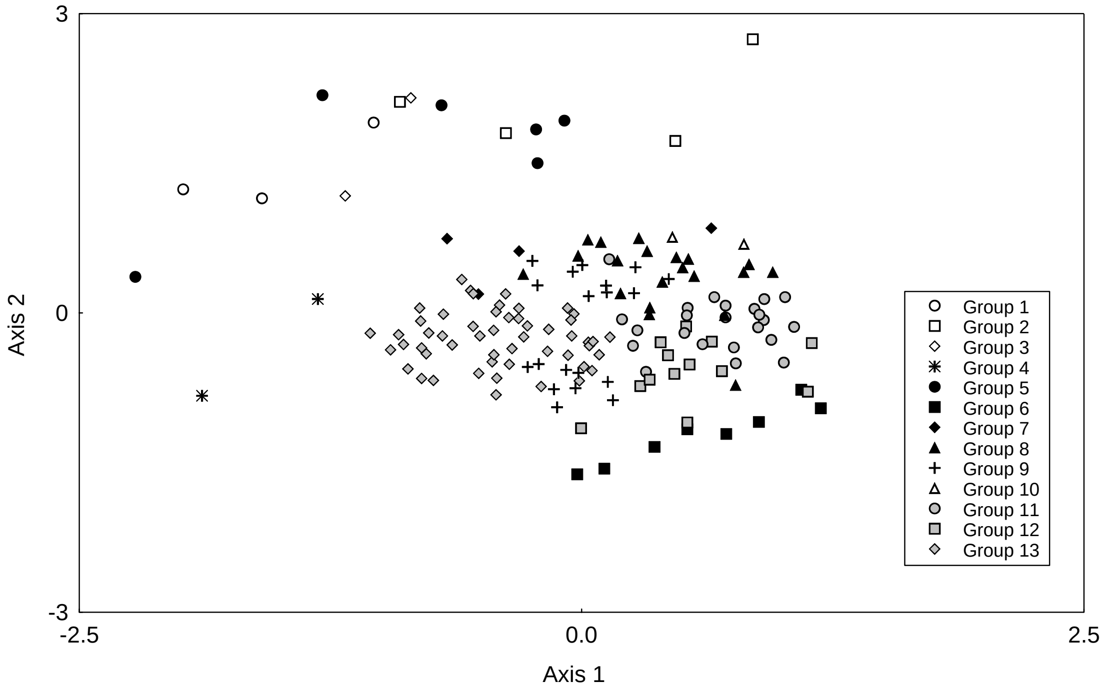
Vertebrate species composition and groups

Classification of the 158 wet season sample quadrats by their vertebrate fauna composition identified the best truncation at 13 groups (Figure 3.1). The subsequent ordination on two axes (stress = 0.32) indicated a broad primary separation of sites into a condensed clump in the centre of the ordination and central to the axes (groups 8, 9, 11, 12, 13), and those on the periphery of this cluster (groups 4, 6, 7, 10) and those at the extremes of ordination space (groups 1, 2, 3, 5) (Figure 3.2). The classification and ordination are not particularly consistent, the main split in the classification not being well realised in the ordination. Regardless, the division generally reflects the sites with simple and/or unique structural characteristics (grasslands, heaths), and those widespread open *Eucalyptus* and *Acacia* woodland types with more complex strata. Further classification and ordination of these central woodland sites did not reveal any further clear pattern of separation. Additionally group definition at lower levels of truncation of the dendrogram (8-10 groups) failed to assemble the groups represented by very few sites (n=2-4), into ones of greater amalgamation, and instead grouped those woodland types already consisting of a large number of sites. This indicates that, despite the low number of non-woodland sites, there is a strong fidelity of species composition to them. The species and environmental characteristics of the groups (Table 3.2, 3.3, 3.7-9, Figure 3.2) are briefly described below. Indicative geographic position of the quadrat and group distribution is also presented (Figure 3.3).

Figure 3.1 Dendrogram derived from Bray-Curtis dissimilarity matrix. Number of quadrats indicated in parenthesis after the group number.

```
Dissimilarity →
0.9120   0.9916      1.0712      1.1508      1.2304      1.3100
            |           |           |           |           |           |
Group 1 ( 3)______________
Group 2 ( 4)_____________|___________
Group 3 ( 2)_                       |
Group 4 ( 2)|_______________        |
Group 5 ( 6)_______________|________|_______________________
Group 6 ( 8)_______________________________________________|_____________
Group 7 ( 2)___                                                         |
Group 8 (20)__|________________                                         |
Group 9 (19)___               |                                         |
Group 10( 2)__|_______________|______                                   |
Group 11(23)______________          |                                   |
Group 12(13)_____________|__________|_________________                  |
Group 13(52)_________________________________________|__________________|
            |           |           |           |           |           |
       0.9120      0.9916      1.0712      1.1508      1.2304      1.3100
```

Figure 3.2 Two-dimensional ordination of vertebrate species composition for each sample site. Data were standardised and species recorded in only one quadrat were removed from the analysis. Symbols represent the thirteen groups identified from a complementary classification.



Grasslands and associated types

Group 1. This group comprised three hummock grasslands (*Triodia longiceps*) quadrats, associated with saline discharge areas central to the Desert Uplands. The quadrats are characterised by high bare ground and hummock grass cover. The total vertebrate richness for this group is low (n=16), as is the mean quadrat richness (n=8.7), with birds and reptiles equally predominant. Characteristic fauna comprised *Pseudomys desertor*, *Macropus giganteus*, *Tympanocryptis lineata* and *Ctenotus robustus*, Spinifexbird, White-winged Fairy-wren and Nankeen Kestrel. Abundance of terrestrial insectivores, terrestrial omnivores, murids and agamids was relatively high.

Group 2. This group comprises four quadrats of *Astrebla* spp tussock grasslands, all in the western sub-region of the Desert Uplands. The quadrats are characterised by high areas of bare ground and tussock grass, and grey cracking clay soils. The total vertebrate richness for this group is low (n=25), as is the mean quadrat richness (n=9.0), with birds and mammals predominant. Characteristic fauna comprised the Australian Bustard, Galah, Red-chested Button-quail, *Sminthopsis douglasi*, *Macropus giganteus*, *M. rufus*, *Tympanocryptis lineata* and *Delma tincta*. Abundance of terrestrial omnivores, dasyurids and pygopodids was relatively high.

Group 3. This group comprises two quadrats of *Astrebla* spp tussock grasslands, in the north-western Desert Uplands. Though identical regional ecosystems to those within group 2, they are structurally different with much higher tussock grass cover (59%) and correspondingly low bare ground cover. Their fauna composition is also distinct. The total vertebrate richness for this group is very low (n=12), and as is the mean quadrat richness (n=7.0), with birds predominant. Characteristic fauna comprised the Black-faced Woodswallow, Red-chested Button-quail, *Denisonia devisi* and *Rattus villosissimus*. Abundance of hawkers and murids was high, the Black-faced Woodswallow and *Rattus villosissimus* contributing the most in these guilds.

Group 5. This group comprises six quadrats of lake-edge samphire vegetation from both Lake Buchanan (*Lawrencia buchananensis* and *Halosarcia* spp) and Lake Galilee (*Halosarcia* spp) in the central region of the Desert Uplands. The quadrats are characterised by an extensive cover of bare ground and samphire, and correspondingly relatively sparse cover of tussock grass. Soils were white sands overlying grey clay-loams. The total vertebrate richness for this group is low (n=24), as is the mean quadrat richness (n=7.3), with birds predominant. Characteristic fauna comprised the Richard’s Pipit, Nankeen Kestrel, Cockatiel, Australian Magpie, *Macropus rufus*, *Ctenophorus nuchalis* and *Menetia greyii*. Abundance of terrestrial omnivores, granivores and skinks was relatively high, as was the richness of wetland bird species.

Heaths and low open woodlands

Group 4. This group comprises two quadrats of low *Melaleuca* spp, *Acacia* spp and *Thryptomene parviflora* shrubland, from the central region of the Desert Uplands. The quadrats are characterised by extensive cover of bare ground (55%), a correspondingly sparse vegetation cover of *Triodia* sp, and dense canopy cover to 2 m of a variety of small shrubs. The total vertebrate richness for this group is low (n=19), as is the mean quadrat richness (n=12.5), with birds and reptiles predominant. Characteristic fauna comprised the Brown Honeyeater, Singing Honeyeater, Spotted Nightjar, Variegated Fairy-wren, *Pseudomys desertor*, *Ctenophorus nuchalis*, *Ctenotus pantherinus*, *Diplodactylus williamsi* and *C. ingrami*. Abundance of terrestrial insectivores, nectarivores, murids and skinks were relatively high.

Group 6. This group comprises seven quadrats of mixed *Eucalyptus quadricostata*, *C. erythrophloia*, *C. leichhardtii*, *E. exilipes* and *C. lamprophylla* tall open woodlands and *Melaleuca tamariscina* shrublands on deep red sands. All sites are from the very north of the Desert Uplands in White Mountain National Park. The quadrats are characterised by broadly similar areas of bare ground (21%), tussock (21%) and hummock grass (27%) cover, extensive litter cover, and a complex mid-storey and canopy strata with a high cover, basal area and height. The total vertebrate richness for this group is intermediate (n=49), and the mean quadrat richness low (n=16.6), with birds and reptiles predominant. Characteristic fauna comprised the Weebill, White-throated Honeyeater, Brown Honeyeater, Noisy Friarbird, Striated Pardalote, Rufous Whistler, *Pseudomys delicatulus*, *P. patrius*, *Proablepharus tenuis*, *Menetia timlowi*, *Ctenotus spaldingi Diplodactylus steindachneri* and *D. conspicillatus*. Abundance of nectarivores, foliage gleaners, murids, skinks and geckos was relatively high, as was species richness of murids and skinks.

Group 7. This group comprises four quadrats of low mixed *Grevillea striata*, *G. parallela*, *Acacia coriacea* woodlands, and *Corymbia dallachiana* and *C. plena* open woodlands on unconsolidated sandy dunes. The quadrats are characterised by high area of bare ground, tussock grasses, litter and fallen logs, and an open canopy of small trees. Soils are white and very sandy. The total vertebrate richness for this group is intermediate (n=49), and the mean quadrat richness low (n=19.5), with birds predominant. Characteristic fauna comprised Little Friarbird, Striated Pardalote, Grey-crowned Babbler, Pied Butcherbird, Cockatiel, Galah, Magpie-lark, *Macropus giganteus*, *M. rufus* and *Ctenotus hebetior*. Abundance of terrestrial omnivores, granivores, macropods and skinks are relatively high, as was species richness of Typhlopidae (blind snakes).

Group 10. This group comprises two quadrats representing very low, lake-edge *Acacia stenophylla* woodlands on Lake Galilee. The quadrats are characterised by extensive areas of bare ground (70%), with sparse forbs and tussock grass cover, and a moderate cover of low *Acacia* trees. The total vertebrate richness for this group was very low (n=21), as was the mean quadrat richness (n=15.5), with birds predominant. Characteristic fauna comprised the Australian Raven, Magpie-lark, Willie Wagtail, Mistletoebird, Pied Butcherbird, Spiny-cheeked Honeyeater, Crested Pigeon, Bush Stone-curlew, *Gehyra catenata* and *Cryptoblepharus plagiocephalus*. Abundance of all species groups was low, though terrestrial omnivores and dasyurids were moderately high.

Open *Eucalyptus* and *Acacia* woodlands

Group 8. This group comprises 20 quadrats consisting of 10 regional ecosystems, and is thus the most diverse group in regards to regional ecosystems represented. All quadrats were open woodlands on very sandy soils, including a mix of *Eucalyptus, Corymbia* and *Acacia* species. The quadrats are characterised by intermediate to high canopy height and cover, and an intermediate area of bare ground and tussock grass cover, and low but equable cover of litter, fallen logs, hummock grass and forbs. The total vertebrate richness for this group was high (n=110), as was the mean quadrat richness (n=22.2), with birds predominant, but relatively high reptile and mammal species compared to other groups. Characteristic fauna comprised Pied Butcherbird, Apostlebird, Australian Magpie, Grey-crowned Babbler, Galah, Weebill, Magpie-lark, Yellow-throated Miner, Brown Treecreeper, *Macropus rufus*, *Pseudomys desertor*, *Lagorchestes conspicillatus*, *Ctenotus hebetior*, *Gehyra catenata*, *Menetia greyii*, *Cryptoblepharus plagiocephalus*, *Heteronotia binoei* and *G. dubia*. Abundance and species richness of terrestrial omnivores, granivores, geckos and skinks were especially high.

Group 9. This group comprises 19 quadrats, all open woodlands of *Eucalyptus brownii*, *E. coolabah, E. camaldulensis*, *Corymbia dallachiana*, *C. tessellaris* and *A. argyrodendron* on texture-contrast alluvial soils, associated with drainage lines and seasonally flooded areas. The quadrats in this group had low canopy height and cover, and were characterised by extensive cover of bare ground, and intermediate cover of tussock grasses, litter, fallen logs and forbs. The total vertebrate richness for this group was high (n=113), as was the mean quadrat richness (n=29.6), with birds predominant (>60%), though also a high reptile and mammal count. Characteristic fauna comprised Magpie-lark, Apostlebird, Jacky Winter, Little Friarbird, Rufous Whistler, Grey-crowned Babbler, Peaceful Dove, Striped Honeyeater, Weebill, Grey Shrike-thrush, Crested Pigeon, *Macropus rufus, M. giganteus*, *Trichosurus vulpecula*, *Diplodactylus steindachneri*, *Gehyra catenata*, *Morethia boulengeri* and *Amphibolurus gilberti*. Abundance of terrestrial omnivores, foliage gleaners/salliers, foliage gleaners, frugivores, macropods and geckos was high, as was granivores, foliage gleaners/salliers, macropod and gecko species richness.

Group 11. This group comprises 23 quadrats representing predominantly *Eucalyptus brownii* and *E. melanophloia* open woodlands, with most sites in the north-east sub-region of the Desert Uplands. The quadrats are characterised by extensive cover of tussock grasses and a tall but open canopy cover. The total vertebrate richness for this group was moderately high (n=97), though the mean quadrat richness was moderately low (n=18.4), with birds predominant. Characteristic fauna comprised Pied Butcherbird, Black-faced Cuckoo-shrike, Australian Magpie, Australian Owlet-nightjar, Noisy Friarbird, Red-backed Fairy-wren, Rufous Whistler, Peaceful Dove, Striated Pardalote, *Menetia greyii*, *Ctenotus robustus*, *Carlia munda*, *Gehyra dubia* and *Heteronotia binoei*. Though the vertebrate guilds and families were well represented, none were particularly abundant or species-rich compared to other groups, except terrestrial omnivores.

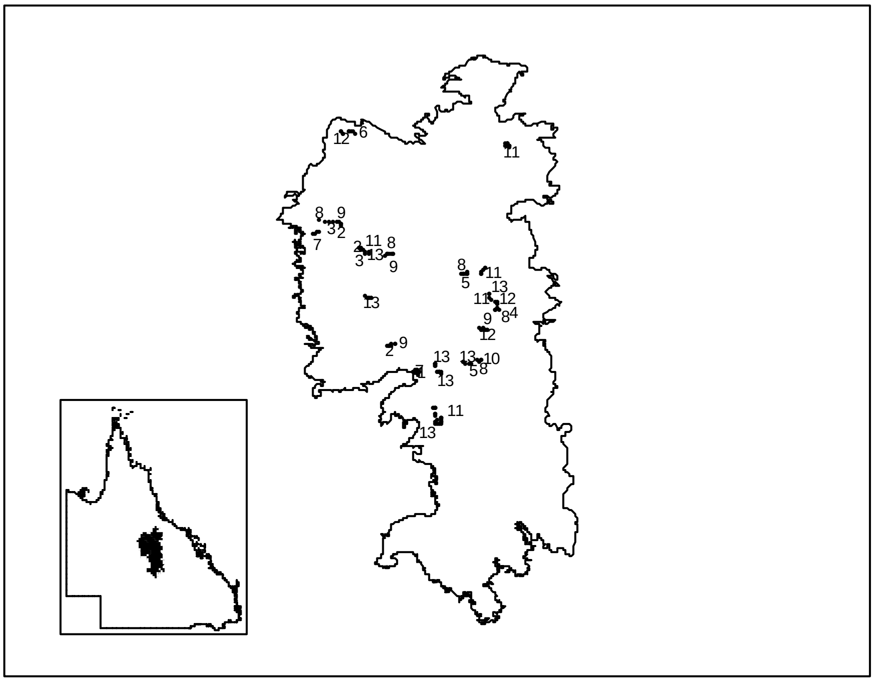
Group 12. This group comprises 13 quadrats representing open *Eucalyptus cambageana*, *Acacia argyrodendron*, *Eucalyptus brownii*, *Acacia shirleyi*, *E. thozetiana*, *A. cambagei* woodlands on shallow clay, colluvial and skeletal soils. These quadrats are characterised by high canopy cover and basal area, intermediate and equable cover of bare ground, tussock grasses, hummock grasses, and high number of fallen logs and dead trees. The total vertebrate richness for this group was moderately high (n=94), as was the mean quadrat richness (n=22.4), with birds predominant (>60%), and a moderate number of reptile and mammal species. Characteristic fauna comprised Pied Butcherbird, Striped Honeyeater, Noisy Friarbird, Striated Pardalote, Weebill, Australian Magpie, Australian Owlet-nightjar, *Gehyra catenata*, *Morethia boulengeri*, *Ctenotus strauchii* and *Carlia pectoralis*. Abundance of skinks, nectarivores, foliage gleaners and nectarivore/gleaners was high, as was species richness of skinks, terrestrial omnivores and nectarivores/gleaners.

Group 13. This group comprises 52 quadrats representing predominantly *Eucalyptus similis*, *E. whitei*, *Corymbia setosa*, *E. melanophloia*, *C. dallachiana*, *E. brownii* open woodlands on deep red and yellow earths. The quadrats are characterised by extensive cover of bare ground and hummock grasses, and a moderate to low canopy height and cover. The total vertebrate richness for this group was high (n=133), as was the mean quadrat richness (n=26.2). Characteristic fauna comprised Singing Honeyeater, Crested Bellbird, Rufous Whistler, Pied Butcherbird, Jacky Winter, Australian Owlet-nightjar, Weebill, Yellow-rumped Thornbill, Common Bronzewing, Pallid Cuckoo, Red-browed Pardalote, *Pseudomys desertor*, *P. delicatulus, Macropus giganteus, Ctenotus hebetior, C. pantherinus, Varanus tristis, Ctenotus rosarium, Lialis burtoni* and *Menetia greyii*. Abundance and species-richness of skinks, geckos, pygopodids, salliers, hawkers, nectarivore/gleaners, foliage gleaners and murids were all high.

Table 3.2 Characteristic fauna for each group identified via SIMPER routine and Bray-Curtis dissimilarity measures. Data indicate the percentage contribution from each species and only the top ten (if applicable) tabulated. Groups ordered to reflect structural groups, and species data are sorted in ascending order from group 1 to aid interpretation. Additional data included are the number of quadrats, total site species richness and average sample richness per group. g= guild or genera (Table 3.10).

SPECIES	g	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13
Number of quadrats		3	4	2	6	2	2	4	8	20	19	23	13	52
Species richness		16	25	12	24	19	21	49	49	110	113	97	94	133
Bird richness		7	14	8	15	9	18	33	25	64	71	59	59	86
Reptiles richness		7	4	2	7	7	2	12	20	35	32	29	29	37
Mammal richness		2	7	2	2	3	1	4	4	11	10	9	6	10
Sample species richness		8.6	9.0	7.0	7.3	12.5	15.5	19.5	16.6	22.1	29.6	18.4	22.4	26.1
Sample bird richness		3.3	4.5	4.5	4.5	6.0	12.5	12.7	9.1	14.6	21.7	13.1	16.5	17.5
Sample reptiles richness		3.3	2.3	1.0	2.2	4.5	2.0	5.2	5.6	6.1	5.7	4.3	5.1	6.4
Sample mammal richness		2.0	2.3	1.5	0.7	2.0	1.0	1.5	1.8	1.4	2.2	1.1	0.9	2.2
BIRDS														
Spinifexbird	TI	29.7												
Galah	GR		39.2					2.7		6.2				
Australian Bustard	TO		8.9											
Red-chested Button-Quail	GR		6.2											
Black-faced Woodswallow	H			38.8										
Richard's Pipit	TO				55.9									
Nankeen Kestrel	TO				13.2									
Cockatiel	GR				5.9			2.5						
Australian Magpie	TO				1.7				1.6	5.12		6.2	5.2	
Variegated Fairy-wren	TI					27.2								
Singing Honeyeater	NL					20.4								9.3
Brown Honeyeater	N					15.2			13.4					
Australian Raven	TO						34.3							
Magpie-Lark	TO						12.3	2.3		3.2	3.5			
Mistletoebird	F						8.2							
Spiny-cheeked Honeyeater	NL						8.2							
Willie Wagtail	S						6.8							1.9
Pied Butcherbird	TO						4.1	3.1		8.4		20.2	7.0	4.1
Little Friarbird	N							11.1			11.3		2.1	
Striated Pardalote	L							5.5	3.13			5.7	10.9	
Grey-crowned Babbler	TI							4.7		7.7	4.4			
Weebill	L								18.7	1.6	3.3		2.6	2.0
White-throated Honeyeater	N								10.6					
Noisy Friarbird	N								10.4			8.5	2.8	
Rufous Whistler	L								4.1		6.7	3.2		15.6
Apostlebird	TO									3.2	5.4			
Peaceful Dove	GR										5.2	4.43		
Striped Honeyeater	NL										4.5		7.9	
Jacky Winter	S										3.3			5.4
Black-faced Cuckoo-shrike	L											1.1		
Red-backed Fairy-wren	TI											7.4		
Australian Owlet-nightjar	S											5.1	2.2	3.9
Crested Bellbird	TO													11.2
Yellow-Rumped Thornbill	L													1.18
MAMMALS														
Pseudomys desertor	MU	46.5				15.2			0.94	0.8				4.7
Macropus giganteus	MA	8.7	3.4					4.4			1.2			1.1
Macropus rufus	MA		9.1		3.7			1.6		0.8	1.3			
Sminthopsis douglasi	DA		5.3											
Rattus villosissimus	MU			5.7										
Pseudomys delicatulus	MU								10.8					1.6
REPTILES														
Ctenotus robustus	SC	7.4										0.6		
Tympanocryptis lineata	AG	4.3	8.34											
Delma tincta	PY		16.7											
Ctenophorus nuchalis	AG				6.4	6.8								
Menetia greyii	SC				5.8					2.1		3.5		0.9
Ctenotus pantherinus	SC					15.2								1.4
Gehyra catenata	GE						13.7			1.4	3.8		2.2	
Ctenotus hebetior	SC							20.5		5.0				3.1

Figure 3.3 Location of the quadrats sampled in the Desert Uplands, and indicative distribution of the groups. Not all quadrats are labelled as, due to the scale of the map, many overlap. However any group represented in a cluster of quadrats is shown.



Environmental gradients

Twenty-one of the environmental variables were significantly correlated with the ordination of vertebrate species composition (Table 3.3). However due to the potential complexity of interpretation of so many variables, some filtering to identify the most significant vectors was required. The pattern of correlations within these variables was examined using a simple correlation matrix. Sixteen were considered highly inter-correlated with one or more of the other vectors. The variables were then ranked in descending order of the magnitude of the PCC correlation coefficient. The first variable (that with the highest coefficient) from an inter-correlated group was therefore selected (e.g. tussock cover r=0.51 and ground-storey richness r=0.35) (Table 3.3). The remaining four uncorrelated variables (litter cover bare ground cover, FPC 1-3 m, forb cover, hummock grass cover) were also used. These are considered representative of major environmental gradients measured by the data, and are illustrated on a separate ordination with all quadrat sites labelled with group number (Figure 3.4). It is clear there are a few distinctive gradients of fauna composition change relating to the vectors (e.g. turnover from high tussock cover to high hummock grass cover at opposite ends of the ordination), whereas others such as those relating to upper vegetation strata (e.g. basal area and foliage projective cover for plants 1-3 m and 3-5 m) are less well defined and possibly interacting.

These relationships between environmental variation and the ordination space defined by vertebrate species composition largely summarise and recapitulate the group descriptions given above. For example there are distinctive simple treeless groups defined clearly by ground cover structure, low species richness, but with a corresponding specialised and unique fauna assemblage (groups 1-5). Conversely there are ranges of woodland groups that share a number of common fauna species, and intergrade structurally and floristically (groups 8-12). Perhaps the most notable feature of these illustrations is the complexity of patterns. There is no single strong environmental gradient structuring the variation in species composition, but rather, a multitude of unrelated gradients for different environmental factors, implying that variation in species composition is complex, and subject to idiosyncratic influences from a highly disparate set of factors.

The interplay between the environmental variation and the subtle change in the species composition and abundance across groups can be illustrated by plotting quadrat abundances for those species within the ordination space. The patterns of turnover in species and guilds reflect the relationship between fauna assemblage and the shifting habitat resources across the quadrat groups. A number of guild and species pairings illustrate this neatly:

- comparing two terrestrial insectivores, Crested Bellbirds were more abundant in quadrats (group 13) with low basal area, high bare ground, hummock and shrub cover, whereas Australian Magpies, though widespread and present in sites lacking tree cover, were more abundant in quadrats (groups 11, 12), with higher tussock grass cover, basal area and clay soils (Figure 3.5 a-b);
- comparing two granivores, Crested Pigeons were patchily distributed, but generally more abundant in quadrats (groups 8, 9) with lower basal area, high bare ground cover, forb cover and cracking clay soils, whereas Peaceful Doves were distributed across woodland quadrats central to the ordination (Figure 3.5 c-d);

- comparing species typical of open environments, Galahs were more abundant in quadrats (groups 7-9) with intermediate bare ground and forb cover, and low basal area, whereas and the Nankeen Kestrel, though uncommon, occurred in treeless quadrats, with extensive bare ground (Figure 3.5 e-f);
- comparing two related nectarivores, the smaller Little Friarbird was more abundant in quadrats with intermediate bare and hummock grass cover, and lower shrub layer (groups 8, 9, 13), whereas the larger Noisy Friarbird occurred more frequently in quadrats (groups 6, 11, 12) with higher basal area, tussock grass cover and mid-storey tree layer (Figure 3.5 g-h);
- comparing two small foliage gleaner species, a similar pattern to the friarbirds was recorded, with the Weebill more abundant in intermediate and shrubby woodlands, and Striated Pardalote more abundant in taller woodlands (Figure 3.5 i-j);
- comparing two guilds of bird species, there is a quite expected pattern of higher Terrestrial Insectivore abundance in quadrats representing treeless, and less well-developed woodlands with a range of grass and bare ground cover, whereas Nectarivore abundance is notably clumped in quadrats characterised by high basal area of more complex vegetation structure (Figure 3.5 k-l);
- comparing two mammal families, the Muridae and Dasyuridae, there is overlap in quadrats of high abundance associated with high hummock grass cover, intermediate canopy cover and sandy soils. However rodents are numerous in treeless hummock grass quadrats or sites characterised by high basal area, whereas dasyurids by more abundant in tussock grasslands (Figure 3.5 m-n);
- quadrats with high abundances of three skink species are distributed along a gradient of changing ground cover and soil type. *Carlia munda* is more common in quadrats characterised by higher tussock grass cover and clay soils, *Ctenotus hebetior* widespread across varying ground cover and soil types, and *C. pantherinus* abundant typically in quadrats with high hummock grass cover (Figure 3.5 o-q); and
- three widespread gecko species follow suite to the skinks illustrated with *Heteronotia binoei* more typical of quadrats central in the ordination reflecting a distribution across woodlands types, *Gehyra catenata* more abundant in quadrats with high basal area, shrub, litter cover or cracking soils and *Diplodactylus steindachneri* generally uncommon, but present more typically in the sandy, hummock grass quadrats of group 13 (Figure 3.5 r-t).

Table 3.3 Mean scores for all habitat measures identified as significant vectors in the fauna ordinations. Data provided is the sample mean per group, the correlation coefficient and the significance in variation in abundance tested via Kruskal-Wallis ANOVA. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant. Bold indicates highest score and underlined indicates lowest score. Those highly correlated (r>0.5, p<0.05) are indicated by matching letters in column I. As such only a single variable of this set is illustrated on ordination.

Variable	Code	r	I	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Basal area	BASAL	0.75***	a	0	0	0	0	0	5	4.56	11.44	9.1	11.9	10.08	**14**	7.6	61.4	***
Canopy height	CANHT	0.67***	a	0	0	0	0	2	4	11.5	13.8	12	10.5	**13.5**	12.46	9.1	73.2	***
Basal area (live)	LIVE	0.60***	a	0	0	0	0	0	4	3.75	**10.1**	7.6	9.38	6.76	8.87	6.3	53.2	***
Foliage projective cover >10m	FPC >10	0.59***	a	0	0	0	0	0	0	0.7	**1.1**	1	0.7	0.9	**1.1**	0.4	47.8	***
Foliage projective cover 3-5m	FPC 3-5	0.51***	c	0	0	0	0	0	**2**	1.2	1.3	1.1	1.7	1.1	1.8	1.3	38.4	***
Tussock grasses	TUSS	0.51***	b	3.3	45	**59**	10.5	2.5	10	33.7	21.5	25	26.1	48.4	20.7	13	56.3	***
Canopy cover	CANCOV	0.50***	a	0	0	0	0	**30**	18	17.5	24.3	17	22.1	11.4	29.2	14	57.9	***
Hummock grass	HUMM	0.50**		**35**	0	0	0	15	0	1.2	26.8	9.2	0.2	1.3	10.3	29	72.8	***
Foliage projective cover 1-3m	FPC 1-3	0.49**		0.3	0.2	0.5	0	**4**	1.5	2	2	1.2	1.5	1.1	1.7	1.5	50.4	***
Foliage projective cover 5-10m	FPC 5-10	0.48**	c	0	0	0	0	0	0	1.2	1	1.5	**1.8**	1.13	1.7	1.1	76.9	***
Fallen tree >10cm	FALL>10	0.47**	a	0	0	0	0	0	8.5	31	8.1	11	13.7	8.1	**36.8**	6.9	27.5	**
Basal area (dead)	DEAD	0.46**	a	0	0	0	0	0	1	0.81	1.31	1.5	2.53	3.36	**5.1**	1.3	44.1	***
Soil type	SOILTYPE	0.44**	e	3	**6.5**	5	1	1.5	6	1.2	2.2	1.5	3.7	2.9	3.9	1.4	71.6	***
Dead tree >10cm	DEAD>10	0.40**	a	0	0	0	0	0.5	7	3.2	6.5	6.2	7.3	7.1	**16.9**	5.1	27.2	**
Crack size mode	CRACMODE	0.38*	d	0	**15**	13	0	0	5	0	0	0	6.3	0	0	0	95.5	***
Litter cover	LITT	0.37*		0	1.2	1	0.8	7.5	5	**14**	11.8	8.2	10.7	6.5	9.2	8.8	54.2	***
Ground richness	GSRICH	0.35*	b	8.3	13	15	10.5	3	5.5	12.5	10.6	13	14.3	14.6	**15.3**	10	28.1	***
Forb cover	FORB	0.34*		5	3.2	5	**24**	0	10	7	3.7	6.9	6.9	4.6	8.5	4	29.6	***
Soil colour	SOILCOLO	0.33*	e	4	6	**7**	6	2	6	5	3.3	4.7	5	2.7	4.6	3.2	69.3	***
Crack size	CRAC	0.33*	d	0	2.5	2.5	0	0	**5**	0	0	0	0.78	0	0	0	93.4	***
Bare ground	BARE	0.31*		55	49	33	58.3	55	**70**	43.7	21.6	45	51.5	34.7	38.8	45	23.2	**

Figure 3.4. Two-dimensional ordination of quadrats by fauna composition illustrating the direction of the significant environmental vectors identified via the PCC. Vector codes and significance level identified in Table 3.3. Not all variables are illustrated, and those inter-correlated are listed in Table 3.3.

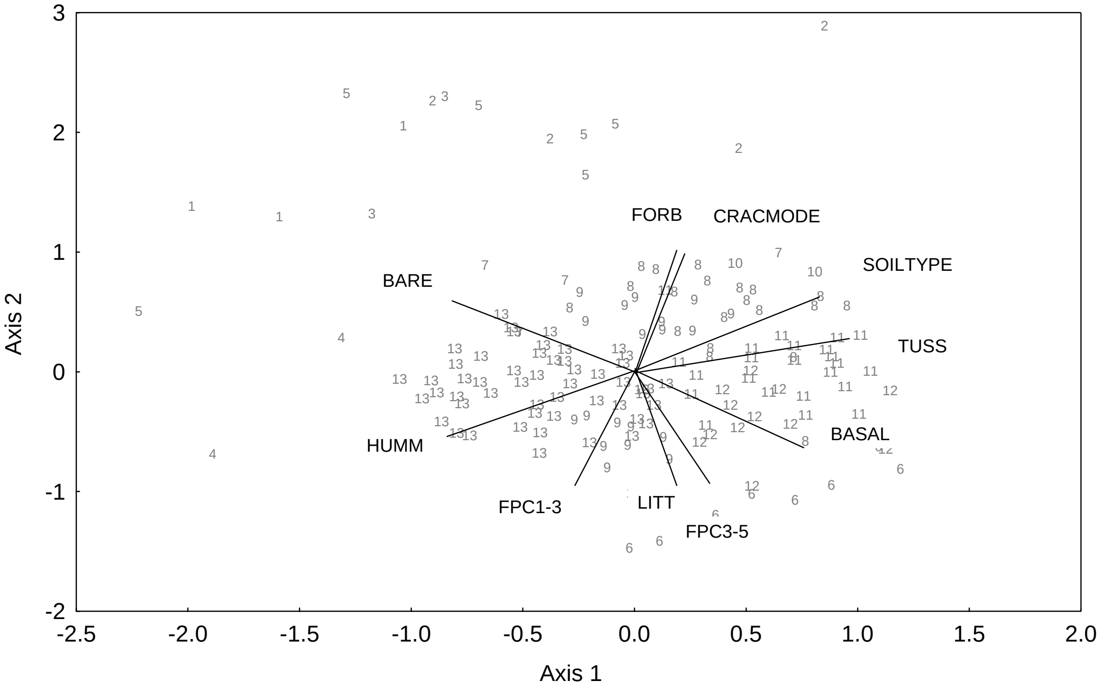


Figure 3.5 (a-t) Total abundance of selected species recorded in each quadrat. Abundance is superimposed on the quadrat within the ordination and increasing size of symbol indicates a higher abundance.

Figure 3.5 (a) Ordination indicating relative abundance of Crested Bellbirds at each quadrat.

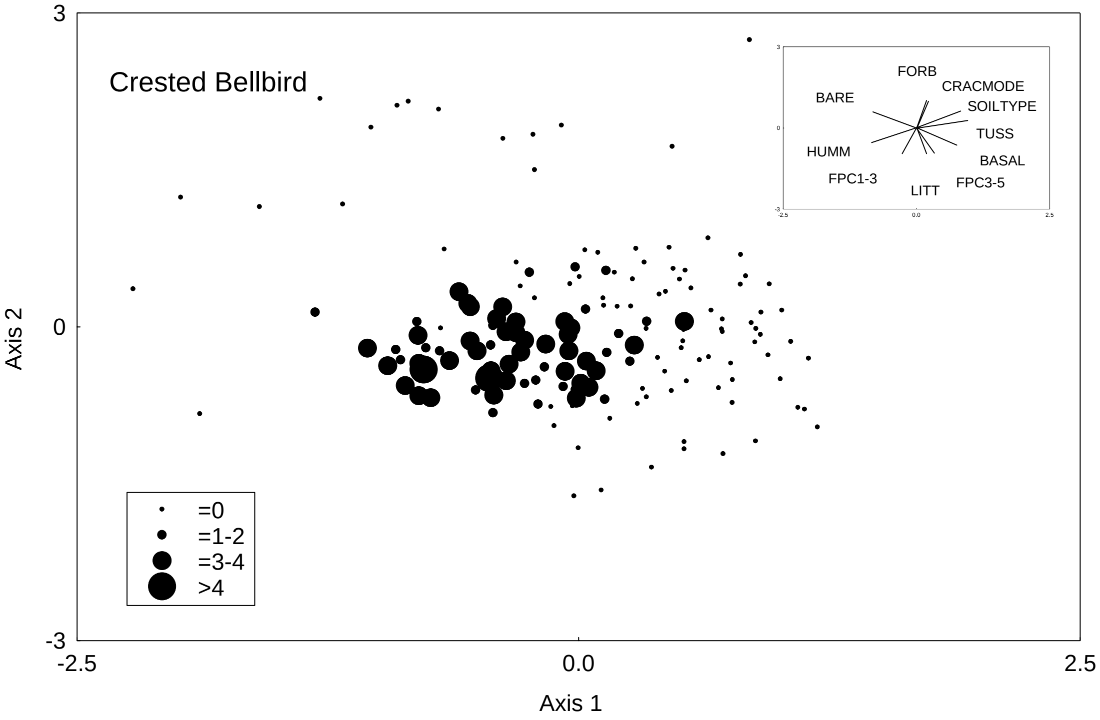


Figure 3.5 (b) Ordination indicating relative abundance of Australian Magpies at each quadrat.

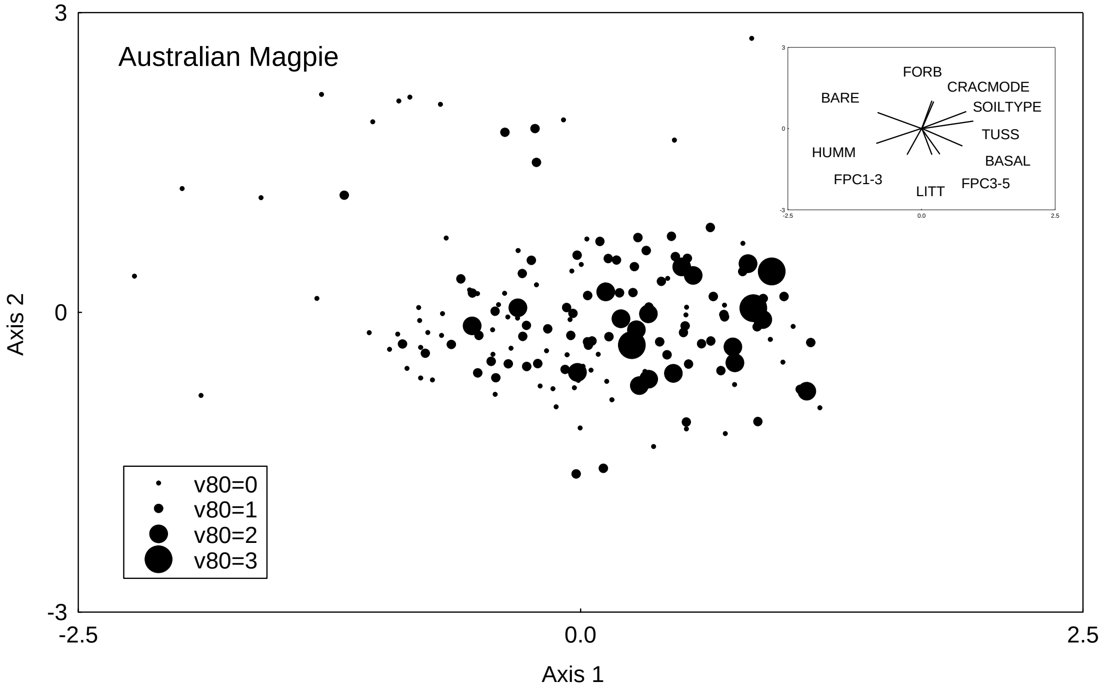


Figure 3.5 (c) Ordination indicating relative abundance of Crested Pigeons at each quadrat.

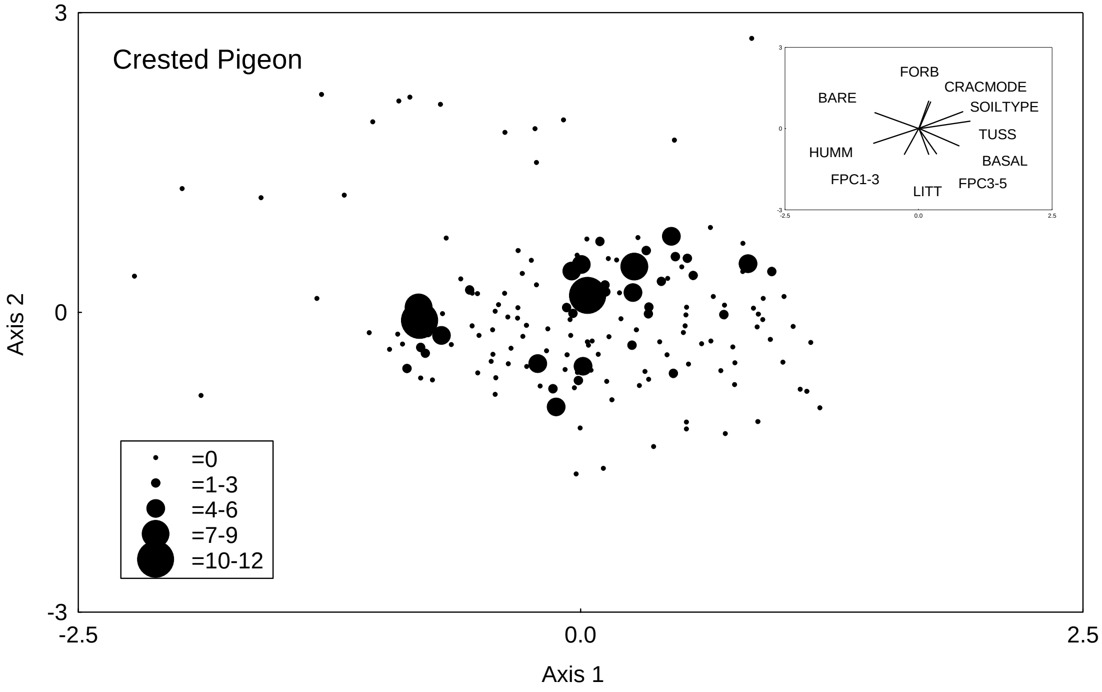


Figure 3.5 (d) Ordination indicating relative abundance of Peaceful Doves at each quadrat.

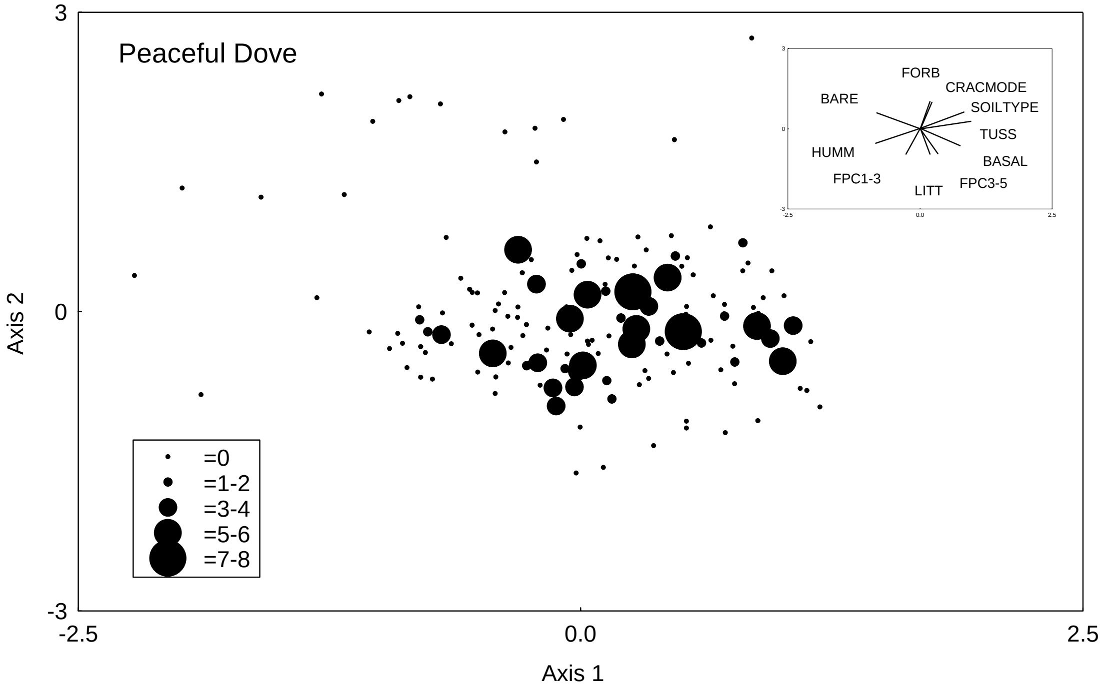


Figure 3.5 (e) Ordination indicating relative abundance of Galahs at each quadrat.

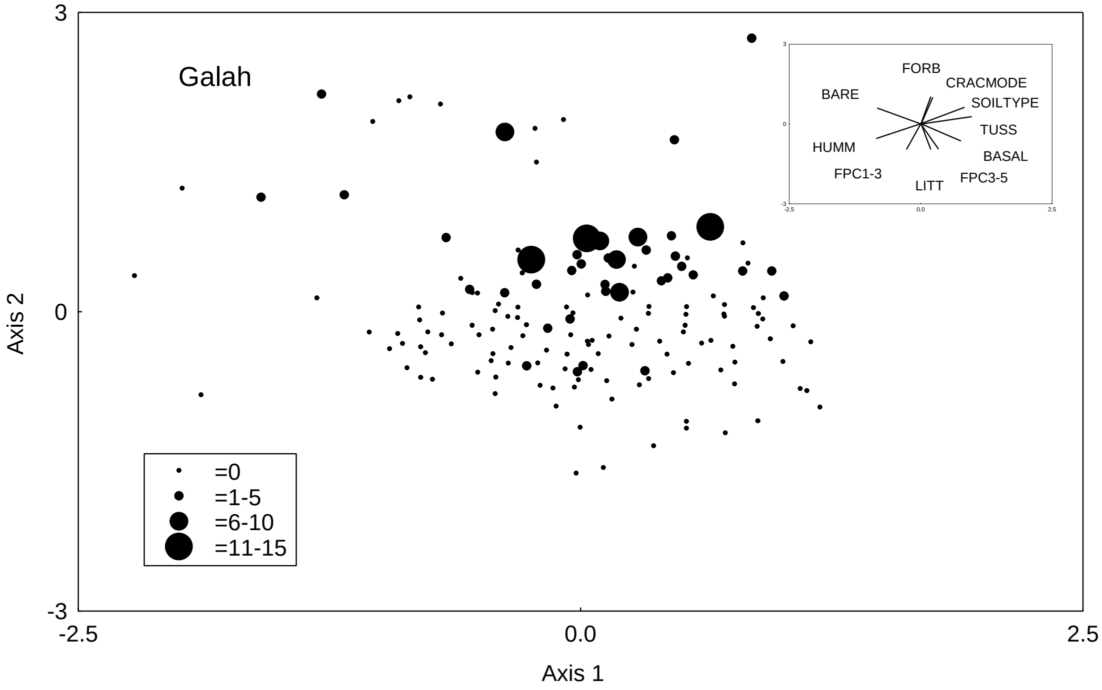


Figure 3.5 (f) Ordination indicating relative abundance of Nankeen Kestrels at each quadrat.

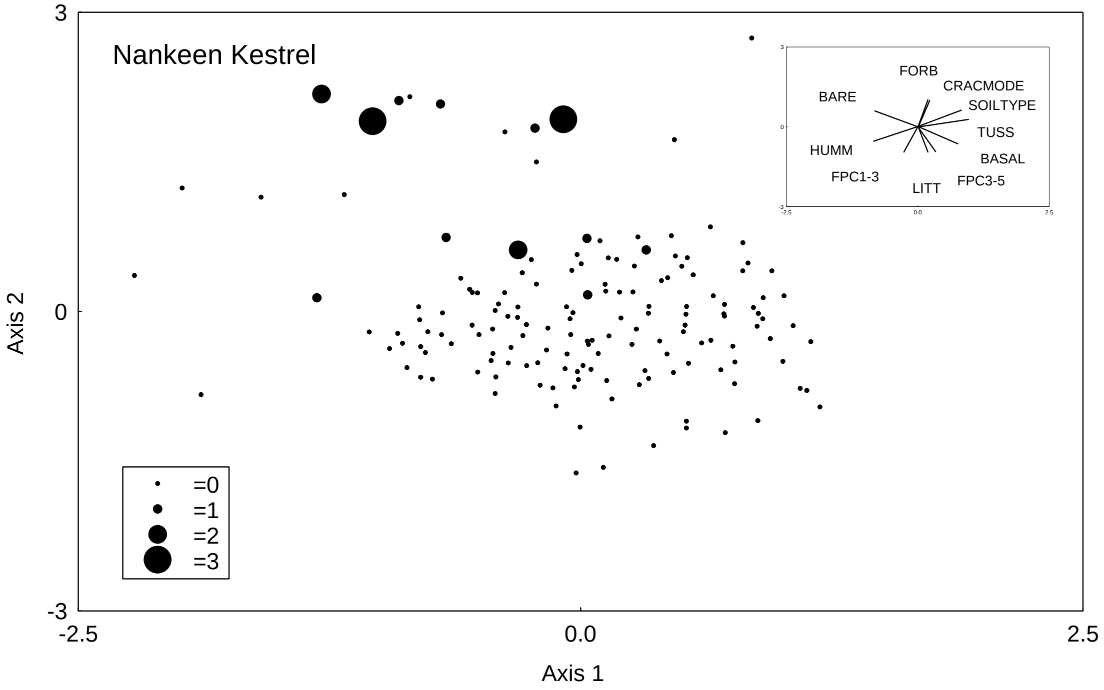


Figure 3.5 (g) Ordination indicating relative abundance of Little Friarbirds at each quadrat.

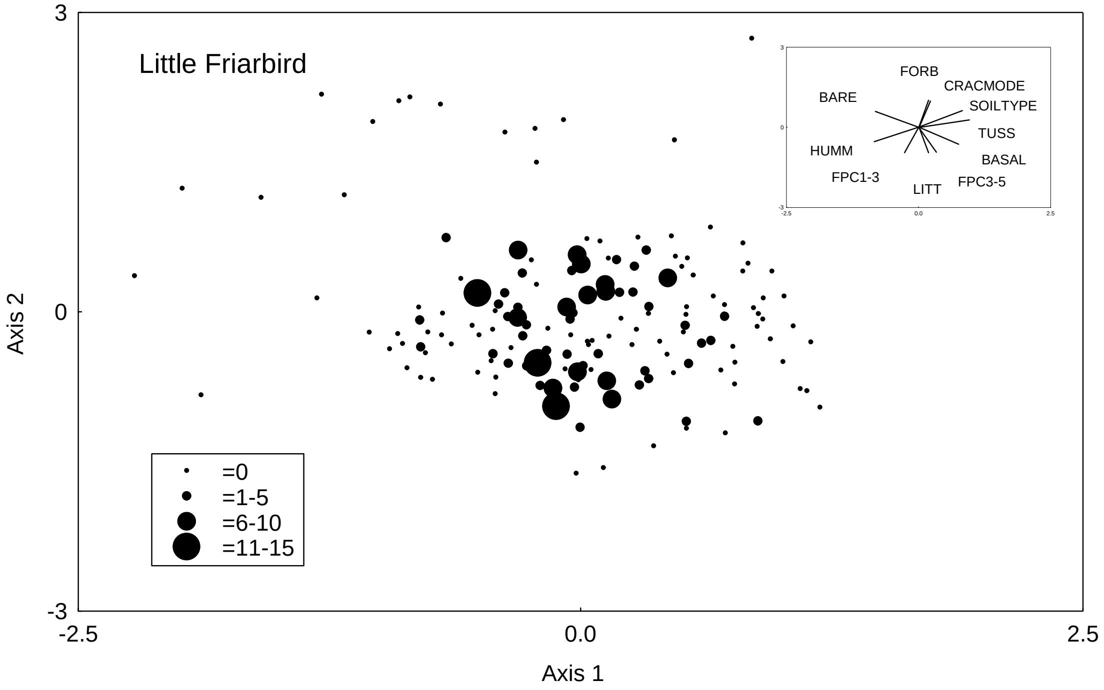


Figure 3.5 (h) Ordination indicating relative abundance of Noisy Friarbirds at each quadrat.

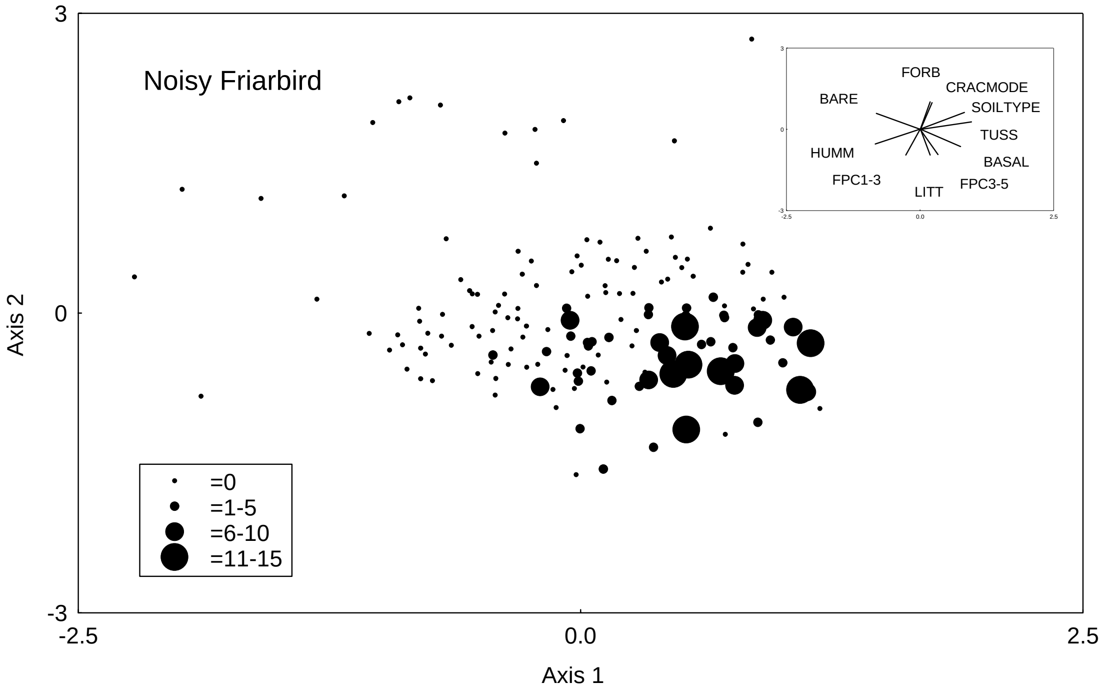


Figure 3.5 (i) Ordination indicating relative abundance of Weebills at each quadrat.

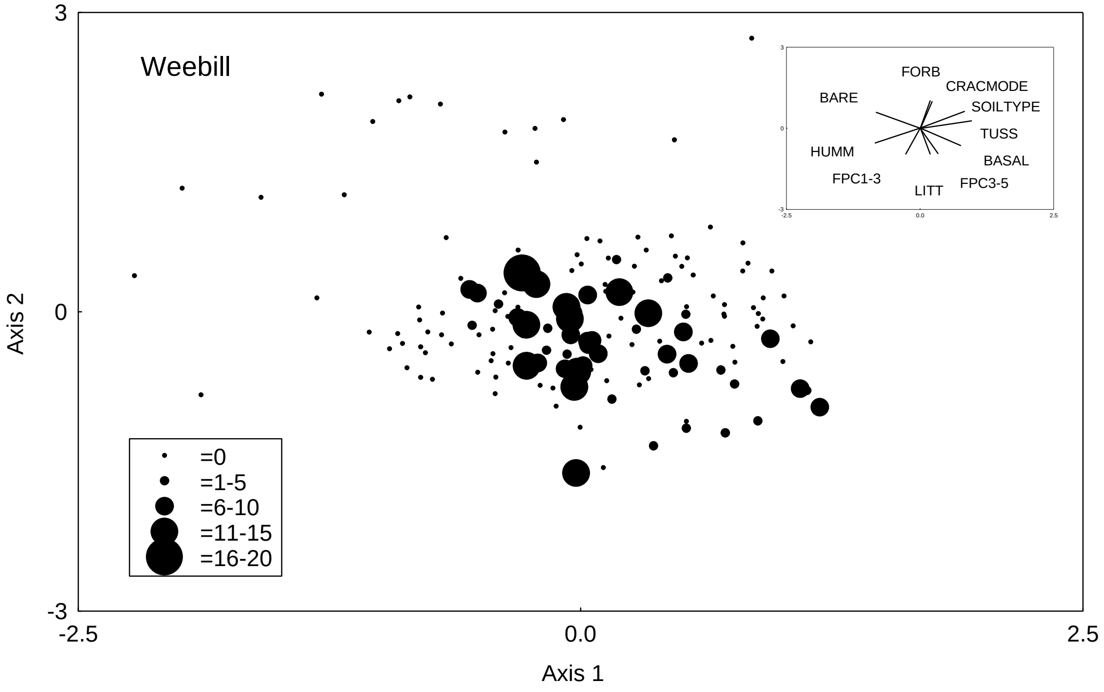


Figure 3.5 (j) Ordination indicating relative abundance of Striated Pardalotes at each quadrat.

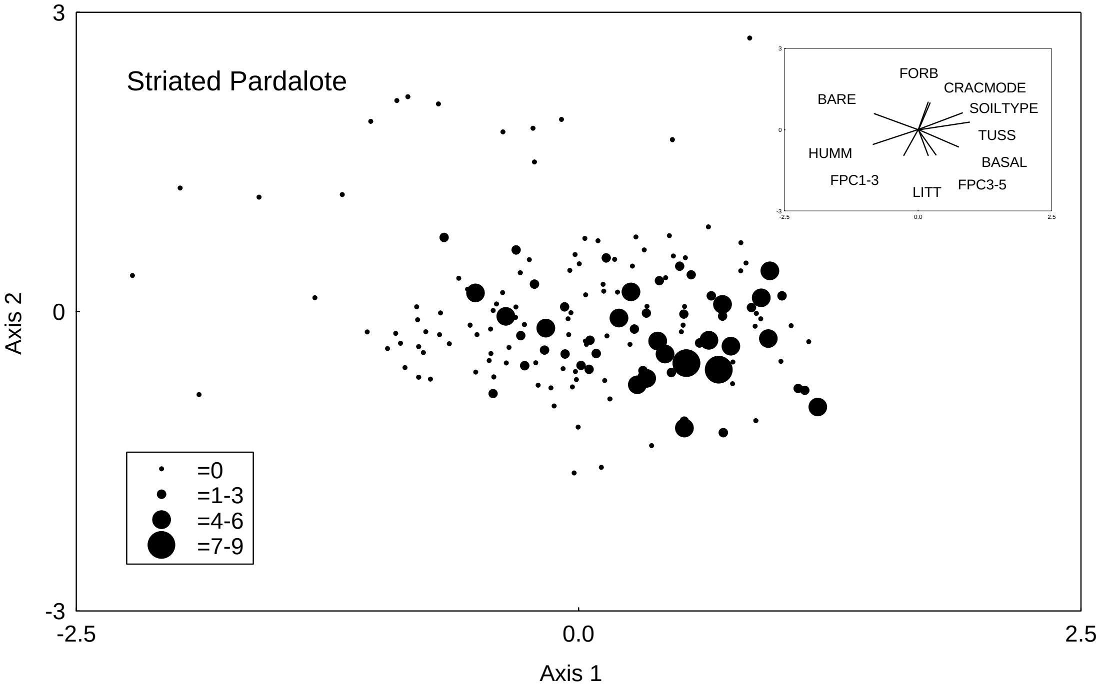


Figure 3.5 (k) Ordination indicating relative abundance of Terrestrial insectivores at each quadrat.

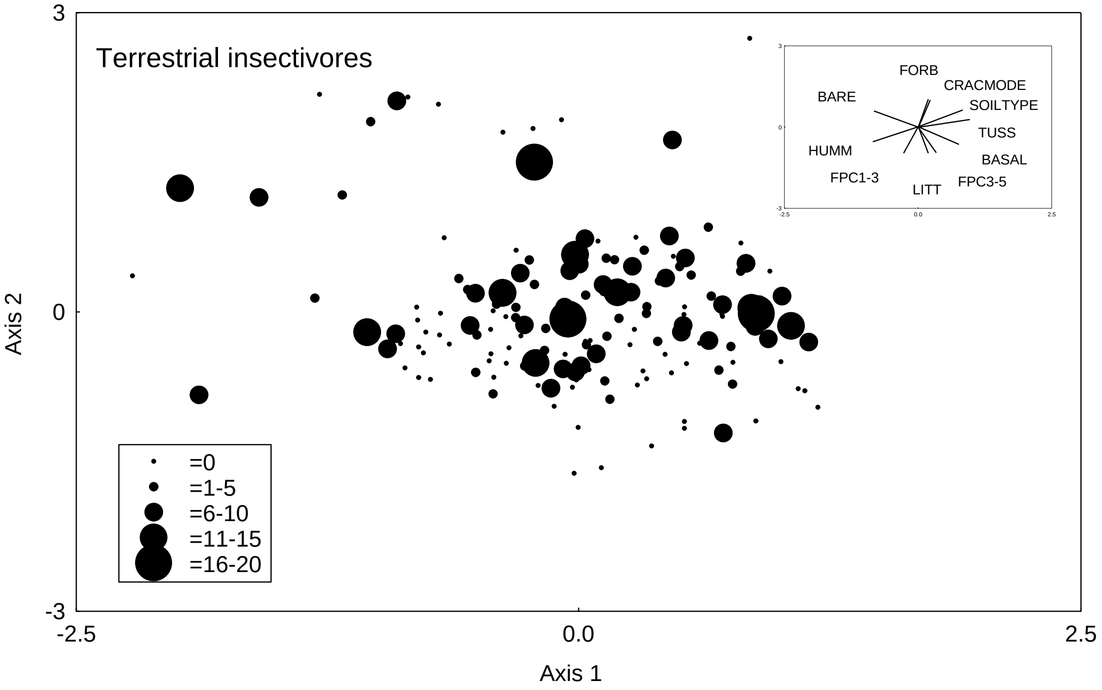


Figure 3.5 (l) Ordination indicating relative abundance of nectarivores at each quadrat.

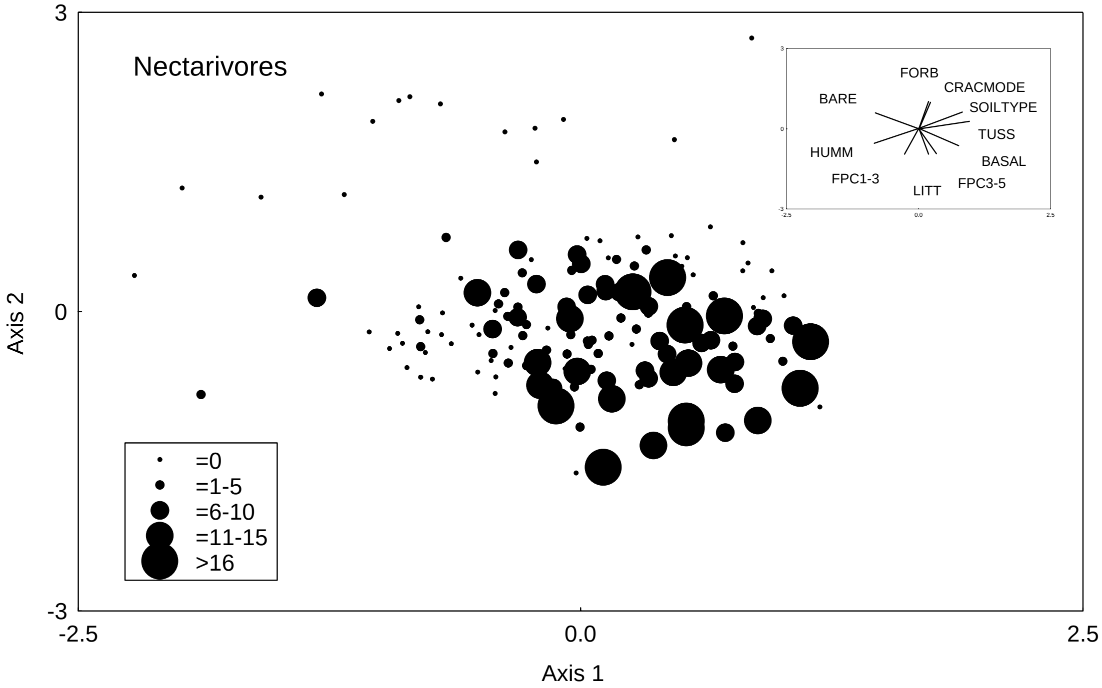


Figure 3.5 (m) Ordination indicating relative abundance of Muridae at each quadrat.

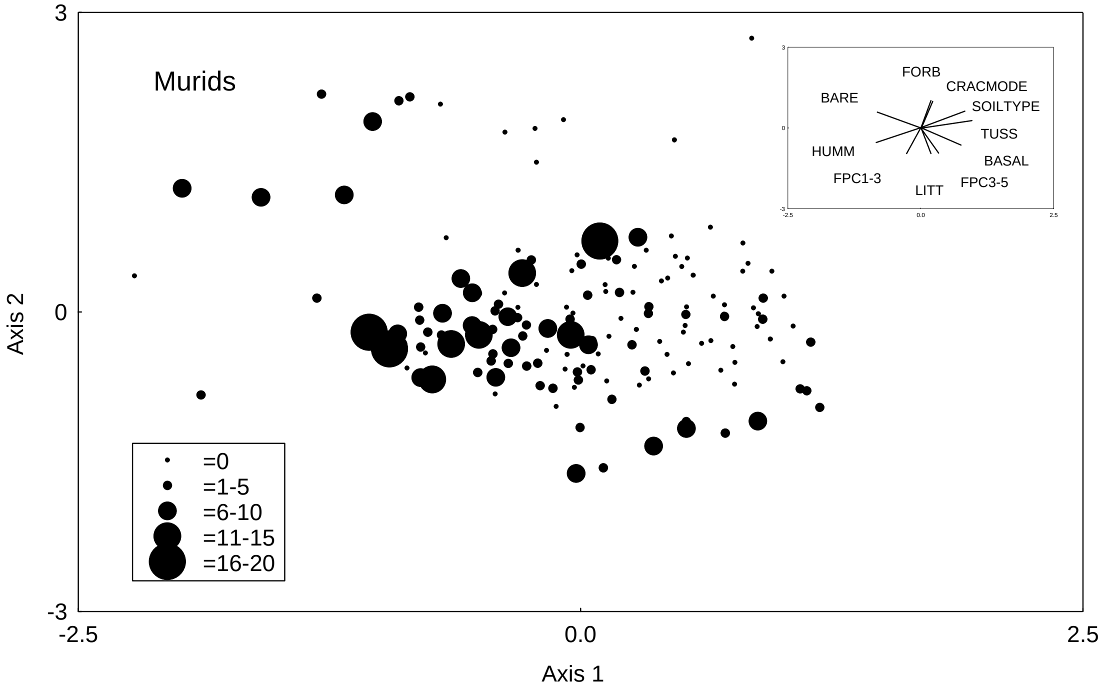


Figure 3.5 (n) Ordination indicating relative abundance of Dasyuridae at each quadrat.

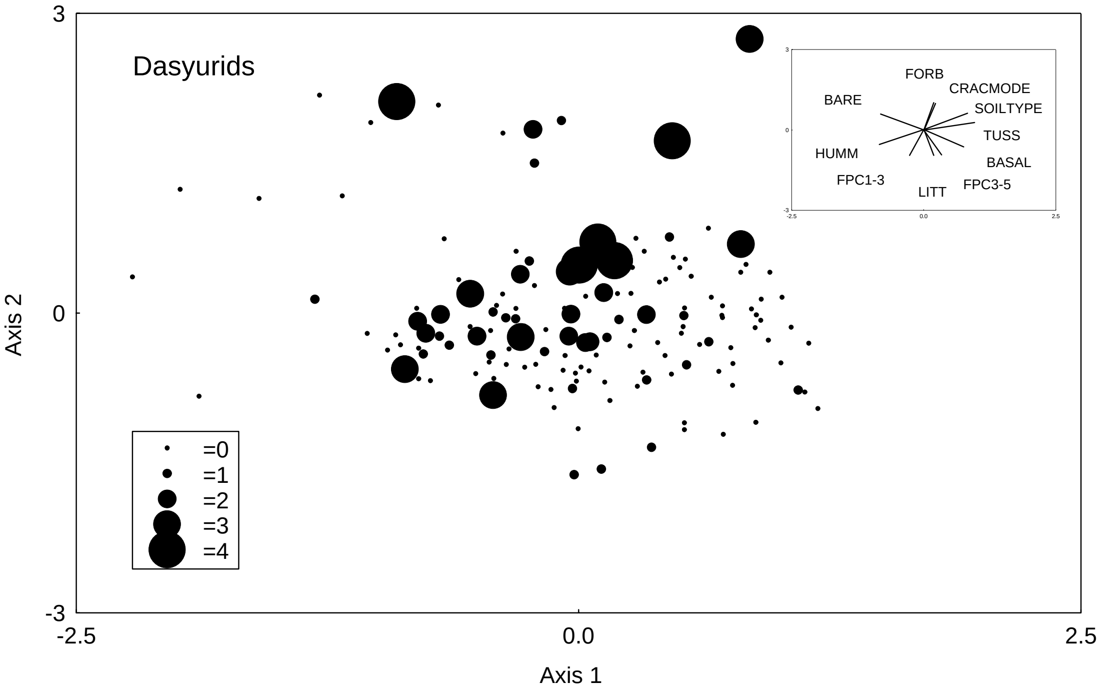


Figure 3.5 (o) Ordination indicating relative abundance of *Carlia munda* at each quadrat.

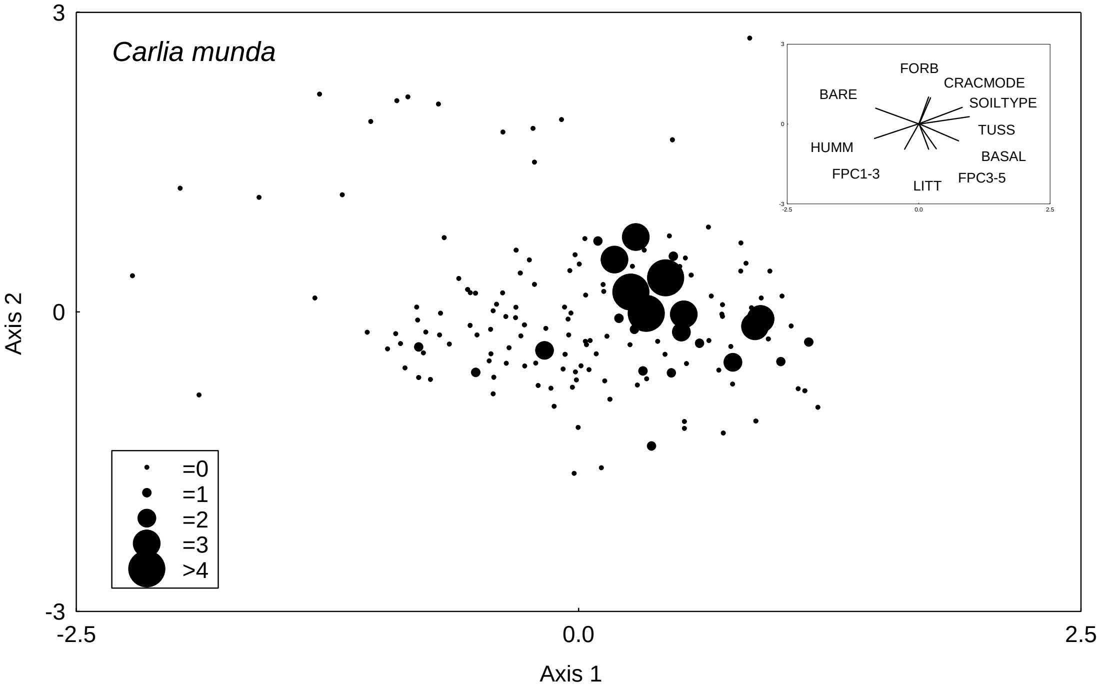


Figure 3.5 (p) Ordination indicating relative abundance of *Ctenotus hebetior* at each quadrat.

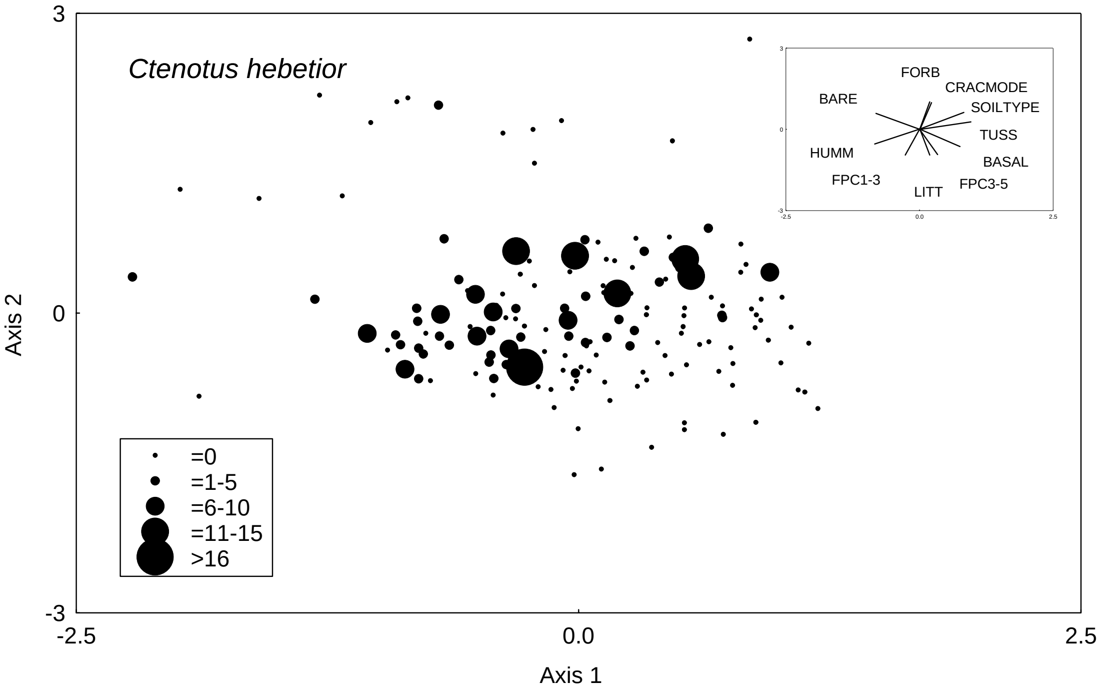


Figure 3.5 (q) Ordination indicating relative abundance of *Ctenotus pantherinus* at each quadrat.

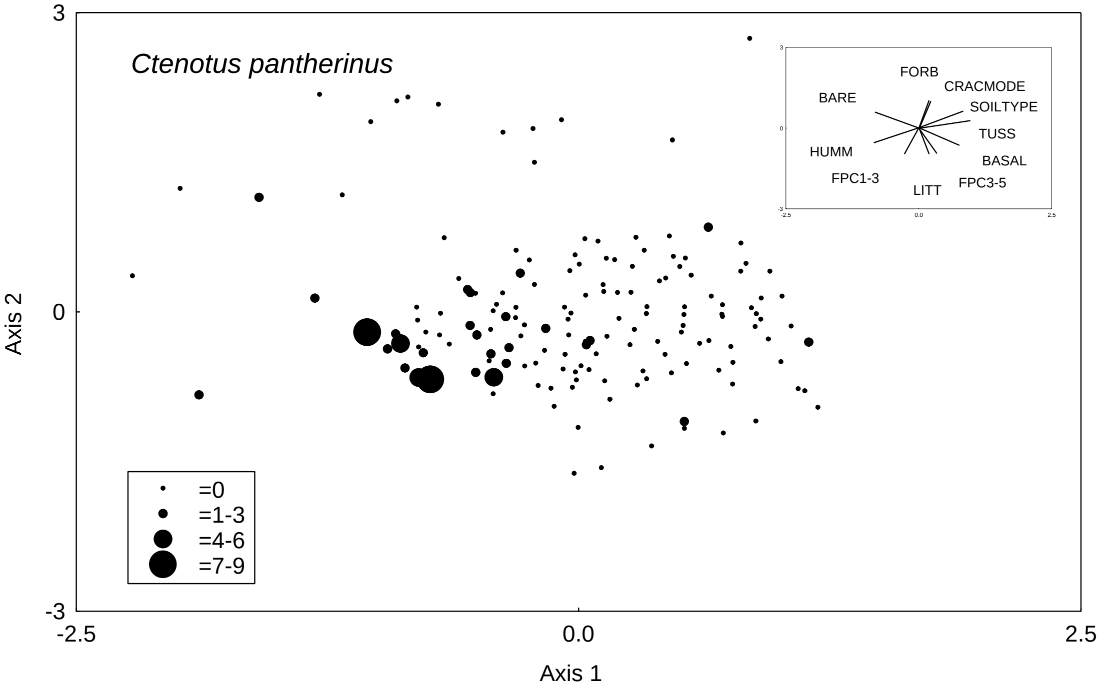


Figure 3.5 (r) Ordination indicating relative abundance of *Heteronotia binoei* at each quadrat.

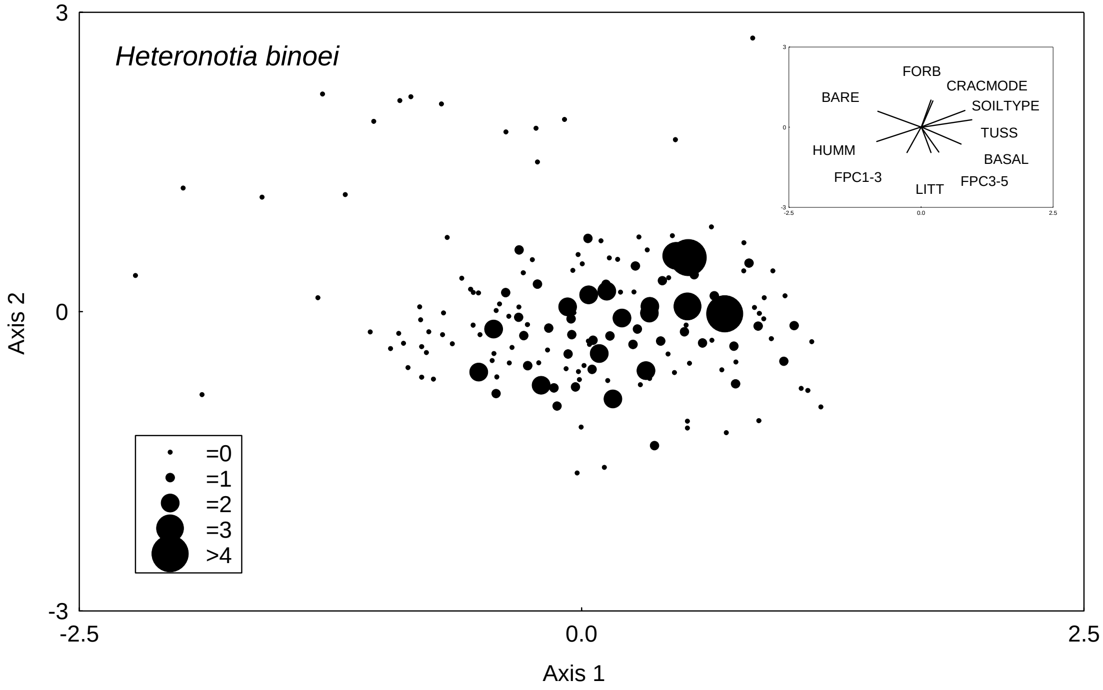


Figure 3.5 (s) Ordination indicating relative abundance of *Gehyra catenata* at each quadrat.

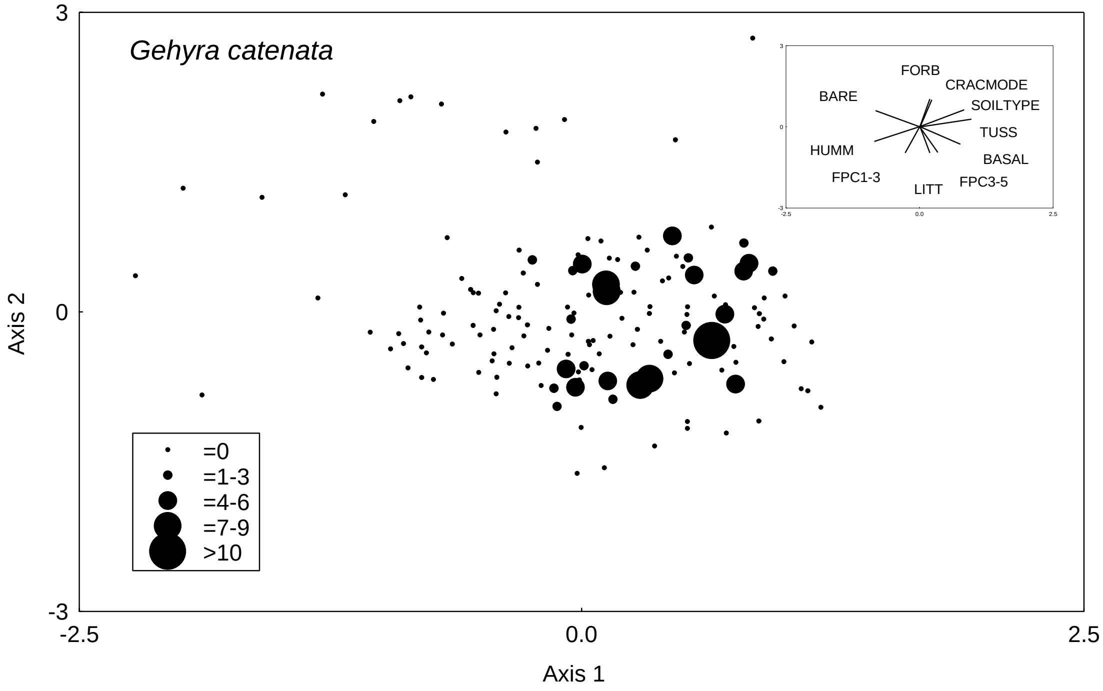
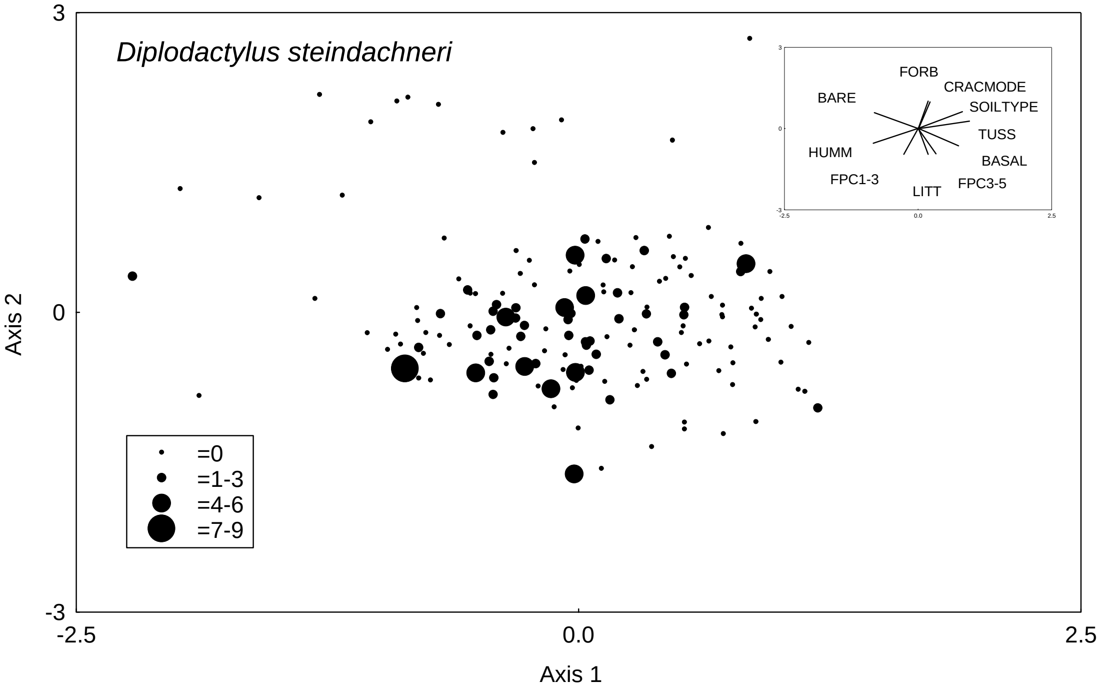


Figure 3.5 (t) Ordination indicating relative abundance of *Diplodactylus steindachneri* at each quadrat.



Plant species composition and correlation to fauna

The ordination of plant composition using cover abundance scores was labelled with the fauna classification groups (Figure 3.6). This indicated some general correspondence between plant assemblages at quadrat sampling sites and the fauna assemblages recorded. Analysis of similarity using the fauna groups was undertaken to further test the relationship. Similarity between quadrats as defined by plant composition using cover abundance scores, average height of each species, and ground cover composition using cover abundance scores, were the most strongly associated (all Rho>0.5) (Table 3.4).

The correlation between vertebrate taxa and vegetation dissimilarity matrices was significant for all comparisons except for mammals and basal area, and mammals and canopy cover. The strongest assemblage fidelity was again between all vertebrates, birds, mammals and reptiles and plant composition (as scored by cover abundance), and ground cover (cover abundance). There was also a strong relationship between birds and canopy composition cover abundance (Table 3.4).

Figure 3.6 Two-dimensional ordination of plant species composition at each sample site. Data standardised and species recorded in only one quadrat removed from analysis. Stress=0.32. Sites labelled with the thirteen fauna groups to illustrate correspondence between plant and fauna site composition.

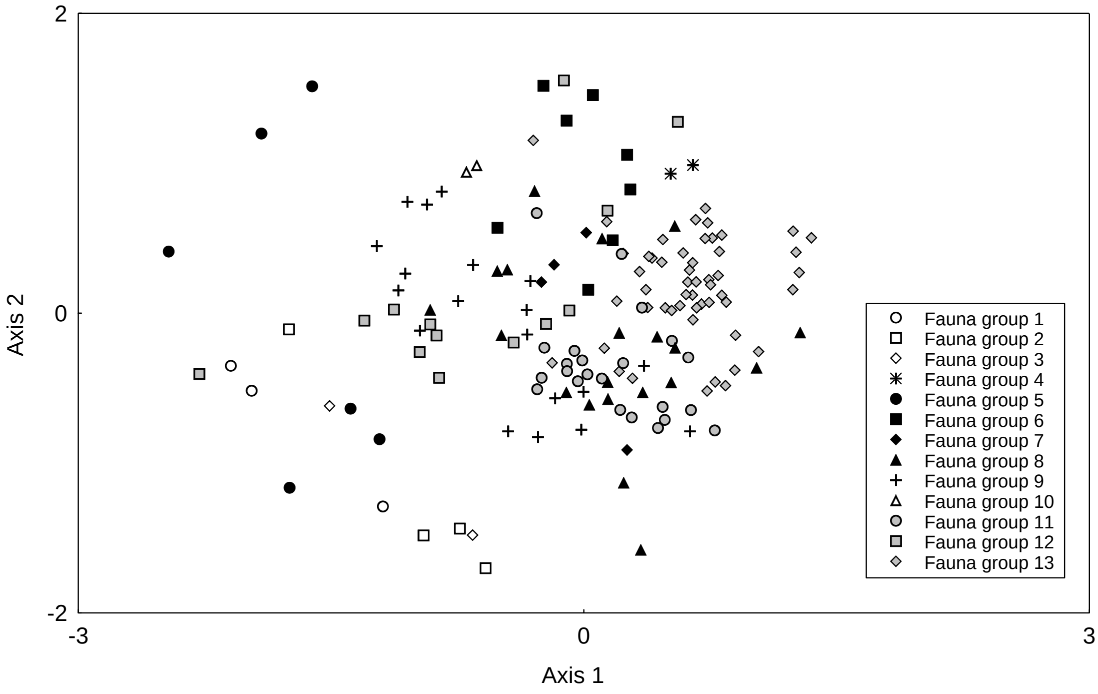


Table 3.4 Analysis of similarity (ANOSIM) relationships between fauna group classification and a range of dissimilarity matrices derived for plant species composition using cover abundance, height and basal area scores. Mantel tests estimating correlations between composition of vertebrate taxa and plants groups are also tabulated. Data indicates rank correlation coefficient using standardised Bray-Curtis dissimilarity matrices derived from abundance (fauna) or cover abundance, total basal area or average height (plants). Significance identified via permutation tests. Probability levels are *p<0.5, **p<0.01, ***p<0.001, ns=not significant.

Groups	Quadrat cover	Quadrat basal area	Quadrat height	Canopy cover (>5m)	Mid-storey cover (1-5m)	Ground cover (<1m)
ANOSIM						
Fauna groups	0.71***	0.371***	0.576***	0.393***	0.281***	0.641***
MANTEL						
All	0.558***	0.349***	0.515***	0.386***	0.213***	0.482***
Bird	0.51***	0.363***	0.511***	0.397***	0.193***	0.424***
Reptiles	0.446***	0.169***	0.318***	0.194***	0.16***	0.427***
Mammals	0.182***	0.047 ns	0.075*	0.045 ns	0.107***	0.192***

Predictive models for fauna guilds, families and species

Minimum adequate models were derived for abundance and species richness for the bird foraging guilds, and mammal and reptile families, using the six significant environmental vectors (Table 3.10). Between one and four variables were used in the models, though most used only two terms, and deviance explained ranged from 4-47%. For abundance data, the variation in 12 foraging guilds, five mammal families and four reptile families could be modelled, whereas ten guilds, three mammal and two reptile families were modelled for species richness. Typically bird guild abundance and richness was predicted by basal area and bare ground cover, whereas all other variables were evenly spread as accounting for variation recorded in reptile and mammal abundance and species richness.

Minimum adequate models were also derived for 89 species most frequently recorded (reported from 10 or more quadrats) using the same six variables (Table 3.10). Total deviance explained for species ranged from 2-56%, and models generally provided a sensible description of the habitat requirements and biology of the species selected. A number of these relationships are plotted to illustrate the direction and degree of response to individual model terms (Figure 3.7a-m). Some of the key patterns include:

Birds (Figures 3.7a-e)

Basal area and foliage projective cover were the most significant predictors of the abundance of many bird species, though bare ground and soil type were also common predictive factors. The relationships are predominantly positive. The Mistletoebird (frugivore), Brown Treecreeper (trunk gleaner), Rufous Whistler (gleaner), Weebill (gleaner) and Noisy Friarbird (nectarivore), all increased in abundance with increasing basal area. The latter two were still abundant where basal area was low. In comparison smaller nectarivores (Singing Honeyeater, Brown Honeyeater, Little Friarbird) and terrestrial insectivores (Variegated Fairy-wren) were strongly associated with high mid-storey foliage projective cover. Conversely, the Nankeen Kestrel (raptor) and Torresian Crow (terrestrial omnivore) declined with increase in canopy and mid-storey cover. For some species the relationship was more complicated. Striped Honeyeaters (nectarivore/gleaner) had a positive relationship with basal area, FPC 1-3 m and bare ground, and this reflects this species habitat preference, being more abundant in dense *Acacia* spp dominated communities.

For the Apostlebird (terrestrial omnivores), Pale-headed Rosella (granivore), Red-backed Fairy-wren and Grey-crowned Babbler (both terrestrial insectivores), abundance was positively related to increasing mid-storey (Apostlebird) or canopy cover (the remainder), differentially patterned according to ground cover type (Pale-headed Rosella and Red-backed Fairy-wren increasing with tussock grass cover, the other two bare ground). This pattern reflects their guild membership and hence foraging preferences: open ground (Apostlebird, Grey-crowned Babbler), and high grass cover (Pale-headed Rosella, Red-backed Fairy-wren).

Other species were best predicted by ground cover variables alone. Known disturbance increasers (Willie Wagtail, a sallier and the Diamond Dove and Crested Pigeon, both granivores) increased with higher percentage of bare ground cover, as did the Barn Owl, a nocturnal terrestrial omnivore. Other relationships were complementary. Peaceful Dove (granivore) and Yellow-throated Miners (terrestrial omnivores) both increased in abundance with increasing bare ground cover and tussock grass cover. This suggests that these species occur in environments that may have either high bare ground cover or high tussock grass cover, without any singular preference for either, and irrespective of other factors tested (basal area, hummock grass cover). Other variables may determine their presence and abundance in sites of either high ground or tussock cover that were not measured or tested.

Figure 3.7 (a-m) Modelled relationships between selected species and guilds abundance and significant predictive terms. Only the response to single terms for representative species is plotted, the effect of other significant terms being held constant.

Figure 3.7 (a) Modelled relationship between six bird species and basal area. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

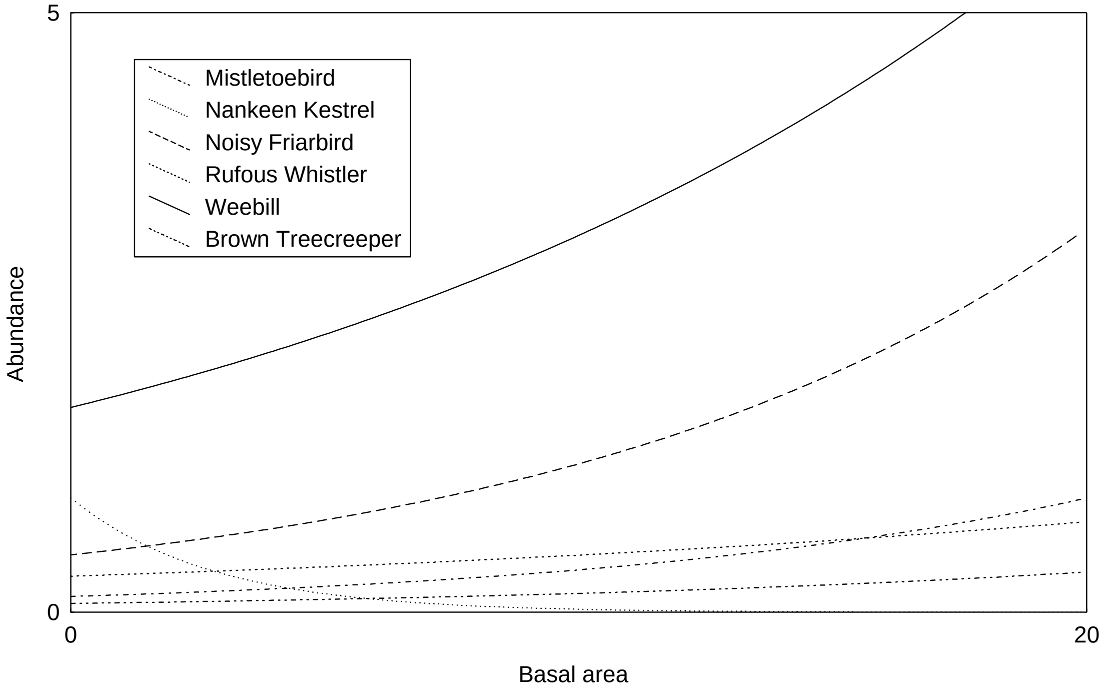


Figure 3.7 (b) Modelled relationship between six bird species and FPC 1-3 m. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

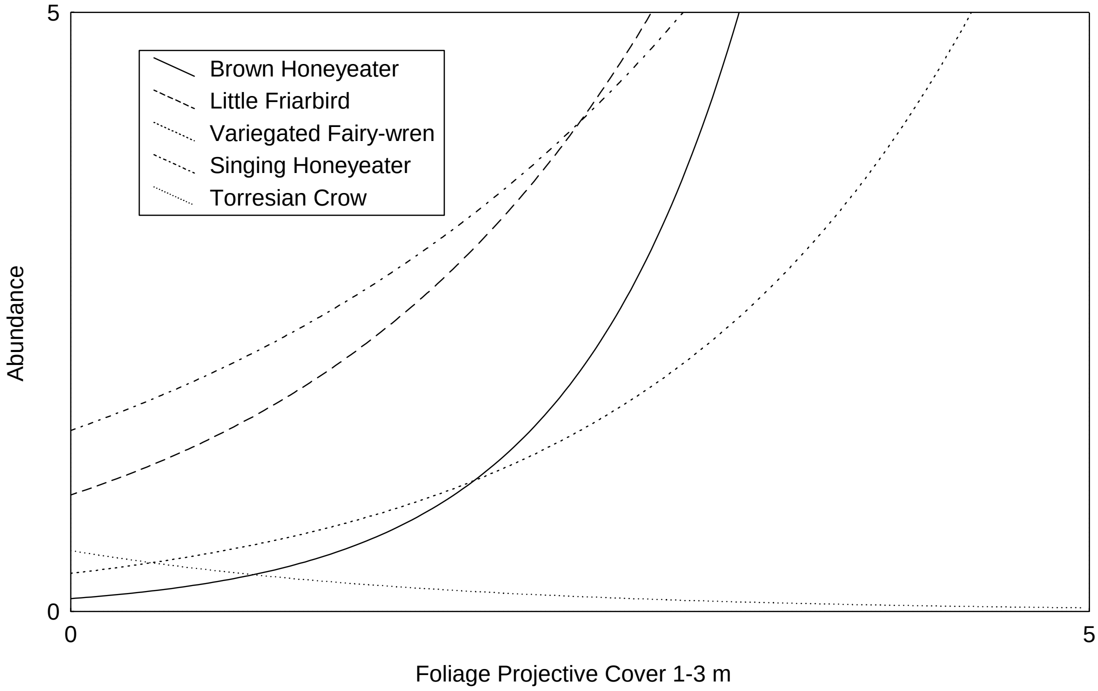


Figure 3.7 (c) Modelled relationship between five bird species and bare ground cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

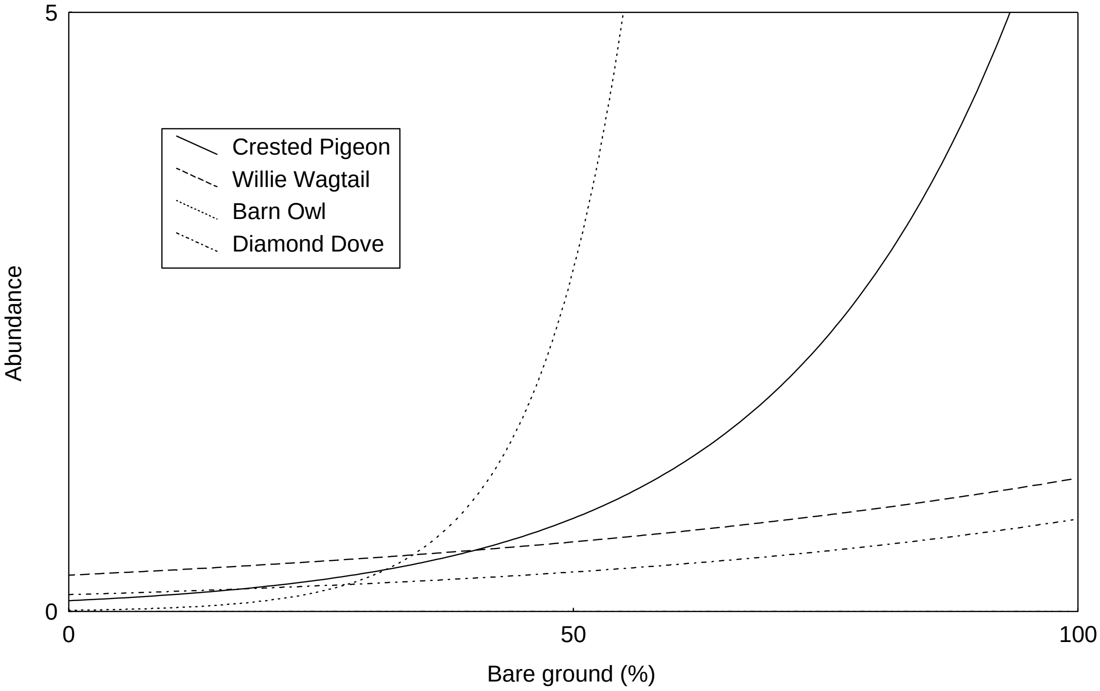


Figure 3.7 (d) Modelled relationship between two bird species, hummock and tussock grass cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

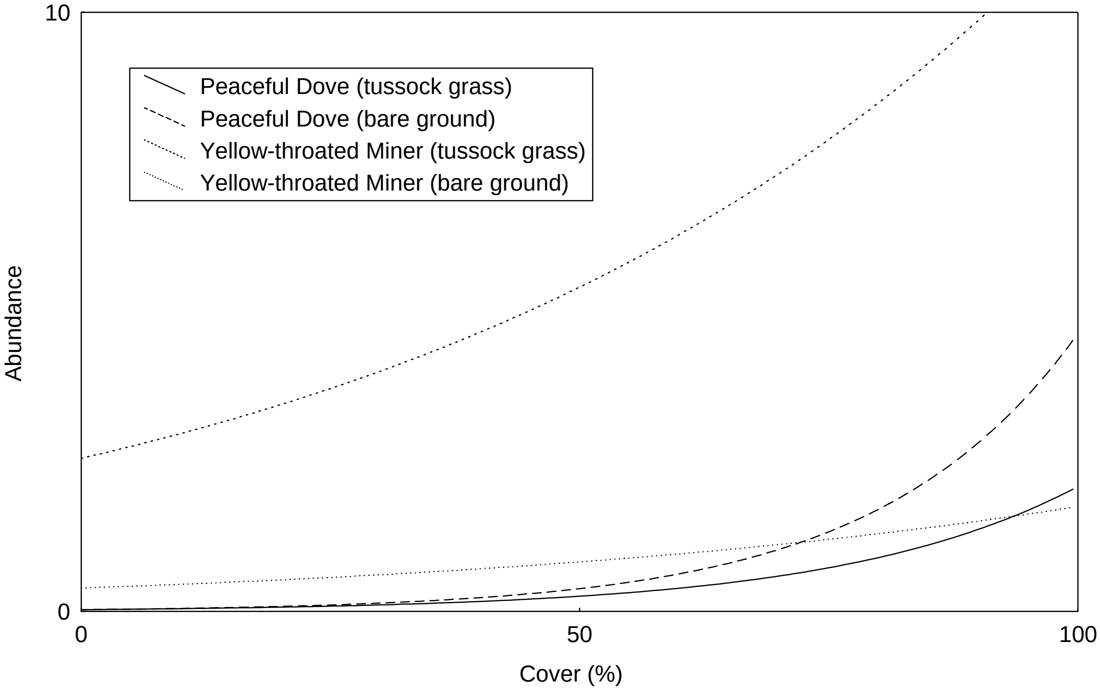
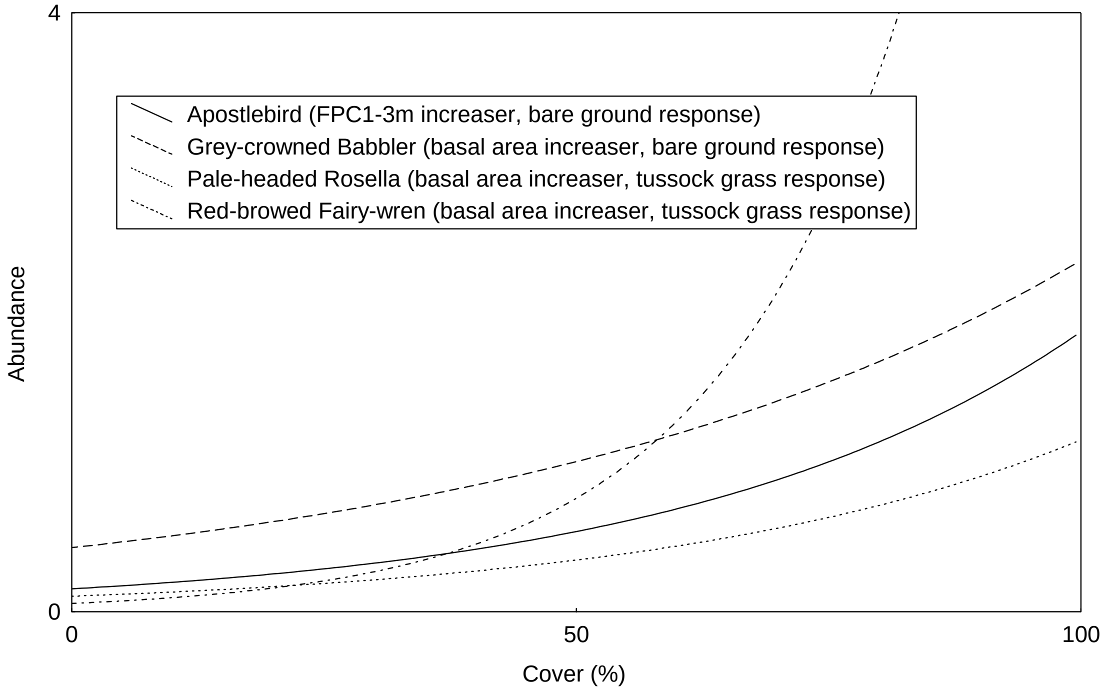


Figure 3.7 (e) Modelled relationship between four bird species, tussock grass and bare ground cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.



Mammals (Figures 3.7 f-h)

Mammal species responded to the range of variables tested, without any consistent tendency for one set of variables to be explanatory. This reflects perhaps a greater variation in body size and biology. *Macropus robustus* and *Tachyglossus aculeatus* abundance increased with increasing basal area; while *M. robustus* also increased with higher bare ground, *T. aculeatus* was more abundant where tussock grass cover was between 0-50%. Conversely *Pseudomys desertor* declined with tree-cover, but showed a strong relationship with increasing hummock grass cover. *Sminthopsis macroura* abundance was predicted by hummock grass cover, but also by decreasing bare ground cover, indicating that sites with high ground cover of other species (e.g. tussock grasses) may also have reasonable *S. macroura* numbers. *Macropus giganteus* follows suit in that though abundance increased slightly in sites with high hummock grass cover, measured abundance was most strongly associated with high area of bare ground.

Figure 3.7 (f) Modelled relationship between three mammal species and basal area. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

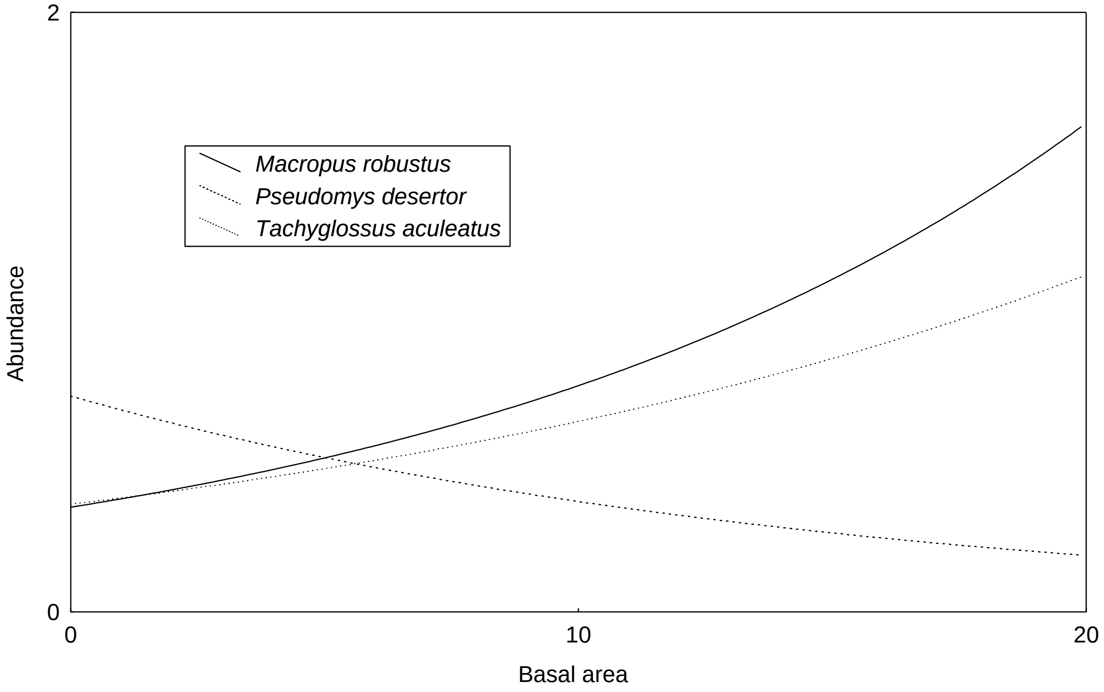


Figure 3.7 (g) Modelled relationship between four mammal species and hummock grass cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

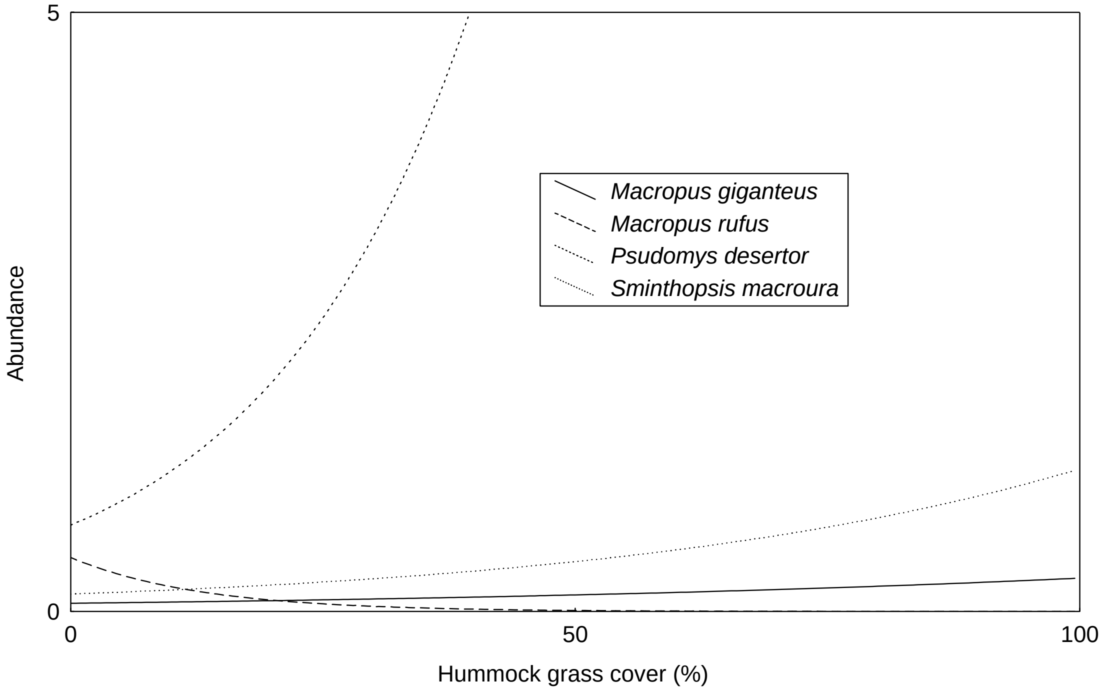
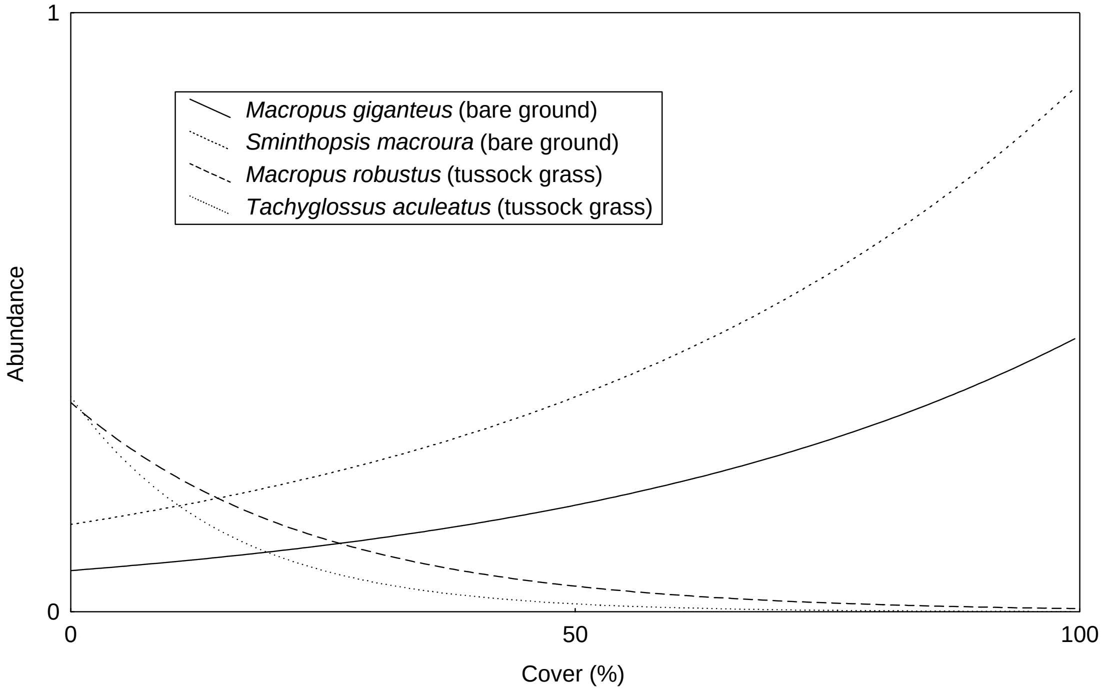


Figure 3.7 (h) Modelled relationship between four mammal species, tussock grass and bare ground cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.



Reptiles (Figures 3.7 i-m)

On the whole reptile species abundance was best predicted by substrate variables such as ground cover (hummock, tussock, bare) and notably soil type (in comparison to mammals and birds). Simple relationships between abundance of arboreal (*Gehyra catenata*, *Egernia striolata*) and terrestrial species (*Ctenotus hebetior* and *C. pantherinus*) with increasing or decreasing basal area were identified. *Morethia boulengeri* was also associated with basal area, but this terrestrial species preferred densely timbered *Acacia* woodlands with large extent of bare ground and ample fallen timber. *Ctenotus robustus* declined with increasing mid-storey foliage projective cover, in contrast to the scansorial, basking dragon *Amphibolurus nobbi*, and the fossorial *Lerista punctatovittata*. Mid-storey cover (FPC 1-3 m) must provide a microclimate (e.g. daytime shade) or microhabitat (e.g. surrogate measure for high litter cover) for this species. Abundance of a number of species that are typically associated with hummock grassland environments was strongly related to this variable (*Ctenotus pantherinus*, *C. rosarium*, *Lialis burtoni* and *Rhynchoedura ornata*), whereas widely distributed more catholic species (*Heteronotia binoei*) identified a negative pattern. A similar case occurred for bare ground cover: those associated with open ground habitats increased (*Ctenophorus nuchalis*, *Morethia boulengeri*, *Suta suta*), and fossorial species declined (*Proablepharus tenuis*).

As indicated earlier, soil type as a measure of substrate type was a consistent predictor for many reptiles. Many species were more abundant in sandy soils, and these included nocturnal and diurnal species that burrow to shelter (*Ctenophorus nuchalis*, *Diplodactylus steindachneri*), or for breeding (*Pogona barbata*, *Amphibolurus nobbi*). Fossorial species such as *Menetia greyii* were also more prevalent in sandier soils, whereas *Gehyra catenata* and *Suta suta* were not, being more abundant in clay soils. Some species identified a strong preference to a soil type (*Ctenophorus nuchalis* absent in clay soils, *Suta suta* absent in sandy soils), whereas others were more universal, and simply more abundant in one particular type (*Gehyra catenata* and clays, *Menetia greyii* and sands). This suggests other habitat variables concurrently determine presence or absence (e.g. basal area for the arboreal *G. catenata*, and ground cover factors for the fossorial *M. greyii*).

Figure 3.7 (i) Modelled relationship between five reptile species and bare ground cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

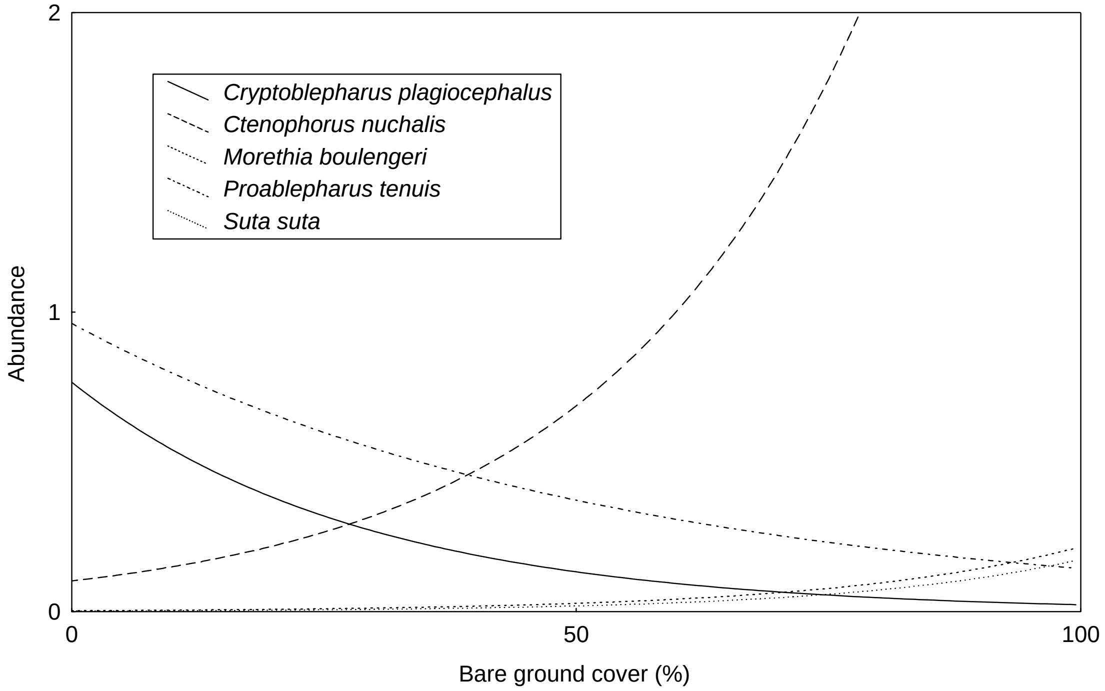


Figure 3.7 (j) Modelled relationship between five reptile species and basal area. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

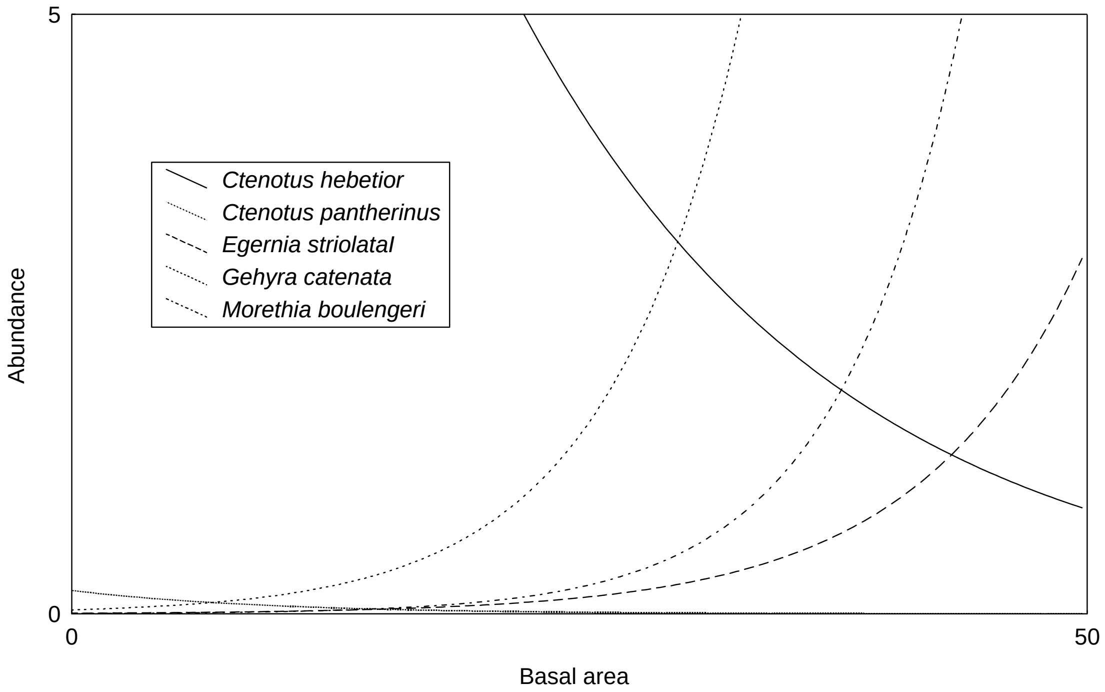


Figure 3.7 (k) Modelled relationship between three reptile species and FPC 1-3 m. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

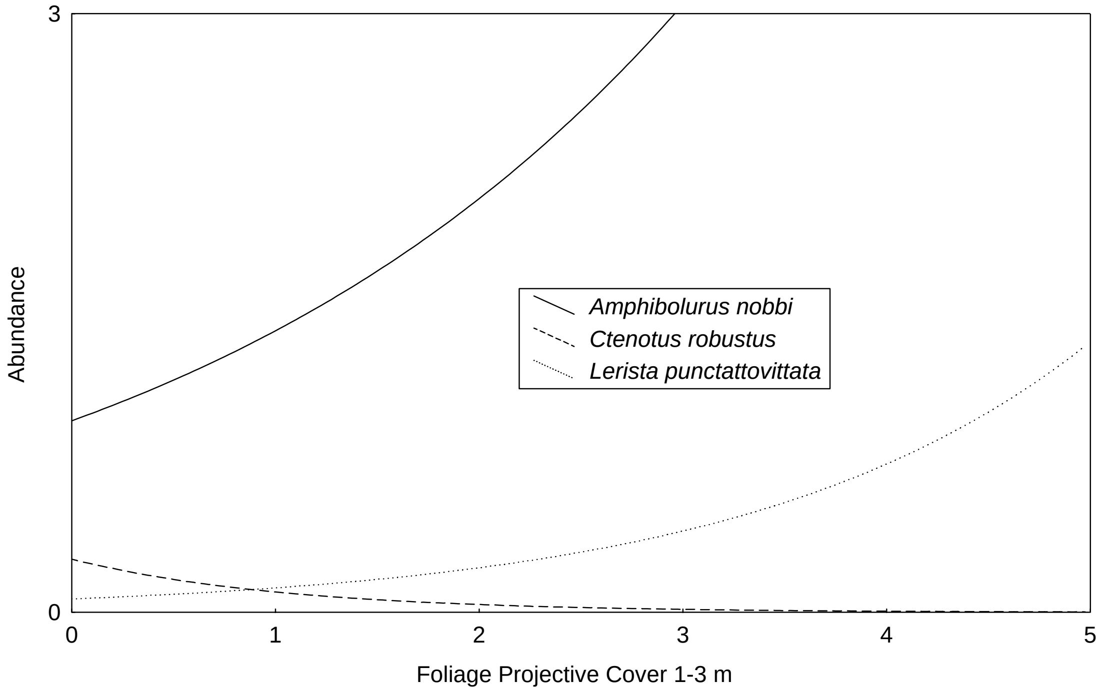


Figure 3.7 (l) Modelled relationship between five bird species and hummock grass cover. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.

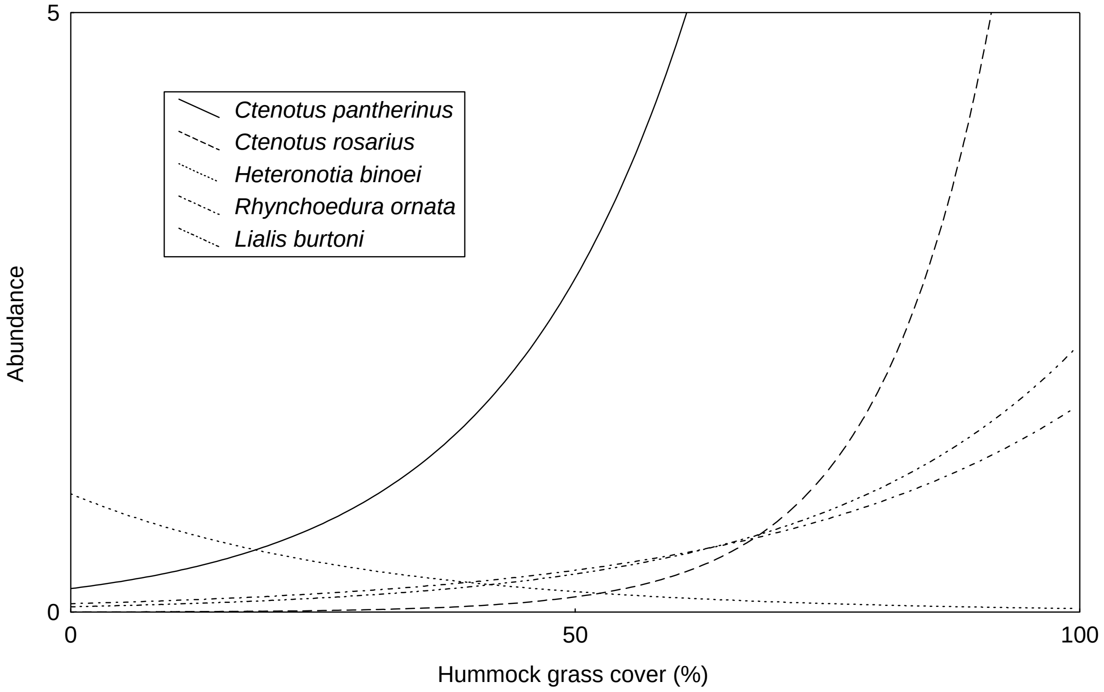
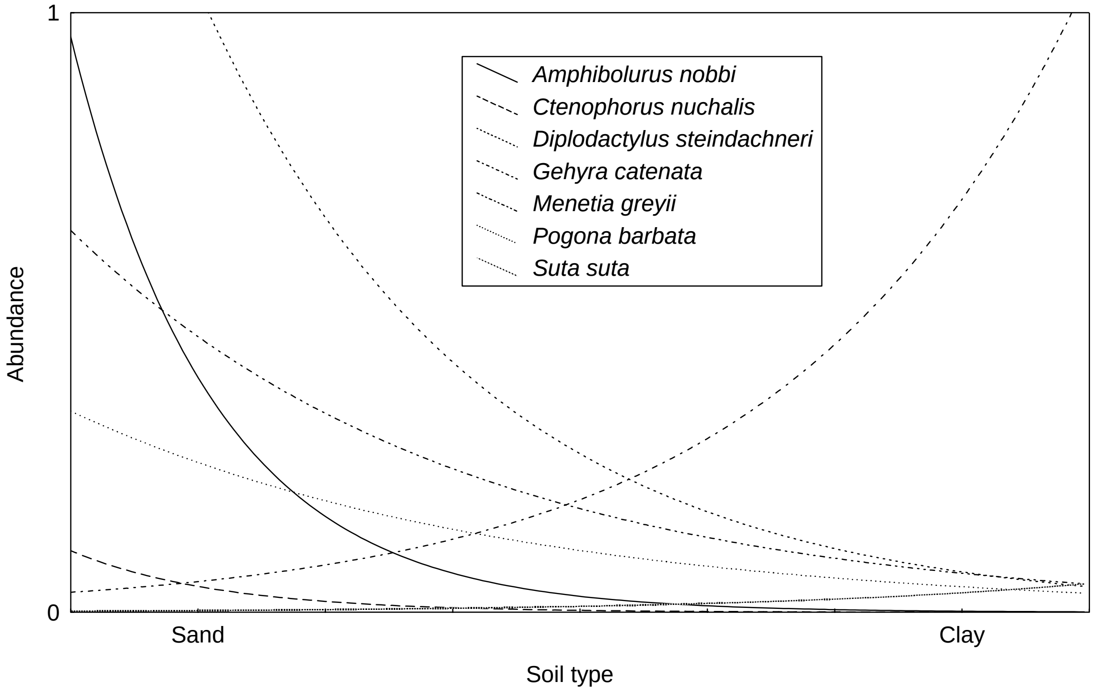


Figure 3.7 (m) Modelled relationship between seven reptile species and soil type. Model terms (variable, intercept, estimates and significance levels) are listed in Table 3.9 and 3.10.



Area, habitat heterogeneity and productivity influence on species richness

Variables representing productivity and area were tested independently for significance and percentage deviance explained against vertebrate, bird, mammal, and reptile quadrat species richness. All indicated significant relationships with vegetation structure and basal area, though these were generally weak (Table 3.5). Reptile richness was also related to the area of regional ecosystem polygon sampled, as was mammals by total area of regional ecosystem over bioregion. Bird richness was predicted by all factors, though most strongly by the productivity surrogates (basal area, ground cover, landzone rank and structure). Total richness patterns were similar to birds, indicating interdependence of bird and total richness.

Minimum adequate models for vertebrates, birds, reptiles and mammals indicated structural class was consistently associated with species richness (Table 3.6). The best models were for all vertebrates (62% explained) and birds (61%). Generally, measures of area and productivity were less successful in accounting for mammal (26%) and reptile (37%) richness. Landzone rank also contributed to the vertebrates and bird models only, while basal area and average bioregion shape were included in the mammal model, inversely related to richness. Generally, it seems there is a consistent relationship between increasing vegetation complexity (class 1 represents grasslands, class 5 represents riparian vegetation) and increasing species richness (Figure 3.8). Predicted mean species richness for birds and reptiles increased rapidly in the lower structural class and then remained fairly uniform with increasing complexity. Mammal richness did not increase to its highest level until the final structural class. The model for bird species richness also identified a relationship with productivity. The pattern was idiosyncratic with highest and lowest richness predicted for intermediate land zone classes (hence productivity).

Table 3.5 Variance in species richness explained by each variable individually for birds, mammals and frogs. Poisson (log-linear) error distribution used. Significance levels include *p<0.05, **p<0.01, ***p<0.001, ns=not significant.

Group	All	Birds	Mammal	Reptiles
Basal area	8.6***	10.6***	3.1*	4.3**
Ground cover	0.5 ns	17.8***	0.7 ns	0.7 ns
Landzone rank	28.3***	32.8***	8.1 ns	4.7 ns
Structure	40.8***	34.2***	7.8***	36.6***
Regional ecosystem sample area	14.8***	6.6***	0.5 ns	3.1*
Regional ecosystem sample shape	9.1***	3.3***	0.03 ns	0.3 ns
Regional ecosystem total area	15.2***	6.6***	5.9**	2.1 ns
Regional ecosystem average shape	16.2***	2.6***	2.4 ns	2.1 ns

Table 3.6 Minimum adequate models derived for fauna species richness (vertebrates, birds, mammals, reptiles) per site using utilising generalised linear modelling. Table indicates parameter estimate and significance (Wald statistic *p<0.05, **p<0.01, ***p<0.001, ns=not significant), degrees of freedom of model and total deviance explained (%). Aliased term and significance of each class for categorical data also indicated.

Summary of all effects	df	Wald statistic	p	Variable and level of effect	Estimate	se	p
Vertebrates							
Total deviance explained 62%							
Intercept	1	10636.31	***	Intercept	3.246	0.026	***
Structural class	4	106.9	***	Structural class 1	-0.685	0.058	***
Category 5 aliased				Structural class 2	0.128	0.056	ns
				Structural class 3	0.229	0.047	***
				Structural class 4	0.141	0.031	**
Landzone rank	5	78.5	***	Landzone rank 1	-0.019	0.032	ns
Category 6 aliased				Landzone rank 2	0.058	0.039	ns
				Landzone rank 3	-0.404	0.047	***
				Landzone rank 4	0.016	0.040	ns
				Landzone rank 5	0.242	0.032	***
Birds							
Total deviance explained 61%							
Intercept	1	5398.6	***	Intercept	2.839	0.031	***
Structural class	4	81.8	***	Structural class 1	-0.747	0.072	***
Category 5 aliased				Structural class 2	0.144	0.069	ns
				Structural class 3	0.293	0.056	***
				Structural class 4	0.123	0.038	**
Landzone rank	5	91.4	***	Landzone rank 1	-0.055	0.040	ns
Category 6 aliased				Landzone rank 2	0.107	0.048	ns
				Landzone rank 3	-0.514	0.060	***
				Landzone rank 4	0.012	0.049	ns
				Landzone rank 5	0.333	0.039	***
Mammals							
Total deviance explained 26%							
Intercept	1	89.3	***	Intercept	2.335	0.319	***
Basal area	1	20.9	***	Basal area	-0.049	0.014	***
Average shape	1	11.5	**	Average shape	-1.181	0.450	**
Structural class	4	43.7	***	Structural class 1	-0.440	0.169	**
Category 5 aliased				Structural class 2	-0.696	0.185	***
				Structural class 3	0.200	0.154	ns
				Structural class 4	0.057	0.083	ns
Reptiles							
Total deviance explained 37%							
Intercept	1	1051.8	***	Intercept	1.665	0.059	***
Structural class	4	66.9	***	Structural class 1	-0.817	0.133	***
Category 5 aliased				Structural class 2	0.194	0.106	*
				Structural class 3	0.239	0.085	**
				Structural class 4	0.300	0.066	***

Figure 3.8 (a-b) Relationship between species richness, structural and landzone classes. Values shown are the mean richness as predicted by the estimate in the generalised linear model. Whiskers are the 95% confidence limits.

Figure 3.8 (a) Predicted mean species richness of all vertebrates, birds, mammals and reptiles for each structural class (SC), where 1 represents the least complex (grasslands) and 5 the most (riparian)

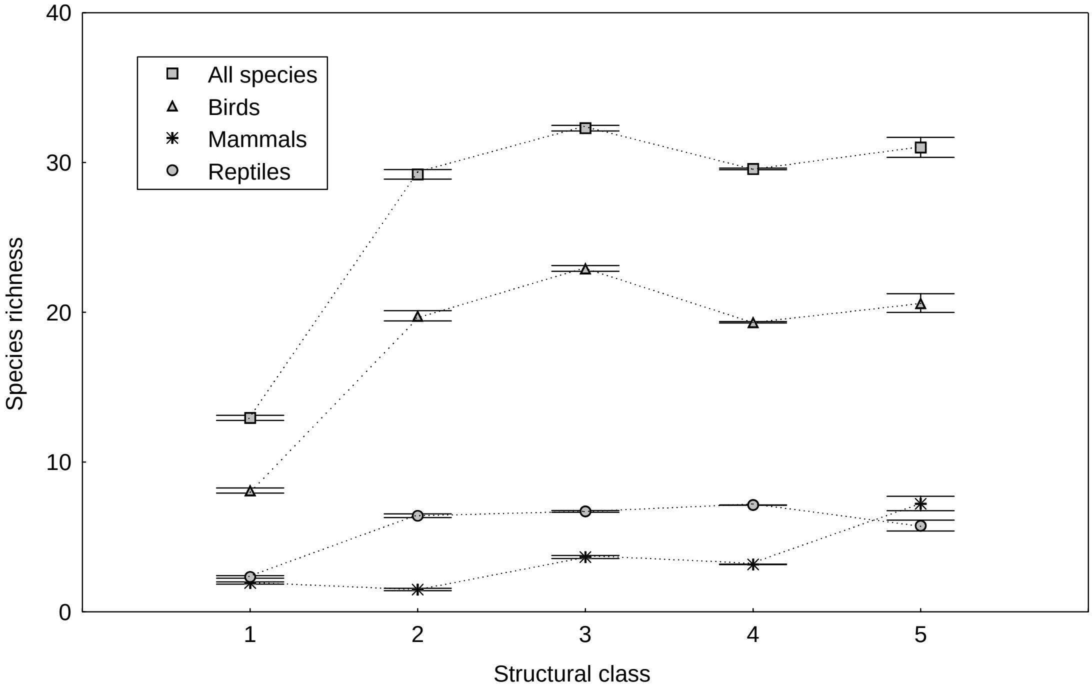
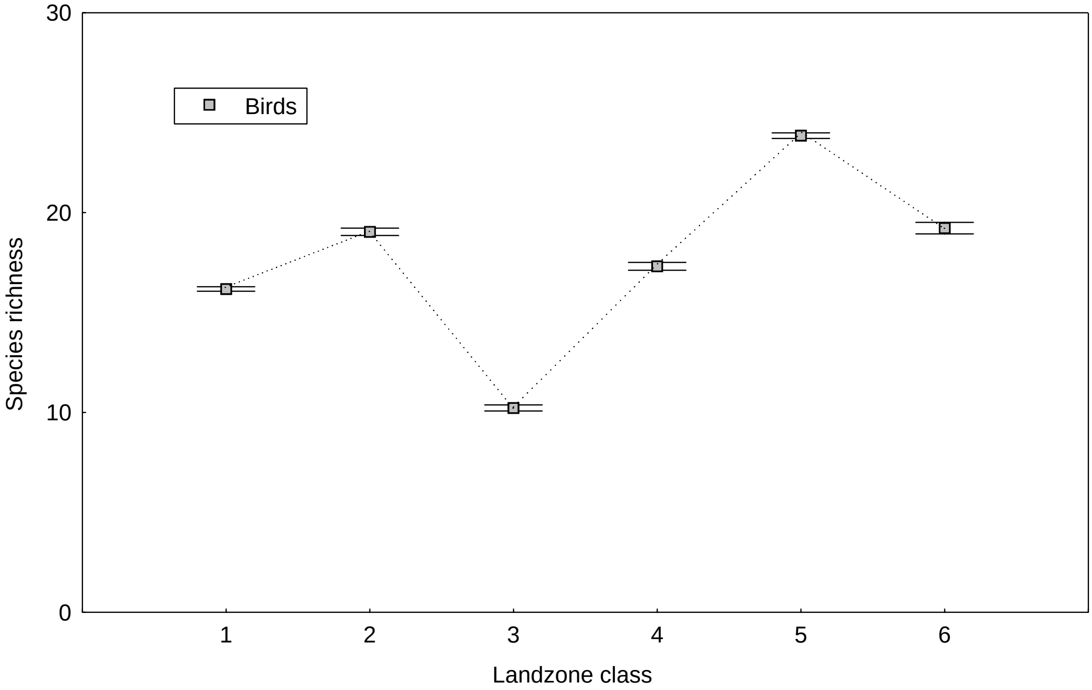


Figure 3.8 (b) Predicted mean species richness of birds for each landzone class (LC), where 1 represents the least productive and 6 the most.



Discussion

Species richness

The composition and species richness of the vertebrate fauna of the Desert Uplands bioregion reflects a mixture of species representative of both the range of vegetation structural types sampled and the biogeographic location (see Chapter 2) with a high fidelity of some assemblages and species to particular habitat types and environmental extremes (e.g grasslands). Additionally there is an indistinct, overlapping suite of woodland species and sites. This latter group, though the most species-rich, is characterised by having a core assemblage of species and functional groups that varies in abundance between different woodland types, and which is complemented by a series of less common species whose abundance varies with relatively subtle environmental shifts (e.g sand to clay soils, *Acacia* versus *Eucalyptus* woodland, hummock versus tussock ground cover).

On a landscape scale, the processes that drive patterns of species abundance and composition will include competitive interactions and habitat factors (e.g. heterogeneity and more elusive impacts such as productivity) (Schluter and Ricklefs 1993). In tropical savannas it has been suggested that resource availability, its seasonal variation, and the strategies used by individual species to cope with this unpredictability, is more strongly influential (Woinarski 1999b). The relative effect of each process seems variable in the case of the quadrats surveyed here. In the most structurally simple environments such as the grasslands, competitive and habitat factors possibly predominate. That is, these environments support relatively few species, but they typically have very strict niche requirements or habitat relationships (e.g. *Sminthopsis douglasi*, *Tympanocryptis lineata*), and are possibly specialised and competitively dominant. Conversely, in the more structurally complex woodlands, there is interconnectivity and gradual variation in habitat, and hence in the fauna. The higher number and overlapping arrangement of the species suggest that habitat heterogeneity coupled with subtle resource variation couple to drive assemblage patterns.

In tropical savannas, the high mobility and transitory pattern of bird communities throughout mosaic landscapes has been well established for birds (Woinarski and Tidemann 1991; Woinarski 1993; Woinarski *et al.* 2000a, b), and is proposed as a strategy to cope with the seasonal and longer periods of resource ebb and flow (Woinarski 1999b). Species richness is also maintained through rainfall gradients for other taxa, as long as vegetation structure remains more or less constant (Woinarski *et al.* 1999b). The results of this study (see Chapter 2 also) tend to support this contention: in tropical savannas local species richness and abundance is a function of both widespread habitat interconnectivity and species redundancy (Shmida and Wilson 1985; Walker 1997).

Local species richness, apart from habitat heterogeneity (Pianka 1969; 1986), has been variably linked to factors of habitat area (Rosenzweig 1995) and productivity (Hutchinson 1959; Currie 1991). Generally the relationship between these factors and richness is positive (Currie 1991; Southwood 1996; Gaston and Blackburn 2000; Williams *et al.* 2002). There is a confounding inter-relatedness of area and habitat heterogeneity, and structural complexity and productivity (Gaston and Blackburn 2000), which can mask any clear independent response (Gaston and Blackburn 2000). Minimum models for site species richness in the Desert Uplands indicated consistent trends in response to vegetation structure, namely that the increase in the architectural complexity of habitat was a good predictor of increased site species richness for all taxa. In all cases, the clearest disparity was between treeless and treed sites. The increase was likely due to the increase in the number of, for example, foraging strata and therefore guilds for birds, and the increase in arboreal and timber-sheltering species in reptiles. This pattern was noted for Mitchell Grass Downs (Fisher 2001a). Though structure was a predictor for mammal richness, it was only weakly so, perhaps due to the constancy and widespread distribution of many unspecialised terrestrial woodland species (e.g. *Pseudomys* spp, *Macropus* spp). The addition of arboreal species (*Phascolarctos cinereus*, *Petaurus norfolcensis, Trichosurus vulpecula*), which are restricted in semi-arid areas to the most well developed woodlands or riparian areas, accounts for the increase in richness in the final structural class category. In tropical savannas, as in other tropical environments such as the wet tropics, structural complexity is the most significant determinant of local species richness, though there must be some interaction with area, as the more heterogeneous habitats (e.g. woodlands) are generally more widespread.

One interesting comparison was the non-linear relationship of bird richness with land zone category, which is a more traditional measure of productivity in terms of soil type, nutrient status and moisture retention capacity (Sattler and Williams 1999; Dr M. Lorimer Environmental Protection Agency, pers. comm., 2000). Though no universal rule exists, there is ample evidence for humped relationships with productivity, though this is often scale-dependent (Abramsky and Rosenzweig 1984; Tilman and Pacala 1993; Williams *et al.* 2002). The suggestion is that high productivity creates a homogenous and monodominant vegetation structure (Tilman and Pacala 1993), which in turn supports a reduced diversity (Williams *et al.* 2002). In this study, low productivity habitats included woodlands on sand and sandy-clay soils, and habitat of higher productivity were grasslands and *Acacia* woodlands on clays. As such structural complexity did not reflect the measure of soil productivity, and as bird species richness generally increased with structural complexity, the relationship with productivity was skewed. In tropical savannas Woinarski *et al.* (1999) identified higher species richness on high fertility, high rainfall clay soils, with a decline in species richness with decreasing rainfall and decreasing vegetation structure. Species richness in woodlands on less productive sands and loams remained relatively consistent within the rainfall gradient (Woinarski *et al.* 1999). These results suggest that though vegetation structure is an adequate surrogate for productivity where rainfall is high (and hence species richness is also high), along strong climatic gradients (e.g. rainfall), there may be a threshold for this relationship. Though soils may still be productive, rainfall is too low to permit complex vegetation growth and therefore restricts species diversity. The prediction that vegetation biomass alone may act as a surrogate for productivity (Southwood 1996) may not necessarily hold true, at least on a regional scale.

Seasonal variation

The tropical savanna woodlands of northern Australia are important seasonal habitat for a suite of migratory bird species (Blakers *et al.* 1984; Schodde and Mason 1999). The Desert Uplands is no exception and a number of species were recorded in varying wet and dry season abundances. These can be classified as (1) species whose distribution is typically patchy, irruptive or dispersive (Buff-rumped Thornbill, Red-chested Button-quail, Spotted Bowerbird); (2) species that are locally and regionally nomadic, following water, food and breeding resources (Sulphur-crested Cockatoo, Pale-headed Rosella, Jacky Winter, Brown Treecreeper, Emu, Singing Honeyeater); (3) winter inland to coastal migrants (Black-faced Cuckoo-shrike; Red-backed Kingfisher) and (4) south-eastern Australian winter and summer migrants (Australian Bustard, Brown Songlark, Red-capped Robin, Sacred Kingfisher, Pallid Cuckoo, Olive-backed Oriole, Grey Fantail) (Blakers *et al.* 1984; Schodde and Mason 1999). The only exception to these patterns was the high abundance of a typical summer breeding migrant from New Guinea (Dollarbird) in the dry season samples. This may possibly be due to the early arrival of this species in some sampled quadrats.

The characterisation of wet and dry season used in this study is too broad to adequately capture the enormous temporal and spatial variation in tropical savanna bird communities, which is typically driven by seasonal, annual and long term cycles of resource pulse and decline (Woinarski *et al.* 1988; Woinarski and Tidemann 1991). Timing of migration and movement is wholly dependent on the onset of seasons. Therefore, some of the elements in the pattern recorded here were confounding (e.g. higher Pallid Cuckoo and Olive-backed Oriole abundance in wet season). Naturally within the large geographic extent of the northern savannas, some species may be more sedentary or locally nomadic than previously reported, shifting between wetter and drier parts of the region, rather than following large scale movements (e.g. Australian Bustard, Red-chested Button-quail). The presence of this suite of species with pronounced seasonal variation in abundance emphasises the significance of these sub-humid woodlands for bird communities. The fragmentation of woodland in south-eastern Australia has impacted heavily on woodland species, including many migrating species (Robinson and Traill 1996; Barrett 2000; Ford *et al.* 2001). The Desert Uplands is still a relatively intact landscape, but it is under increasing and dramatic land clearing pressure (Rolfe *et al.* 2001; Accad *et al.* 2002). Continued loss of these woodlands at the current rate will cause further deleterious effects both on species reliant on northern Australia as a seasonal destination, and on sedentary woodland bird species, such as has already occurred in the south (Ford 2001).

The significantly higher captures of a number of reptile species in the wet season is entirely expected - heliothermic organisms are most active in higher diurnal and nocturnal temperatures (Heatwole and Taylor 1987). Other surveys have also reported higher activity in hotter periods (Fisher 2001a). Though all species captured at higher abundances in the wet season were also captured in the dry season, surveys in conditions that cause increased reptile activity ensure the highest likelihood of recording all species present at a site, particularly large -bodied or arboreal species that spend periods of time in torpor within timber and tree-hollows, and nocturnal thigmothermic species reliant on warm substrates to remain active (Heatwole and Taylor 1987).

Vertebrate species assemblages, composition and environmental gradients

The vertebrate fauna of the Desert Uplands is distinguished by the grouping of characteristic assemblages at the extremes of the sampled environment gradients of the bioregion, and a more species-rich but poorly defined set of species in the subtly variable savanna woodlands. What is notable was the strength of the classification - regardless of an attempt to force the site-poor groups to lump together and refine the woodland sites further, the pattern remained firm. This is not surprising however, as the pattern essentially reflects vegetation structural change accompanied by turnover in fauna composition. Three broad clusters of sites are apparent: grassland communities of low species richness, but with a high proportion of characteristic species unique to this group; low heaths and woodlands associated with the lake and dune landscapes, and shallow soils on escarpments; and a species-rich mixed *Eucalypt* and *Acacia* woodland conglomerate with few characteristic species for each group, but distinguished by subtle variation in species composition, abundances and environment.

Though there have been no similar quantified surveys in savanna woodlands of northern Queensland, a range of studies examining the patterns of flora and fauna along climatic and other environmental gradients in the tropical savannas of the Northern Territory provide a useful comparison for the Desert Uplands. There is a clear biogeographic continuity of the tropical savannas across northern Australia, indicated by the coastal and widespread dominance of poorly differentiated *Eucalypt* woodlands (chapter 2; Woinarski 1992; Woinarski *et al.* 1999b). As such there is common semblance in tropical savanna woodlands, though there is a marked climatic shift in the Northern

Territory to monsoonal patterns, and communities more attuned to regular burning (Yibarbuk *et al.* 2002). Intermediate bioregions between the Northern Territory and Queensland (Gulf Plains, North-west Highlands) have been unstudied.

Gradual ecological variation and widespread connectivity, punctuated by patches of distinct vegetation such as monsoon forest, sandstone outcrops, swamps and woodland variants such as *Acacia*, is characteristic of northern Australia's tropical savanna woodlands (Woinarski 1992; 1999b). A number of studies have attempted to describe the patterns of fauna variation within this mosaic and elucidate the underlying local (e.g. Woinarski *et al.* 1992a), and regional (e.g. Woinarski and Fisher 1995 a, b), environmental mechanisms that control any measured change in composition. A number of consistent themes are very evident from these studies:

- assemblages were strongly associated with substrate and moisture availability as expressed by broad habitat types (sandstone, swamp, woodland, monsoon rainforest), rather than floristic variation (Woinarski and Gambold 1992; Woinarski *et al.* 1992a);
- local scale factors in these communities (moisture, substrate, soil, complexity) were more predictive of fauna composition than patch size, a relationship sufficiently strong to override external influences such as timing of fire (Woinarski and Menkhorst 1992; Trainor and Woinarski 1992; Woinarski 1993; Woinarski and Fisher 1995 a, b);
- smaller patchy vegetation types such as monsoon rainforest or *Acacia* woodland are generally impoverished, and largely comprise a subset of surrounding widespread woodland species (Woinarski and Menkhorst 1992; Woinarski 1993; Woinarski and Fisher 1995a, b);
- for widespread communities (e.g. *Eucalypt* woodlands, rainforest patches) there was a clear effect of the latitudinal rainfall gradient, with attenuation of species richness and composition to the south, though within-habitat species composition was idiosyncratic and dependant on surrounding sources of species or again local factors such as soil (Woinarski and Menkhorst 1992; Woinarski and Fisher 1995b; Woinarski *et al.* 1999b).

Most recently the patterns of biota in the extensive Mitchell Grass Downs, a bioregion that abuts both the Desert Uplands and the *Eucalypt* woodlands of the monsoonal tropical savannas, have been examined (Fensham *et al.* 2000; Fisher 2001a). Temperature and rainfall seasonality was the best indicator of floristic composition (Fensham *et al.* 2000) and broad fauna assemblage (Fisher 2001a), though on a local scale, latitude-climate gradient (wetter-drier species incursions), local substrate characteristics and vegetation composition defined vertebrate composition (Fisher 2001a).

This survey of the Desert Uplands fauna did not examine the variation and composition within the range of all vegetation to the detail of the targeted studies listed above. However, there are a number of strong parallels in the determinants of tropical savanna fauna assemblage, namely: the correspondence of species richness and composition to broad habitats; lesser within-habitat variation in woodland types; and some degree of vegetation structure, substrate and possible climate control. The clarity of the climatic gradients in the Desert Uplands is not as readily apparent on a bioregional scale (compare with state-wide patterns considered in chapter 2), because of its elongate shape and relatively short longitudinal range (the orientation of the rainfall gradient). The change in vegetation structure from east to west acts as a partial surrogate. There is a gradual shift from eastern wetter regions with more consistent open woodlands cover, across the Alice Tableland, comprising Tertiary sandstone communities, west to a more varied mix of *Acacia*, *Eucalypt* and grassland vegetation, tending towards semi-aridity and inland biogeographic influence (chapter 1). There is a concomitant shift within the fauna assemblage (chapter 2).

There is an especial set of grassland sites, tussock, hummock and chenopod communities, that comprised the lowest species richness, but (at least for the grasslands) the most distinctive species composition of all communities. These were naturally situated on the extremes of the gradients of tussock, hummock and forb cover as well as bare ground, crack and clay soil types. The low diversity is typical of these environments, as is some specialisation of the fauna that inhabits them (Brock 2000; Fisher 2001a). Six sites sampled in tussock grasslands or Mitchell Grass Downs yielded species similar to those recorded in an extensive survey of this habitat in northern Australia (Fisher 2001a): for example, Red-chested Button-quail, Black-faced

Woodswallow, *Tympanocryptis lineata*, *Planigale ingrami*, *Delma tincta*. Though unexpected, the occurrence of *Sminthopsis douglasi* in the Desert Uplands is also consistent, given that the tussock grasslands there are broadly connected to the more extensive Mitchell grasslands in Queensland which the species was hitherto thought to be restricted (see Chapter 2; Kutt 2003a, Appendix 2). Despite the low number of sites sampled, the Mitchell Grass Downs was clearly split into two groups (2 and 3) with distinct composition and species richness (group 2 with high bird and mammal richness, group 3 with lower). There is no geographic distinction between the groups, and variation can only be accounted for by differences in floristic composition, ground cover and microhabitat features (e.g. soil crack size), though land management history may have some influence. Though the sample size is small, it provides a hint that subtle variation in local conditions may pattern composition within seemingly uniform environments, a conclusion similarly drawn from a more extensive Mitchell Grass Downs fauna survey (Fisher 2001a).

Fauna composition of the lakeside chenopod communities comprised generalists (e.g. *Ctenophorus nuchalis*, *Menetia greyii*, *Sminthopsis macroura*) or birds typical of open or treeless environments (e.g. Nankeen Kestrel, Australian Magpie, Richard’s Pipit). Sites were generally depauperate representing a small subset of fauna from adjacent habitats; a pattern recorded for other chenopod communities (Brock 2000). Very low abundances of White-winged Fairy-wrens were recorded, a species with known association with this environment, and considered to be declining (Reid and Fleming 1992), though this wren was identified in tussock and hummock grass communities as well. Fauna of the hummock grasslands (*Triodia longiceps*) was also impoverished, in contrast to central Australia where this environment is the most extensive and species-rich, not the least due to long, evolved association between this characteristic vegetation type, invertebrates and vertebrates (Schodde 1982; Pianka 1986; Morton and James 1988). The Desert Uplands communities are again obviously small-scale outliers, but significant nonetheless as habitat for disjunct (Spinifexbird, *Tiliqua multifasciata*) and poorly known species (*Leggadina lakedownensis*), and typical hummock grass species recorded in unexpectedly high numbers (*Pseudomys desertor*, Kutt *et al.* in press 2003, Appendix 6). “Soft spinifex” *Triodia pungens* on the other hand formed a significant ground cover component in a number of woodlands types sampled, the most species rich communities in the Desert Uplands.

The structurally intermediate woodlands (heath, low dune woodlands: groups 4,6,7, and 10) support a moderate species richness reflecting the transition from the more extreme environments to the more extensive woodland types. In contrast to the distinctive fauna associated with the even less species-rich treeless communities, the fauna of these habitats was not indistinct, but rather comprised a subset of species recorded uniformly across the woodland communities, or in the grasslands, albeit in lower abundances (e.g. Emu, Galah, *Sminthopsis macroura*, *Pseudomys delicatulus*, *Gehyra catenata*, *Ctenotus pantherinus*, *C. hebetior*, *Ctenophorus nuchalis*). As an entity there is only loose correspondence between the structural and floristic characteristics of each group, though they are better related to the woodland groups with which they are adjacent in the ordination (e.g. group 4 and 13, group 7 and 8/9). Regardless, the composition and abundance of their vertebrate assemblage is governed by simple habitat features (e.g. group 4 heaths over open hummock grass on sands, with species such as *Pseudomys desertor*, *Ctenotus pantherinus*, Brown and Singing Honeyeaters; group 7 sandy dunes with sparse tussock cover and low, but densely timbered *Acacia*, *Grevillea*, *Corymbia*, over-storey, with coincident species such as *P. delicatulus*, *C. hebetior*, *Gehyra dubia* and terrestrial omnivorous birds). Fisher (2001a) identified a similar increasing species richness with structural complexity on clay woodlands and shrubby rises in comparison to the adjacent tussock grasslands, with an increase in arboreal reptiles, foliage gleaners and nectarivores. Woinarski and Fisher (1995 b) noted that in the low diversity *Acacia* woodland associations, species presence was significantly related to particular features of each community (e.g. substrate, ground cover, vegetation density).

The sites within group 6 are slightly anomalous, and are an amalgam of tall woodlands and heaths. All are derived from the White Mountains National Park at the very north of the bioregion and in some respects represent an outlier, with some strong affinity to the adjacent Einasleigh Uplands (Stanton and Morgan 1977). Location on the bioregion boundary, high altitude, and a mix of tall forest and heaths on typically shallow sandstone-derived soils distinguish them. These sites contain many unique and outlier species that reflect both the sandstone environments (e.g. *Pseudomys patrius*, *Diplodactylus vittatus*, *Nephrurus asper*), tall, dense vegetation with high litter cover (e.g. high fossorial skink and foliage gleaner numbers) and the affinity to the north-east coastal bioregions, but were predominantly recorded in low abundance (e.g. Noisy

Miner, Pied Currawong, *Planigale maculata*, *Menetia timlowi*, *Glaphyromorphus punctulatus*, *Lerista wilkinsi*, *Carlia schmeltzii*). The high murid richness is due to the sympatry of three species of *Pseudomys* (*delicatulus*, *desertor* and *patrius*) and these along with other incidental species recorded in this region also reinforce the notion of this location as a refugial environment with high species turnover (Kutt *et al.* 2003c, Appendix 4).

The largest, most diverse and least clearly distinguished group were the *Eucalypt* and *Acacia* woodland types, all clustered within the centre of the ordination. Though this rightly suggests a high degree of overlap and a rather inchoate differentiation in both the fauna composition and habitat characteristics, there is some subtle variation. The contrasting examples of species abundance variation and turnover between quadrats on the ordination illustrate the nature of the changes, as does the generalised linear modelling (see discussion below). Not surprisingly, where the contrast is marked, the composition change is also more varied. For example, the shift from hummock to tussock grass cover and sandy soils to clay soils has a concomitant shift from terrestrial, burrowing and shelter-dependent species (*Ctenotus* spp; Heatwole and Taylor 1987; James 1991) to fossorial animals (*Carlia munda, Menetia greyii*; Heatwole and Taylor 1987). For mammals there is a change from crack-dwelling dasyurids in tussock grasslands (*Sminthopsis* spp, *Planigale* spp; Fisher 2001a), to burrowing rodents in sandy hummock grasslands (*Pseudomys* spp; Dickman *et al.* 1999). Similarly, arboreal reptiles inhabit quadrats with high basal area or foliage projective cover (e.g. *Gehyra dubia, Cryptoblepharus plagiocephalus, Egernia striolata*), being absent, or uncommon in other sites. Variation in vegetation structure also influences the abundance of bird species: more open country birds in treeless sites (Nankeen Kestrel, Galah, Australian Bustard), increased abundance of nectarivores and gleaners in quadrats with complex structure (Singing Honeyeater, Weebill, Yellow-rumped Thornbill), and a range of species associated with a tall canopy stratum in the taller woodland quadrats (Striated Pardalote, Pied Butcherbird, Australian Magpie). There is an associated change in the richness of contrasting bird guilds such as nectarivores and terrestrial insectivores along gradients of basal area and ground cover.

Conversely, a more subtle drift of species manifests itself within the *Acacia* and *Eucalyptus* woodlands found in the centre of the ordination space. Here the environmental transition is less contrasting. Many quadrats have equable and indistinguishable abundances of a number of generalist species (Grey Shrike-thrush, Apostlebird, Rufous Whistler, *Varanus tristis, Macropus giganteus*) common in open *Acacia*/*Eucalypt* woodland complexes. In other cases already illustrated and described (Figures 3.5 a-m), differences in the abundance of some species are explained by smaller changes in structural and habitat features. This matches the known ecology of many species. For example, Little Friarbirds can occur where there is less canopy cover than compared to Noisy Friarbirds (Reid 1999). Striated Pardalotes are canopy foraging species compared to Weebills that utilised mid-storey strata (Fisher 2001a). Crested Bellbirds are cryptic terrestrial omnivores compared to gregarious Australian Magpies that prefer open ground. Crested Pigeons similarly are grazing increasers occurring in open ground, whereas Peaceful Dove, though still tolerant of disturbance, relies on a degree of ground shelter and cryptic behaviour to avoid predators (Landsberg *et al.* 1997; Fisher 2001a). In regards to reptiles the medium-sized *Ctenotus hebetior* can tolerate more open ground, whereas the large bodied *C. pantherinus* requires better shelter, and in particular long unburnt *Triodia* for shelter and control of thermoregulation (James 1991; Thurgate 1997). Though it is cavalier to simply dismiss other examples and patterns of species recorded as typical of known biology and habitat preferences, this is predominantly the case and does not warrant further laborious review.

These features are in keeping with more extensive studies examining the patterns of tropical savanna fauna distribution in the Northern Territory. Woinarski *et al.* (1999b) identified limited vertebrate fauna variation in seemingly ubiquitous and unvarying *Eucalyptus* vegetation on different sands and loams along an extensive rainfall gradient, though diversity declined in clay soils, but generally as a function of declining vegetation structure and productivity. Most variation in *Eucalyptus* woodlands was typically associated with pockets of unusual vegetation and substrate. Woinarski and Fisher (1995 a, b) examined vertebrate fauna composition of Lancewood *Acacia shirleyi* communities across the Northern Territory and reported an intangible assemblage, mostly related to geographic and landscape position, and intrusion from neighbouring vegetation types. Species present were largely a subset of the fauna of the surrounding *Eucalyptus* woodland (terrestrial omnivores, arboreal geckoes and trunk, branch gleaners), able to utilise resources in Lancewood (low ground cover, high litter cover and greater stem density). Though the *Acacia* communities sampled in the Desert Uplands rarely were independent in regards to their group-membership, the mixing and interrelatedness of much of the fauna in woodland types in general suggest a similar situation occurs.

Bird communities in tropical savannas are most notoriously unpredictable and driven by fluctuations in resource availability (Woinarski *et al.* 1988; Woinarski and Tidemann 1991). There is clear evidence that in fairly uniform woodland environments, bird composition and abundance varies with sometimes little repeated pattern over seasons and years, controlled by varying fires, climatic conditions and resultant flowering and seeding phenology (Woinarski and Tidemann 1991). Though the current survey does not have a strong temporal component, it is also evident, except where the contrast is dramatic (e.g. treeless communities), the bird assemblage is fluid and partially indistinct - 138 woodland sites sampled clustered into only five groups, with little variation in bird guild structure, species richness and abundance. Of the five groups, at least 12 out of the 13 guilds were recorded in each. Furthermore 32 bird species were recorded in all groups, 18 in four, and 15 in three. That is, approximately 60% of all birds recorded in woodlands occurred in three or more of the groups. Only nine species were not recorded in the woodland complexes. No aspect of woodland type would ever really preclude a species being present, yet there is naturally a differential advantage for various foraging guilds within varying structural types. Granivorous, nectarivores, salliers, hawkers and foliage-gleaners are abundant and species richness is high, with terrestrial feeding guilds less abundant, a pattern reported as a feature of tropical woodland bird communities (Woinarski and Tidemann 1991). Though assessment of genuine rarity and transience is difficult for species recorded at low abundances without long-term sampling, the conclusion of a core species mass coupled with a peripheral assemblage for these woodlands, does not seem unreasonable.

Modelled species response to environment variables

The predictive models generated for the guilds, families and species fortify the patterns of relationship with the environmental gradients, which were previously inferred from the groups' position in the ordination space. The discussion here concentrates on broad environmental determinants of species abundance. On a local scale, the influence of fire and grazing on vegetation patterns and species abundance is examined in more detail in chapter 5.

Birds

Overall the significant model terms for bird foraging guild patterns coalesce with detailed studies of bird communities in temperate woodlands and tropical savannas (Loyn 1985; Recher and Holmes 1985; Recher *et al.* 1991; Woinarski and Tidemann 1991; Woinarski and Fisher 1995a; Catterall *et al.* 1997a, b; Sewell and Catterall 1998; Reid 1999; Catterall *et al.* 2001; Fisher 2001a, b). The relationship between environmental variables and guild abundance and richness reflects a group's foraging or breeding preferences. Naturally guilds that are predominantly arboreal were related to increasing basal area and hence canopy cover (foliage gleaners, salliers), with other significant factors depending on the guild in question (terrestrial omnivores and bare ground). Nectarivores and nectarivore/gleaners were more abundant in quadrats with more complex vertical structure (basal area and FPC 1-3 m significant), and this includes *Acacia*-type communities and the *Eucalyptus* woodlands. Other guilds demonstrated a logical relationship with ground cover features such as high abundance of terrestrial insectivores and granivores in sites where tussock grassland cover is high. Structural diversity is a well-accepted coarse predictor of bird community richness and composition (Wiens 1989).

The species relationships reported also have ample precedence. Bird community composition shifts due to variation in complexity caused by any number of forces including forestry, tree-clearing and urban development and fire (Loyn 1985; Recher *et al.* 1991; Catterall *et al.* 1997a, b; Sewell and Catterall 1998; Reid 1999; Catterall *et al.* 2001; Fisher 2001b; Woinarski and Ash 2002). More specifically, species respond to habitat factors that complement their life history traits. Some bird species are more abundant in sites with high area of bare ground, either with some canopy cover (Yellow-throated Miner, Willie Wagtail, Torresian Crow) or without trees (Australian Magpie, Galah, Crested Pigeon, Nankeen Kestrel) (Landsberg *et al.* 1997; Catterall *et al.* 2001; Fisher 2001a; Woinarski and Ash 2002). Yellow-throated Miners are slightly anomalous in that they inhabit a variety of disturbed or intact habitats, (Catterall *et al.* 2001; Fisher 2001b; Woinarski and Ash 2002), and this is reflected in this study by the relationship with high bare ground or tussock cover. Honeyeaters and fairy-wrens are generally abundant in sites where ground cover and mid-strata cover is extensive (Woinarski 1990; Catterall *et al.* 2001), while pardalotes and the Weebill are associated in woodlands with mature form and structure (Catterall *et al.* 1997b; Reid 1999). Granivore species respond differentially to impacts that alter vegetation cover and structure, depending on both diet and cover requirements (Woinarski 1990; Franklin 1999; Reid 1999; Fisher 2001a). The predictive models reported here identify similar variation, gregarious generalists responding to the lack of canopy cover (Galah, Sulphur-crested Cockatoo), disturbance tolerant species to bare ground cover (Crested Pigeon, Diamond Dove) or smaller, more cryptic species to a mixture of vegetation with both grass cover and open ground (Peaceful Dove, Common Bronzewing).

<u>Mammals</u>

The significant model terms identified for mammal abundance also have a clear relationship with species life history, and because of most of the mammals recorded in the survey are terrestrial and herbivorous, variation in their abundance is generally related to vegetation cover at ground level. Among large macropods, *M. robustus* is typically associated with dense vegetation on more bare undulating terrain (Woinarski and Fisher 1995a). Conversely other macropods increase in response to increased ground cover, linked to availability of palatable tussock grasses and forbs (Griffiths *et al.* 1974; Ellis *et al.* 1977).

Small mammal assemblages have been correlated to changes in vegetation cover, as driven by fire or rainfall (Reid *et al.* 1993; Masters 1993; Dickman *et al.* 1999). *Pseudomys desertor* abundance increased in treeless hummock grasslands as expected (Masters 1993), as did *Sminthopsis macroura*, though this species is more a widespread generalist that inhabits a range of semi-arid woodlands and grasslands (Menkhorst and Knight 2001). The relationship of *P. delicatulus* to sandy soils reflects its burrowing habit and preference for sparse vegetation associated with this substrate (Braithwaite and Brady 1993). The monospecific *Tachyglossus aculeatus* was abundant in sites with high basal area, this being simply a surrogate for high termite and ant numbers (their preferred food source).

Reptiles

As with birds and mammals, abundance of predominantly terrestrial reptiles was predicted by ground cover variables (*Ctenotus hebetior* and *C. pantherinus*). Abundance of arboreal and scansorial species was related to basal area and mid-storey cover (*Gehyra catenata*, *Egernia striolata*). The abundance of *Morethia boulengeri* was also associated with basal area, but this terrestrial species prefers densely timbered *Acacia* woodlands with high area of bare ground and ample fallen timber (Fisher and Woinarski 1995a). In general many of the patterns recorded reflect thermoregulatory and sheltering behaviour, and activity periods (Heatwole and Taylor 1987; Cogger 2000). *Ctenophorus nuchalis* was abundant on sandy grassless sites, matching its known heat tolerance and burrowing trait (Bradshaw and Main 1968; Read 2002). Fossorial species (*Menetia greyii, Proablepharus tenuis, Lerista punctatovittata*) require litter and shrub cover and generally decline with the increase of bare ground (Caughley 1985; Thurgate 1997; Fisher 2001a; Woinarski *et al.* 2002). At the other extreme *Ctenotus pantherinus* is vulnerable to rapid over-heating without adequate shelter (Heatwole and Taylor 1987), and required dense regenerating *Triodia* (Reid *et al.* 1993; Masters 1996). A similar sized skink *Ctenotus robustus* also declines with loss of ground cover (Thurgate 1997), though in this study the relationship was with mid-canopy vegetation.

Furthermore the relationship of skink species richness and abundance with hummock grass on sandy soils reflects the well-established association of this herpetofauna with evolutionary determinants of their diversity (Pianka 1966; James 1991). There is debate as to whether this relationship is one of adaptation to the ecological opportunities provided by *Triodia* and associated high termite richness, or a long history of isolation (Morton and James 1988). Regardless, species such as *Ctenotus pantherinus*, *Lialis burtoni* and *Rhynchoedura ornata* abundant in the hummock grasslands in arid Australia (Reid *et al.* 1993) were associated with hummock grassland environments in the Desert Uplands also.

Soil type was a significant predictive term for the abundance of many reptile species. This is in keeping with the previously reported contention that substrate exerts a deeper influence on reptile composition than changes in cover in tropical savannas (Woinarski and Gambold 1992; Trainor and Woinarski 1994). As vegetation can be a direct expression of soil or substrate, it is difficult to tease out which factor may be the primary determinant of a species presence. However many species abundant in sandy soils were burrowing species (*Ctenophorus nuchalis*, *Diplodactylus steindachneri*, *Pogona barbata* and *Amphibolurus nobbi*), whereas those related to clay soils forage or shelter in cracks (*Delma tincta*, *Suta suta*). Conversely, species such as *Gehyra catenata* were significantly related to clay soil types, likely due to the presence of dense *Acacia* vegetation providing ample exfoliating bark for shelter.

Correlations with vegetation composition

Vegetation pattern often underpins patterns of fauna distribution and composition (e.g. Braithwaite *et al.* 1984). However many studies of tropical savanna environments have indicated that floristic variation is not necessarily a useful predictor of fauna diversity, but rather substrate, climatic gradients, broad habitat types or fire patterns are generally more influential (Woinarski *et al.* 1991). In this study, fauna grouping significantly predicted variation in vegetation composition, though the direct correlation between fauna and vegetation composition was less defined. Obviously biotic patterns along environmental gradients must parallel each other to some degree due to variation in climate, soils and common biogeographic history (Bowman 1996) though whether it is the floristic variation or shifts in vegetation architecture that best controls fauna assemblage change, is difficult to separate.

Along a broad latitudinal gradient in the Northern Territory, Williams *et al.* (1996b) identified a decline of tree height, cover, basal area, woody and deciduous species richness with decreasing rainfall and increasing clay soil content. In contrast, for the same gradient there was little variation in faunal species richness and composition, at least among the varying *Eucalyptus* woodlands on sand and loam soils across the gradient (Woinarski *et al.* 1999b). A similar pattern is implied in this study - though floristic variation is broadly coincident, structural variation and substrate factors are more significant predictors of shifts in fauna composition. The lack of correlation in the species-poor mammal assemblage is a good example. Detailed work in central and south-eastern Australian indicates structure and density of ground cover as controlled by fire and climate, best determines mammal assemblage composition (Dickman *et al.*

1999; Monamy and Fox 2000). A relationship with vegetation pattern has also been recorded for birds (e.g. Wiens 1989) and reptiles (e.g. Pianka 1986).

Conclusions

This survey represents the first comprehensive examination of vertebrate fauna composition, distribution and environmental pattern for the Desert Uplands. There is a mixture of vertebrate species representative of the range of vegetation types. Some assemblages exhibit a high fidelity to particular habitats and environmental extremes (e.g. hummock and tussock grasslands), while with others there is an indistinct, overlapping suite of *Acacia* and *Eucalyptus* woodland species and sites. This latter group, though the most species-rich, is characterised by having a core assemblage (species and functional groups) that varies in abundance between different floristic and structural types (e.g. changes in substrate, ground and canopy cover dominance). Models for quadrat species richness reinforce the positive relationship with the architectural complexity of habitat and all taxa. These patterns of species composition and distribution were commensurate with those recorded in the Mitchell grass, *Acacia* and *Eucalyptus* woodlands across the northern tropical savannas.

Environmental factors controlling vertebrate species abundance and assemblage in the Desert Uplands coalesced with detailed studies of fauna communities in temperate woodlands and tropical savannas. Predominantly arboreal bird guilds were related to increasing and more complex, vegetation structural variables whereas granivore and terrestrial omnivore species were correlated to bare ground. Vegetation cover also predicted terrestrial small mammal and reptile abundance, though substrate factors exerted a strong influence for reptiles in many cases. The relationship of local and regional variation in vertebrate fauna distribution to the *a priori* land classification used in the sampling stratification, and the implications for conservation planning are pursued further in Chapter 4. The local impact of pastoralism (fire and grazing) on the structural variation of the vegetation and patterns in fauna assemblage is examined in Chapter 5.

Table 3.7 Regional ecosystems codes and descriptions for each group (from Sattler and Williams 1999; Neldner *et al*. 2002).

Description	LZ	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13
Number of quadrats		3	4	2	6	2	2	4	8	20	19	23	13	52
Number of regional ecosystems		1	1	1	2	1	1	2	3	10	7	6	7	9
10.3.1 *Acacia argyrodendron* woodland on clays	6										5			
10.3.3 *Eucalyptus cambageana*, *Acacia harpophylla* or *A. argyrodendron* woodland on clays	6												2	
10.3.4 *Acacia cambagei* woodland on clays.	6										4			
10.3.6 *Eucalyptus brownii* on alluvial plains.	5									2	3	10	1	1
10.3.7 Tussock grassland on gravelly clays.	6		4	2										
10.3.9 *Eucalyptus whitei* on sandy alluvial soil.	5									3	1			
10.3.10 *Corymbia dallachiana* and/or *Corymbia plena* on sandy alluvial soil.	5							1		2	1			1
10.5.5 *Eucalyptus melanophloia* on loam to sandy clay soils.	2									1		9		3
10.3.14 *Eucalyptus coolabah* and *E. camaldulensis* on alluvial soils.	5										3	1		
10.3.17 *Acacia excelsa* and *Grevillea striata*. on weathered sand dunes.	3									3				
10.3.19 *Acacia cambagei* on duplex soils on lake-fringing dunes.	6									2				
10.3.21 *Acacia salicina* and *Grevillea striata* on weathered sand dunes.	1									3				
10.3.22 Shrubland of *Lawrencia buchananensis*, *Halosarcia* spp on alluvial flats and old dunes.	1				4									
10.3.23a Shrubland *Halosarcia* spp on alluvial flats and clays	1				2									
10.3.23b *Acacia stenophylla* with tussock grassland of *Leptochloa fusca* on alluvial flats and clays	1						2							
10.3.28 *Eucalyptus melanophloia* on yellow earths.	5											1		2
10.3.29 Hummock grassland of *Triodia longiceps*.	2	3											1	
10.5.1 *Eucalyptus similis* usually with *Corymbia brachycarpa* on deep red sands.	2											1		35
10.5.7 *Grevillea striata*, *G. parallela* and *Acacia coriacea* on sandplains.	2							3						
10.5.9 *Eucalyptus quadricostata* and usually *Corymbia erythrophloia* on red sands.	3								5					
10.5.11 *Eucalyptus whitei* on red sandy soil.	2													2
10.7.1 *Eucalyptus whitei* and *Corymbia dallachiana* on shallow gravelly sandy soil.	4									3				1
10.7.3 *Acacia shirleyi* or *A. catenulata* on skeletal sandstone soils.	3									1		1	2	1
10.7.5 *Eucalyptus thozetiana* on colluvial fans and slopes.	4												2	
10.7.7 Shrubland of *Melaleuca* spp, *Acacia* spp and *Thryptomene parviflora* on shallow soils.	3					2			1					
10.7.10 *Eucalyptus whitei* and *Corymbia setosa* on shallow gravelly sandy soil.	4													6
10.9.1 *Acacia argyrodendron* on clays.	4										2			
10.9.2 *Acacia cambagei* +/- *Eucalyptus thozetiana* or *E. cambageana* on clays.	4												4	
10.10.4 *Corymbia leichhardtii*, *E. exilipes*, or *C. lamprophylla* on sandy soils.	3								2				1	

Table 3.8 Mean abundance and richness of bird guilds and mammal and reptile families recorded in the survey. G1-G13 indicates group number, n= number of sites species recorded. g=guild or family code. Species recorded in the highest abundance indicated in bold. The significance in variation in abundance tested via Kruskal-Wallis ANOVA. H = test statistic. Probability levels *p<0.05, **p<0.01, ***p<0.001, ns= not significant. Species sorted in descending abundance for each taxa. Groups clustered according to general structural complexity.

Guild/Family	g	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
BIRD ABUNDANCE																
Terrestrial insectivores	TI	**8.67**	4.0	2.5	3.0	6.0	3.0	2.50	0.75	4.45	6.11	4.39	2.08	2.79	17.8	*
Terrestrial omnivores	TO	4.67	7.75	2.5	7.83	1.0	15.0	14.75	5.13	**24.55**	17.0	12.09	15.23	10.25	55.1	***
Granivores	G	1.33	4.5	2.5	4.33		4.5	11.5		10.70	**11.84**	4.87	3.31	5.4	32.7	***
Salliers	S	0.33		1.0	0.17	1.0	1.5	1.0	0.38	1.05	5.74	2.74	2.31	**5.87**	74.5	***
Wetland	W		1.5		0.33										26.4	**
Hawkers	H			**3.50**		2.50				0.2	0.37	0.17		3.0	47.6	***
Nectarivores	N					5.50		5.75	**13.25**	2.1	8.16	4.26	11.15	2.13	43.2	***
Nectarivores/gleaners	NL					3.0	2.0	2.5	0.25	1.2	4.16	0.48	**6.62**	5.87	74.3	***
Foliage gleaner/sallier	LS					0.50		0.5	0.75	0.6	**3.95**	0.22	1.23	1.92	49.2	***
Foliage gleaners	L						2.0	8.25	10.75	4.3	**14.37**	6.83	7.46	13.0	66.3	***
Frugivores	F						2.0			0.35	**0.95**	0.26	0.31	0.33	20.3	*
Trunk gleaners	T									0.9	1.05	0.91	0.46	0.87	5.6	ns
Pouncing insectivores	PI									0.2	0.37	0.04	0.15	0.48	21.7	ns
Raptors	R									0.2	0.16			0.08	10.0	ns
MAMMAL ABUNDANCE																
Muridae	MU	**8.33**	0.5	5.5	0.17	2.5		0.25	5.0	2.40	0.63	0.35	0.85	4.69	46.5	***
Macropodidae	MA	2.1	1.6	0.6	0.4	1.1		**2.4**		1.0	2.2	0.1	0.8	1.2	53.9	***
Dasyuridae	DA		**2.75**	0.5	0.67	0.5	2.0		0.50	0.75	0.58	0.09	0.23	0.71	22.9	**
Phalangeridae	PH							**1.0**			0.74	0.09			20.3	*
Tachyglossidae	TA									0.1	0.16	0.04		0.56	25.7	ns
Petauridae	PE									0.05	0.05	0.04			3.6	ns
Potoroidae	PO									0.05					5.8	ns
REPTILE ABUNDANCE																
Agamidae	AG	2.33	0.75		0.67	1.0		1.75	1.0	0.95	1.11	0.52	0.85	1.60	15.8	ns
Scincidae	SC	2.0			1.5	4.0	1.0	8.5	4.0	**8.65**	6.89	3.22	5.62	7.88	54.3	***
Gekkonidae	GE	0.33			0.17	0.5	3.0	1.0	2.63	3.9	**7.47**	1.83	3.62	2.98	52.3	***
Varanidae	VA	0.33						0.75	0.50	0.35	0.16	0.13	0.08	0.52	14.7	ns
Pygopodidae	PY		**2.0**						0.13	0.05	0.16	0.04	0.31	0.52	28.0	***
Elapidae	EL		0.75	0.5	0.17			0.25		0.30	0.21	0.17	0.08	0.19	5.7	ns
Typhlopidae	TY							**0.5**		0.05		0.04	0.08	0.02	25.8	**

Guild/Family	g	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Colubridae	CO									0.05					5.7	ns
Boidae	BO										0.05				6.1	ns
BIRD RICHNESS																
Terrestrial omnivores	TO	1.33	1.75	1.0	1.83	1.0	3.0	3.5	2.0	**4.15**	3.84	3.78	3.77	3.37	29.6	***
Terrestrial insectivores	TI	**1.33**	0.5	0.5	0.17	1.0	0.5	0.5	0.13	0.80	1.11	0.61	0.54	0.5	23.2	**
Granivores	G	0.33	1.25	1.0	1.0		2.0	2.75		3.05	**3.21**	1.52	1.31	1.62	42.0	***
Salliers	S	0.33		0.5	0.17	1.0	1.0	0.5	0.25	0.2	1.63	0.87	0.62	**1.87**	65.5	***
Wetland	W		0.25		**0.5**										32.7	***
Nectarivores/gleaners	NL					1.0	1.0	0.75		0.4	1.37	0.22	**1.54**	1.44	65.9	***
Foliage gleaner/sallier	LS					0.5		0.25	0.38	0.5	**1.53**	0.17	0.85	0.83	46.9	***
Frugivores	F						**1.0**			0.25	0.42	0.13	0.31	0.19	19.0	*
Foliage gleaners	L						0.5	2.0	2.63	1.0	2.42	1.65	1.85	**3.19**	67.1	***
Nectarivores	N							1.25	1.5	0.55	1.11	0.96	1.62	0.62	30.5	***
Pouncing insectivores	PI									0.2	0.37	0.04	0.15	0.23	13.1	ns
Trunk gleaners	T									0.05	0.11	0.04		0.1	2.9	ns
Hawkers	H										0.16			**0.52**	39.3	***
Raptors	R										0.05			0.04	2.9	ns
MAMMAL RICHNESS																
Macropodidae	MA	1.0	1.5	1.5	0.83	1.0		1.75		1.5	**1.84**	0.3	1.23	1.46	45.1	***
Muridae	MU	1.0	0.5	1.0	0.17	1.0	0.5	0.25	**1.38**	0.4	0.42	0.35	0.38	0.94	32.0	***
Dasyuridae	DA		**1.0**	0.5	0.5	0.5	**1.0**		0.5	0.2	0.26	0.09	0.23	0.4	22.4	**
Phalangeridae	PH							**0.25**			0.21	0.04			20.5	*
Tachyglossidae	TA									0.1	0.16	0.04		**0.42**	25.5	**
Petauridae	PE									0.05	0.05	0.04			3.6	ns
Potoroidae	PO									0.05					5.8	ns
REPTILE RICHNESS																
Scincidae	SC	1.67			1.0	3.0	1.0	2.25	3.13	2.85	1.95	2.04	2.54	**3.19**	50.7	***
Agamidae	AG	1.0	0.75		0.67	1.0		0.75	0.5	0.7	0.63	0.48	0.69	0.96	14.3	ns
Gekkonidae	GE	0.33			0.17	0.5	1.0	0.5	1.63	1.85	**2.53**	1.35	1.31	1.69	45.1	***
Varanidae	VA	0.33						0.5	0.38	0.35	0.16	0.13	0.08	0.4	13.9	ns
Pygopodidae	PY		**0.75**						0.13	0.05	0.16	0.04	0.31	0.44	25.6	**
Elapidae	EL		0.5	0.5	0.17			0.25		0.25	0.21	0.17	0.08	0.19	4.9	ns
Typhlopidae	TY							**0.5**		0.05		0.04	0.08	0.02	25.8	**
Colubridae	CO									0.05					5.7	ns
Boidae	BO										0.11				12.3	ns

Table 3.9 Mean abundance of all species recorded in the survey. G1-G13 indicates group number, n= number of sites species recorded. g=bird foraging guild or mammal and reptile genera (Table 3.12). Species recorded in the highest abundance indicated in bold. Significance in variation in abundance tested via Kruskal-Wallis ANOVA. H = test statistic. Probability levels *p<0.05, **p<0.01, ***p<0.001, ns= not significant. Species sorted in descending abundance for each taxa. Groups clustered according to general structural complexity.

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
BIRDS																		
Spinifexbird	*Eremiornis carteri*	TI	4	**5.0**											0.15			
White-winged Fairy-wren	*Malurus leucopterus*	TI	3	**3.67**	2.5		3											
Ground Cuckoo-shrike	*Coracina maxima*	TO	6	2	2.25							0.2				0.15	13.2	ns
Emu	*Dromaius novaehollandiae*	TO	16	1.67						**2**		0.2	0.32	0.22	0.15	0.29	18.2	*
Galah	*Cacatua roseicapilla*	G	39	1.33	3	1	0.67		1	**3.5**		3.3	1.84	0.35		0.29	36	***
Nankeen Kestrel	*Falco cenchroides*	TO	12	1	0.25		**1.17**	0.5		0.75		0.1	0.05				48.9	***
Spotted Nightjar	*Eurostopodus argus*	S	16	0.33			0.17	0.5						0.04	0.15	0.29	15.2	ns
Australian Bustard	*Ardeotis australis*	TO	5		2.25				0.5			0.1		0.04				
Red-chested Button-Quail	*Turnix pyrrhothorax*	G	5		1.5	1.5				1.5					0.08			
Grey-crowned Babbler	*Pomatostomus temporalis*	TI	49		1.5				3	2.5		**3.85**	3.16	0.83	1	1.69	23.9	**
Magpie Goose	*Anseranas semipalmata*	W	1		1.5													
Yellow-throated Miner	*Manorina flavigula*	TO	63		1.25				1	6		**10.65**	0.58	1.87	1.38	1.75	64	***
Magpie-Lark	*Grallina cyanoleuca*	TO	55		0.5				3	1		1.7	**1.74**	0.57	0.54	0.21	46	***
Wedge-tailed Eagle	*Aquila audax*	TO	51		0.5							0.1	0.05			0.04	7.6	ns
Australian Magpie	*Gymnorhina tibicen*	TO	87		0.25	0.5	0.5		1	0.25	0.75	**2**	0.84	1.7	1.77	0.63	28.3	***
Whistling Kite	*Haliastur sphenurus*	TO	5		0.25								0.11					
Spotted Harrier	*Circus assimilis*	TO	1		0.25													
Black-faced Woodswallow	*Artamus cinereus*	H	8			**3.5**		2.5				0.2		0.17		1.31	29.7	***
Variegated Fairy-wren	*Malurus lamberti*	TI	25			2.5		**6**				0.5	2.79	0.35	0.31	0.88	17	*
Richard's Pipit	*Anthus novaeseelandiae*	TO	7			1.5	**3.83**										124.1	***
Willie Wagtail	*Rhipidura leucophrys*	S	58			1		0.5	1.5	1		0.05	**1.68**	0.48	0.23	1.1	32.3	***
Pheasant Coucal	*Centropus phasianinus*	TO	9			0.5						0.1	0.16	0.22		0.04	9.7	ns
Cockatiel	*Nymphicus hollandicus*	G	22				1.67			1.5		1.55		1.17	0.62	0.69	11.9	ns
Sulphur-crested Cockatoo	*Cacatua galerita*	G	11				1.5					0.15	0.26	0.09	0.23	0.08	5.5	ns
Apostlebird	*Struthidea cinerea*	TO	25				1.33			3		3.45	**5.47**	0.52	2.08	0.13	32.9	***
Little Button-Quail	*Turnix velox*	G	7				0.5									0.13	15.9	ns
Australian Raven	*Corvus coronoides*	TO	43				0.33		**7**	0.25	0.38	0.8	1.21	0.22	0.85	0.44	23.7	**
Brolga	*Grus rubicunda*	W	1				0.33											
Banded Lapwing	*Vanellus tricolor*	TO	1				0.33											
Brown Falcon	*Falco berigora*	TO	20				0.17					0.1	0.37		0.23	0.35	10	ns
Masked Lapwing	*Vanellus miles*	TO	1				0.17											
Brown Honeyeater	*Lichmera indistincta*	N	19					**5.5**			5.38		1.21	0.04	1.92		25.8	**

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Singing Honeyeater	*Lichenostomus virescens*	NL	62					3		1.25		0.25	0.84	0.13	1.23	**3.33**	68	***
Grey Shrike-Thrush	*Colluricincla harmonica*	LS	59					0.5			0.75	0.1	**2**	0.13	1	0.96	50.2	***
Crested Bellbird	*Oreoica gutturalis*	TO	65					0.5				0.1	0.63	0.39		**3.04**	97	***
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	NL	28						**2**	0.25		0.1	0.53	0.17	0.77	0.6	17.3	*
Crested Pigeon	*Ocyphaps lophotes*	G	36						2			1.15	**2.42**	0.04	0.08	0.9	28.4	***
Mistletoebird	*Dicaeum hirundinaceum*	F	32						**2**			0.35	0.95	0.26	0.31	0.33	20.3	*
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	L	74						1.5	0.25	0.25	0.5	1.63	**2.09**	0.54	1.04	41.5	***
Peaceful Dove	*Geopelia striata*	G	37						1	1.5		0.3	**2.89**	2.04	0.15	0.44	44.2	***
Pied Butcherbird	*Cracticus nigrogularis*	TO	110						1	1	0.13	2.9	1.74	**3.61**	2.08	1.75	49	***
Bush Stone-Curlew	*Burhinus grallarius*	TO	2						1					0.09				
Rufous Whistler	*Pachycephala rufiventris*	L	94						0.5	0.5	1	0.5	3.26	1	0.46	**4.71**	78.4	***
Sacred Kingfisher	*Todiramphus sanctus*	TO	17						0.5		0.13	0.3	1.05	0.09	0.23	0.1	16.3	ns
Red-winged Parrot	*Aprosmictus erythropterus*	G	3						0.5			1.05	1.21	0.26	1	0.42		
Little Friarbird	*Philemon citreogularis*	N	55							4.5	0.38	1.15	**5.74**	0.52	1.15	1.25	46.1	***
Yellow-Rumped Thornbill	*Acanthiza chrysorrhoa*	L	26							2.5			**3.11**	0.22		1.31	25	**
Weebill	*Smicrornis brevirostris*	L	10							2	5	2.5	3.68	1.09	2	2.17	12	ns
Double-barred Finch	*Taeniopygia bichenovii*	G	7							**2**			1.89	0.09		0.35	21.5	*
Striated Pardalote	*Pardalotus striatus*	L	44							1.75	1.75	0.5	0.42	1.83	**3.85**	0.52	39.7	***
Rainbow Lorikeet	*Trichoglossus haematodus*	N	7							**1.25**		0.1		0.65	0.46	0.12	22.2	**
Blue-faced Honeyeater	*Entomyzon cyanotis*	NL	2							1	0.25	0.25			1.15			
Chestnut-rumped Thornbill	*Acanthiza uropygialis*	L	4							1						0.37		
Diamond Dove	*Geopelia cuneata*	G	15							0.75			0.63		0.23	0.62	14	ns
Pale-headed Rosella	*Platycercus adscitus*	G	6							0.5		1.35	0.26	0.43	0.15	0.27	13.4	ns
Spotted Bowerbird	*Chlamydera maculata*	LS	14							0.5		0.1	0.58		0.15	0.19	12.7	ns
Grey Butcherbird	*Cracticus torquatus*	TO	63							0.25	1.25	0.75	1.58	0.26	**1.69**	0.63	31.2	***
Common Bronzewing	*Phaps chalcoptera*	G	31							0.25		0.35	0.42		0.08	**0.67**	18.1	*
Southern Boobook	*Ninox novaeseelandiae*	TO	36							0.25		0.15	0.26	0.43	0.92	0.21	12.7	ns
Horsfield's Bronze-Cuckoo	*Chrysococcyx basalis*	L	26							0.25			0.11		0.15	**0.56**	32.1	***
Noisy Friarbird	*Philemon corniculatus*	N	50								4.38	0.85	0.47	2.65	**7.62**	0.77	27.1	**
White-throated Honeyeater	*Melithreptus albogularis*	N	6								3.13						0	ns
Buff-rumped Thornbill	*Acanthiza reguloides*	L	7								**1.75**		1.47				25	**
Pied Currawong	*Strepera graculina*	TO	8								1.38				0.92		0	ns
White-bellied Cuckoo-Shrike	*Coracina papuensis*	L	2								0.75		0.05		0.23			
Red-backed Fairy-wren	*Malurus melanocephalus*	TI	13								0.75			**3.22**	0.62	0.1	40.8	***
Noisy Miner	*Manorina melanocephala*	TO	1								0.75							
Laughing Kookaburra	*Dacelo novaeguineae*	TO	8								0.38	0.05	0.05		1.08	0.02	2.5	ns
Shining Bronze-Cuckoo	*Chrysococcyx lucidus*	L	4								0.25		0.11			0.02		
Australian Owlet-nightjar	*Aegotheles cristatus*	S	99								0.13	0.8	1.11	0.96	1.08	**1.21**	42.7	***
Jacky Winter	*Microeca fascinans*	S	66								0.13	0.2	**2.05**	1.09	0.54	2.33	44.2	***

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Grey Fantail	*Rhipidura fuliginosa*	S	3								0.13				0.23			
Brown Treecreeper	*Climacteris picumnus*	T	16									0.75	0.74	0.52	0.46	0.35	4.4	ns
Red-tailed Black-Cockatoo	*Calyptorhynchus banksii*	G	2									0.75				0.04		
Striped Honeyeater	*Plectorhyncha lanceolata*	NL	50									0.6	2.79		**3.46**	1.12	27.5	**
Squatter Pigeon	*Geophaps scripta*	G	7									0.5		0.09	0.62	0.04	5	ns
Olive-backed Oriole	*Oriolus sagittatus*	LS	17									0.4	**0.84**		0.08	0.04	32.7	***
Torresian Crow	*Corvus orru*	TO	20									0.3		**0.78**	0.77	0.12	23	**
Painted Button-Quail	*Turnix varia*	G	26									**0.25**		0.13			20.3	*
Tawny Frogmouth	*Podargus strigoides*	PI	20									0.2	0.37	0.04	0.15	0.12	14.7	ns
Black-shouldered Kite	*Elanus axillaris*	TO	22									**0.2**					17.5	*
Varied Sittella	*Daphoenositta chrysoptera*	T	9									0.15	0.32	0.39		0.52	2.9	ns
Pallid Cuckoo	*Cuculus pallidus*	L	29									0.15	0.16	0.43		**0.88**	17.8	*
Red-backed Kingfisher	*Todiramphus pyrrhopygia*	TO	19									0.15	0.05	0.74		0.19	13.8	ns
Blue-winged Kookaburra	*Dacelo leachii*	TO	14									0.1	**0.68**	0.26	0.31		27.8	**
Rufous Songlark	*Cincloramphus mathewsi*	TI	4									0.1	0.16			0.12		
Channel-billed Cuckoo	*Scythrops novaehollandiae*	L	7									0.1	0.11	0.17		0.06	2.1	ns
Brown Goshawk	*Accipiter fasciatus*	R	4									0.1	0.05			0.04		
Australian Hobby	*Falco longipennis*	R	2									0.1						
Western Gerygone	*Gerygone fusca*	L	6									0.05	0.05			0.23	8.7	ns
Black Kite	*Milvus migrans*	TO	1									0.05						
Rainbow Bee-eater	*Merops ornatus*	S	25										0.84	0.17		**0.92**	19.9	*
White-plumed Honeyeater	*Lichenostomus penicillatus*	N	5										0.63	0.39			11.6	ns
White-winged Triller	*Lalage sueurii*	LS	12										0.53	0.09		0.73	11.5	ns
Dollarbird	*Eurystomus orientalis*	H	9										0.32			0.13	6.6	ns
Brush Cuckoo	*Cacomantis variolosus*	L	2										0.21					
Varied Lorikeet	*Psitteuteles versicolor*	N	1										0.11					
Barn Owl	*Tyto alba*	TO	10										0.05		0.23	0.13	9.3	ns
Little Woodswallow	*Artamus minor*	H	16										0.05			**0.75**	23.8	**
Collared Sparrowhawk	*Accipiter cirrhocephalus*	R	3										0.05			0.04		
Restless Flycatcher	*Myiagra inquieta*	S	30										0.05			0.02	13.6	ns
Black-breasted Buzzard	*Hamirostra melanosternon*	R	1										0.05					
Grey-fronted Honeyeater	*Lichenostomus plumulus*	NL	4											0.17		0.31		
Zebra Finch	*Taeniopygia guttata*	G	3											0.17		0.17		
Forest Kingfisher	*Todiramphus macleayii*	TO	2											0.09				
Brown Thornbill	*Acanthiza pusilla*	L	1												0.15			
Brown Quail	*Coturnix ypsilophora*	G	4												0.08	0.17		
White-throated Gerygone	*Gerygone olivacea*	L	3												0.08	0.08		
White-throated Nightjar	*Eurostopodus mystacalis*	S	1												0.08			
Masked Woodswallow	*Artamus personatus*	H	5													0.65	8.2	ns

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Red-browed Pardalote	*Pardalotus rubricatus*	L	13													**0.62**	22.7	**
Rufous-throated Honeyeater	*Conopophila rufogularis*	NL	3													0.46		
Inland Thornbill	*Acanthiza apicalis*	L	2													0.37		
Hooded Robin	*Melanodryas cucullata*	PI	6													0.37	9.9	ns
White-breasted Woodswallow	*Artamus leucorynchus*	H	3													0.15		
Black-throated Finch	*Poephila cincta*	G	3													0.12		
Black-eared Cuckoo	*Chrysococcyx osculans*	L	2													0.08		
Black-chinned Honeyeater	*Melithreptus gularis*	NL	1													0.06		
Little Eagle	*Hieraaetus morphnoides*	TO	1													0.02		
MAMMALS																		
Desert Mouse	*Pseudomys desertor*	MU	46	**8.33**				2.5		0.25	1.13	2.05	0.16	0.13	0.23	3.44	31.1	***
Eastern Grey Kangaroo	*Macropus giganteus*	MA	79	**2.1**	0.75	0.2				1.45		0.23	0.86	0.07	0.06	0.53	41	***
Julia Creek Dunnart	*Sminthopsis douglasi*	DA	3		1.25	0.5												
Stripe-faced Dunnart	*Sminthopsis macroura*	DA	39		1		0.67	0.5	**2**			0.75	0.53	0.09	0.15	0.65	17.2	*
Red Kangaroo	*Macropus rufus*	MA	56		0.83	0.4	0.35	0.1		0.5		0.51	**0.97**		0.11	0.1	56.6	***
Long-tailed Planigale	*Planigale ingrami*	DA	1		0.5													
Long-haired Rat	*Rattus villosissimus*	MU	3		0.25	5.5												
Forrest's Mouse	*Leggadina forresti*	MU	1		0.25													
Delicate Mouse	*Pseudomys delicatulus*	MU	41				0.17				**3.5**	0.35	0.47	0.17		1.25	19.1	*
Wallaroo	*Macropus robustus*	MA	50					**1**		0.45		0.25	0.38	0.05	0.69	0.55	24	**
Common Brushtail Possum	*Trichosurus vulpecula*	PH	6							**1**			0.74	0.09			20.3	*
Common Planigale	*Planigale maculata*	DA	5								0.5				0.08		0	ns
Pebble-mound Mouse	*Pseudomys patrius*	MU	5								0.38				0.46		0	ns
Spectacled Hare-wallaby	*Lagorchestes conspicillatus*	MA	4									0.25				0.08		
Short-beaked Echidna	*Tachyglossus aculeatus*	MO	28									0.1	0.16	0.04		**0.56**	25.7	**
Sugar Glider	*Petaurus breviceps*	PE	3									0.05	0.05	0.04				
Rufous Bettong	*Aepyprymnus rufescens*	PO	1									0.05						
Narrow-nosed Planigale	*Planigale tenuirostris*	DA	1										0.05					
Canefield Rat	*Rattus sordidus*	MU	1											0.04				
Lakeland Downs Mouse	*Leggadina lakedownensis*	MU	1												0.15			
Black-striped Wallaby	*Macropus dorsalis*	MA	1													0.17		
Common Dunnart	*Sminthopsis murina*	DA	1													0.06		
REPTILES																		
Lined Earless Dragon	*Tympanocryptis lineata*	AG	5	**2**	0.75												94.4	***
Robust Ctenotus	*Ctenotus robustus*	SC	13	**1.33**										0.35	0.15		65.8	***
Centralian Blue-tongued Lizard	*Tiliqua multifasciata*	SC	2	0.33			0.17											
Leopard Ctenotus	*Ctenotus pantherinus*	SC	28	0.33				**2**		0.25		0.05			0.31	1.21	33.6	***
gecko	*Diplodactylus williamsi*	GE	15	0.33				0.5			0.25			0.09		0.25	14.8	ns
Gould's Goanna/Sand Monitor	*Varanus gouldii*	VA	7	0.33									0.05			0.1	10.2	ns

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
dragon	*Diporiphora winneckei*	AG	1	0.33														
Excitable Delma	*Delma tincta*	PY	3		2													
Myall/Curl Snake	*Suta suta*	EL	10		**0.75**		0.17						0.21			0.06	21.5	*
De Vis Banded Snake	*Denisonia devisi*	EL	1			**0.5**												
Common Dwarf Skink	*Menetia greyii*	SC	52				0.83				0.13	1.05	0.05	**1.09**	0.15	0.81	25.7	**
Central Netted Dragon	*Ctenophorus nuchalis*	AG	19				0.67	**1**				0.15		0.04		0.29	22.5	**
skink	*Ctenotus hebetior*	SC	54				0.5	0.5		**6.25**		3.9	1.79	0.22		2.1	30.3	***
Box-patterned gecko	*Diplodactylus steindachneri*	GE	49				0.17				0.63	0.75	1.26	0.26	0.23	0.98	16.5	ns
Eastern Barred Ctenotus	*Ctenotus strauchii*	SC	17					0.5				0.4	0.37		1.15	0.5	9	ns
Unspotted Yellow-sided Ctenotus	*Ctenotus ingrami*	SC	4					0.5						0.09	0.15			
Barred-sided Skink	*Eulamprus sokosoma*	SC	1					0.5										
Chain-backed Dtella	*Gehyra catenata*	GE	28						**3**			1.25	2.53		2.38	0.08	57.8	***
Callose-palmed Shinning-skink	*Cryptoblepharus plagiocephalus*	SC	15						**1**			0.95		0.13	0.69		43.6	***
Eastern Robust Slider	*Lerista punctatovittata*	SC	14							1.75		0.25	0.68	0.04		0.04	8.2	ns
Nobbi Lizard	*Amphibolurus nobbi*	AG	31							**1.5**		0.1	0.37	0.13	0.15	0.77	22.9	**
Black-tailed Monitor	*Varanus tristis*	VA	33							0.75	0.5	0.3	0.11	0.13	0.08	0.42	13	ns
Spiny-tailed Gecko	*Diplodactylus ciliaris*	GE	5							0.75		0.05	0.16				16.6	ns
Blind Snake	*Ramphotyphlops sp*	TY	2							0.5								
Bynoes Gecko	*Heteronotia binoei*	GE	52							0.25	0.13	**1.05**	0.68	0.74	0.08	0.4	17.8	*
Bearded Dragon	*Pogona barbata*	AG	36							0.25		0.6	0.16	0.09	0.38	0.44	15.6	ns
Spiny-palmed Shinning-skink	*Cryptoblepharus carnabyi*	SC	14							0.25		0.2	0.58			0.13	11.6	ns
Western Brown Snake/Gwardar	*Pseudonaja nuchalis*	EL	4							0.25		0.2						
Eastern Two-line Dragon	*Diporiphora australis*	AG	11								1			0.26		0.1	15.7	ns
Northern Soil-crevice Skink	*Proablepharus tenuis*	SC	24								0.88	0.4	0.42	0.17		0.4	6	ns
Zigzag Velvet Gecko	*Oedura rhombifer*	GE	4								0.75		0.16					
Straight-browed Ctenotus	*Ctenotus spaldingi*	SC	14								0.63	0.4	0.11		0.08	0.12	11.8	ns
skink	*Menetia timlowi*	SC	6								0.63				0.38		0	ns
Wood Mulch-slider	*Lerista muelleri*	SC	1								0.5	0.3			0.23	0.15		
Northern Velvet Gecko	*Oedura castelnaui*	GE	8								0.5		0.37	0.09	0.08	0.02	5.5	ns
Robust Rainbow-skink	*Carlia schmeltzii*	SC	3								0.5							
Wood Gecko	*Diplodactylus vittatus*	GE	5								0.25				0.38		0	ns
Tree-base Litter-skink	*Lygisaurus foliorum*	SC	2								0.25							
Shaded-litter Rainbow-skink	*Carlia munda*	SC	24								0.13	0.6	0.74	**0.83**	0.15	0.08	26.3	**
Fat-tailed Diplodactylus	*Diplodactylus conspicillatus*	GE	21								0.13	0.25	0.21			0.75	14.4	ns
Burton's Legless Lizard	*Lialis burtonis*	PY	16								0.13	0.05	0.05			**0.29**	17	*
Desert Uplands Ctenotus	*Ctenotus rosarium*	SC	15								0.13					**0.94**	45.7	***
Fire-tailed Skink	*Morethia taeniopleura*	SC	6								0.13					0.1	8.2	ns
Fine-spotted Mulch-skink	*Glaphyromorphus punctulatus*	SC	1								0.13							
Dubious dtella	*Gehyra dubia*	GE	14									0.3	0.05	**0.52**			35.6	***

Common name	Species	g	n	G1	G2	G3	G5	G4	G10	G7	G6	G8	G9	G11	G12	G13	H	p
Tree Dtella	*Gehyra variegata*	GE	11									0.1	**1.74**	0.09		0.02	27.4	**
Beaked Gecko	*Rhynchoedura ornata*	GE	17									0.1		0.04		**0.37**	17.1	*
Frill-necked Lizard	*Chlamydosaurus kingii*	AG	2									0.1						
Tree Skink	*Egernia striolata*	SC	14									0.05	**1.58**	0.09	0.08	0.12	38.1	***
South-eastern Morethia Skink	*Morethia boulengeri*	SC	12									0.05	0.58		**1.08**		32.2	***
Eastern Blue-tongue Lizard	*Tiliqua scincoides*	SC	5									0.05		0.04		0.06	2.3	ns
Carpentaria Whip-snake	*Rhinoplocephalus boschmai*	EL	2									0.05		0.04				
Rough Knob-tail	*Nephrurus asper*	GE	4									0.05			0.38			
Claw-snouted Blind Snake	*Ramphotyphlops unguirostris*	TY	2									0.05				0.02		
Brown Tree Snake	*Boiga irregularis*	CO	1									0.05						
Eastern Brown Snake	*Pseudonaja textilis*	EL	1									0.05						
Yellow-spotted Monitor	*Varanus panoptes*	VA	1									0.05						
Gilbert's Lashtail	*Amphibolurus gilberti*	AG	7										**0.42**		0.31		25	**
Tessellated Gecko	*Diplodactylus tessellatus*	GE	3										0.32					
Hooded Scaly Foot	*Pygopus nigriceps*	PY	15										0.11	0.04	0.15	0.23	10.6	ns
Burn's Lashtail	*Amphibolurus burnsi*	AG	2										0.11					
python	*Liasis stimsoni*	BO	1										0.05					
Black-headed Python	*Aspidites melanocephalus*	BO	1										0.05					
dragon	*Pogona vitticeps*	AG	1										0.05					
Capricorn Ctenotus	*Ctenotus capricorni*	SC	25											0.17		**1.08**	41.4	***
Yellow-faced Whipsnake	*Demansia psammophis*	EL	4											0.04	0.08	0.04		
Robust Blind Snake	*Ramphotyphlops ligatus*	TY	2											0.04	0.08			
Red-naped Snake	*Furina diadema*	EL	1											0.04				
Black Whipsnake	*Demansia atra*	EL	1											0.04				
Open-litter Rainbow-skink	*Carlia pectoralis*	SC	3												0.92			
Brigalow Scaly Foot	*Paradelma orientalis*	PY	2												0.15			
Marbled Velvet Gecko	*Oedura marmorata*	GE	5												0.08	0.12	6.5	ns
Two-toed Fine-lined Slider	*Lerista wilkinsi*	SC	1												0.08			
Coral Snake	*Simoselaps australis*	EL	4													0.08		
Unnamed Mulch-slider	*Lerista* sp nov	SC	1													0.06		
NE Plain-nosed Burrowing Snake	*Simoselaps warro*	EL	1													0.02		

Table 3.10 Minimum adequate models derived for vertebrate guilds and families. Model terms include sub-set significant environmental vectors. Table indicates parameter estimate and significance (Wald statistic *p<0.05, **p<0.01, ***p<0.001) and total deviance explained (%).

Guild/Family	%	Intercept	Basal area	FPC 1-3 m	Hummock	Tussock	Bare ground	Soil type
BIRD ABUNDANCE								
Frugivores	12	-2.518	0.093***					0.197**
Foliage gleaner/sallier	12	-1.623	0.087***		0.018***		0.018***	
Nectarivores	27	0.171	0.077***	0.358***				
Nectarivores/gleaners	38	-1.429	0.058***	0.434***	0.018***		0.025***	
Foliage gleaners	9	1.366	0.043***		0.010***		0.006***	
Terrestrial omnivores	7	2.058	0.024***				0.006***	
Salliers	7	0.399	0.023**				0.014***	
Trunk gleaner	5	-2.024		0.449***			0.021***	
Hawkers	14	-0.915			0.023***		0.027***	-0.311***
Granivores	9	2.232			-0.018***			-0.018***
Terrestrial insectivores	4	1.255			-0.009**	0.006*		
Pouncing insectivore	17	-2.043				-0.043**	0.027**	
MAMMAL ABUNDANCE								
Tachyglossidae	21	-1.023	0.058*					
Dasyuridae	8	-0.423	-0.067***					0.153**
Muridae	47	-0.671		0.197***	0.046***	0.013***		
Macropodidae	9	2.301				-0.015***		0.153***
Phalangeridae	11	-0.176					-0.053***	
REPTILE ABUNDANCE								
Gekkonidae	21	1.105	0.058***		-0.016***	-0.013***		
Pygopodidae	8	-2.401			0.021**			0.293**
Agamidae	6	0.566						-0.206**
Scincidae	21	2.824				-0.008***	0.009***	-0.211***
BIRD RICHNESS								
Frugivores	10	-2.577	0.098***					
Nectarivores	13	-0.899	0.069***					
Foliage gleaner/sallier	7	-1.026	0.062***					
Foliage gleaners	9	0.208	0.038***					
Terrestrial omnivores	7	1.019	0.021**					
Nectarivores/gleaners	9	-0.739		0.407***				
Hawkers	27	-0.951			0.025**			-0.714**

Guild/Family	%	Intercept	Basal area	FPC 1-3 m	Hummock	Tussock	Bare ground	Soil type
Salliers	5	-0.627			0.011**		0.012*	
Granivores	9	0.777			-0.016***			
Pouncing insectivore	5	-1.304						-0.026*
MAMMAL RICHNESS								
Muridae	15	-0.825			0.021***			
Tachyglossidae	14	2.399			-0.046***			
Dasyuridae	5	-1.244				-0.016*		0.172*
REPTILE RICHNESS								
Gekkonidae	16	0.124	0.056***					-0.092*
Scincidae	26	1.006			0.009***			-0.133**

Table 3.11 Minimum adequate models derived for vertebrates guilds, families and species (identified as characteristic of fauna groups in SIMPER routine, Table 3.2). Model terms include significant environmental vectors. Table indicates parameter estimate and significance (Wald statistic *p<0.05, **p<0.01, ***p<0.001) and total deviance explained (%). Vector codes in Table 3.3 and guild/family membership listed in Table 3.12.

Species	Guild	n	%	Intercept	Basal area	FPC 1-3 m	Hummock	Tussock	Bare ground	Soil type
Blue-winged Kookaburra	TO	14	13	-3.284	0.135***					
Spotted Bowerbird	LS	14	14	-3.202	0.135***					
Striped Honeyeater	NL	50	31	-3.278	0.125***	0.504***			0.027***	
Mistletoebird	F	32	10	-2.029	0.099***					
Noisy Friarbird	N	50	14	-0.737	0.095***					
Pale-headed Rosella	G	26	11	-2.262	0.093***			0.024*		
Grey Shrike-Thrush	LS	59	12	-1.467	0.089***		0.017**			
Southern Boobook	TO	36	6	-2.073	0.078**					
Magpie-Lark	TO	55	12	-2.085	0.077***				0.021**	
Brown Treecreeper	T	16	39	-2.611	0.076***				0.022**	
Grey Butcherbird	TO	63	13	-1.429	0.075***					0.146**
Striated Pardalote	L	44	8	-1.078	0.067***	0.281**				
Grey-crowned Babbler	TI	49	8	-0.847	0.064***				0.017***	
Weebill	L	51	12	0.535	0.061***					-0.152***
Black-faced Cuckoo-shrike	L	74	7	-0.734	0.052***			0.009*		
Rufous Whistler	L	94	18	-1.201	0.046***		0.028***		0.025***	
Red-backed Fairy-wren	TI	13	30	-2.877	0.045*			0.052***		
Jacky Winter	S	66	5	-1.095	0.034**				0.021***	
Australian Magpie	TO	87	4	-0.431	0.028*			0.008*		
Nankeen Kestrel	TO	12	34	-0.046	-0.364***					
Galah	G	39	6	0.731	-0.056**		-0.024***			
Brown Honeyeater	N	19	6	-2.226		1.169***			-0.033***	0.321***
Variegated Fairy-wren	TI	25	6	-1.145		0.623***				
Olive-backed Oriole	LS	17	12	-2.188		0.588*	-0.053**			
Little Friarbird	N	55	20	-0.027		0.574***	-0.049***			
Emu	TO	16	5	-2.111		0.539**				
Yellow-Rumped Thornbill	L	26	5	-1.658		0.447***			0.018***	
Singing Honeyeater	NL	62	33	0.413		0.398***	0.014***			-0.518***
Apostlebird	TO	25	11	-1.874		0.322***			0.025***	0.222***
Spiny-cheeked Honeyeater	NL	28	2	-1.369		0.291*				
Sulphur-crested Cockatoo	G	11	53	-0.869		-0.788**				

Species	Guild	n	%	Intercept	Basal area	FPC 1-3 m	Hummock	Tussock	Bare ground	Soil type
White-winged Triller	LS	12	3	1.82		-0.688***				-1.336***
Torresian Crow	TO	20	4	-0.675		-0.562*				
Pallid Cuckoo	L	29	40	-7.248			0.079***		0.092***	
Red-browed Pardalote	L	13	25	-7.634			0.071***		0.092***	
Crested Bellbird	TO	65	20	-1.668			0.033***		0.025***	
Horsfield's Bronze-Cuckoo	L	26	28	-1.275			0.031***			-0.534*
Little Woodswallow	H	16	37	0.461			0.029***			-1.769**
Common Bronzewing	G	31	6	-2.44			0.023**		0.020*	
Black-faced Woodswallow	H	22	6	-2.412			0.017**		0.033***	
Sacred Kingfisher	TO	17	5	-1.105			-0.034*			
Red-backed Kingfisher	TO	19	14	-5.979				0.049**	0.063***	
Peaceful Dove	G	37	14	-3.465				0.042***	0.047***	
Yellow-throated Miner	TO	63	10	0.939				0.015***	0.008*	-0.343***
Australian Raven	TO	43	6	-0.612				-0.018*		0.197***
Spotted Nightjar	S	16	14	-1.091				-0.061**		
Barn Owl	TO	10	15	-4.601					0.113*	0.041**
Crested Pigeon	G	36	13	-2.401					0.043***	
Rainbow Bee-eater	S	25	19	-0.687					0.022**	-0.675***
Diamond Dove	G	15	2	-1.958					0.017*	
Willie Wagtail	S	58	4	-1.192					0.013*	0.101*
Western Gerygone	L	10	23	-0.919						-0.863*
Varied Sittella	T	9	8	-0.584						-0.321*
Cockatiel	G	22	4	0.331						-0.294***
MAMMALS										
Macropus robustus	MA	50	19	-1.051	0.077***			-0.042***		
Tachyglossus aculeatus	MO	28	21	-1.023	0.057*			-0.066***		
Pseudomys desertor	MU	46	53	-0.328	-0.067***		0.049***			
Pseudomys delicatulus	MU	41	14	0.288		0.252*				-0.521***
Sminthopsis macroura	DA	39	5	-1.925			0.021***		0.018*	
Macropus giganteus	MA	79	6	-2.676			0.014*		0.019*	
Macropus rufus	MA	56	22	-0.796			-0.078***			
REPTILES										
Morethia boulengeri	SC	12	24	-5.627	0.165***				0.041***	
Gehyra catenata	GE	28	37	-3.404	0.152***					0.433***
Egernia striolata	SC	14	37	-5.132	0.125***					0.676***

Species	Guild	n	%	Intercept	Basal area	FPC 1-3 m	Hummock	Tussock	Bare ground	Soil type
Pygopus nigriceps	PY	15	5	-3.03	0.082*					
Pogona barbata	AG	36	7	-1.092	0.054*					-0.295*
Ctenotus pantherinus	SC	28	56	-1.626	-0.104**		0.053***			
Ctenotus hebetior	SC	54	43	3.012	-0.063***			0.019***		-1.658***
Lerista punctatovittata	SC	14	5	-2.701		0.601**				
Amphibolurus nobbi	AG	31	22	-0.041		0.385**				-0.896***
Ctenotus robustus	SC	13	9	-1.322		-0.959*				
Ctenotus capricorni	SC	25	54	-9.633			0.144***		0.117***	
Ctenotus rosarium	SC	15	49	-6.511			0.089***		0.064***	
Lialis burtonis	PY	16	19	-3.095			0.039***			
Rhynchoedura ornata	GE	17	10	-2.651			0.032***			
Diplodactylus williamsi	GE	15	11	-2.692			0.028**			
Varanus tristis	VA	33	8	-1.802			0.024***			
Ctenotus spaldingi	SC	14	10	-2.334			0.021*			
Heteronotia binoei	GE	52	11	-0.014			-0.035***			-0.162*
Menetia greyii	SC	52	12	-0.451				0.025***		-0.326***
Diporiphora australis	AG	11	5	-2.756				0.022*		
Ctenotus strauchii	SC	17	7	-0.859				-0.032***		0.181*
Gehyra variegata	GE	11	39	-3.644				-0.029**		0.777***
Diplodactylus conspicillatus	GE	21	4	-0.067				-0.026**		
Proablepharus tenuis	SC	24	5	-0.038				-0.015*	-0.019*	
Suta suta	EL	10	23	-6.142					0.044*	0.389**
Ctenophorus nuchalis	AG	19	25	-2.275					0.038**	-0.866**
Cryptoblepharus plagiocephalus	SC	15	7	-0.226					-0.035***	
Diplodactylus steindachneri	GE	49	11	0.494						-0.456***

Table 3.12 Species guild and family membership. Bird guilds after Woinarski and Tidemann (1991) and Fisher (2001a).

FRUGIVORE (F)
Mistletoebird *Dicaeum hirundinaceum*

GRANIVORE (G)
Black-throated Finch *Poephila cincta*
Brown Quail *Coturnix ypsilophora*
Cockatiel *Nymphicus hollandicus*
Common Bronzewing *Phaps chalcoptera*
Crested Pigeon *Ocyphaps lophotes*
Diamond Dove *Geopelia cuneata*
Double-barred Finch *Taeniopygia bichenovii*
Galah *Cacatua roseicapilla*
Little Button-Quail *Turnix velox*
Painted Button-Quail *Turnix varia*
Pale-headed Rosella *Platycercus adscitus*
Peaceful Dove *Geopelia striata*
Red-chested Button-Quail *Turnix pyrrhothorax*
Red-tailed Black-Cockatoo *Calyptorhynchus banksii*
Red-winged Parrot *Aprosmictus erythropterus*
Squatter Pigeon *Geophaps scripta*
Sulphur-crested Cockatoo *Cacatua galerita*
Zebra Finch *Taeniopygia guttata*

HAWKER (H)
Black-faced Woodswallow *Artamus cinereus*
Dollarbird *Eurystomus orientalis*
Little Woodswallow *Artamus minor*
Masked Woodswallow *Artamus personatus*
White-breasted Woodswallow *Artamus leucorynchus*

FOLIAGE GLEANER (L)
Black-eared Cuckoo *Chrysococcyx osculans*
Black-faced Cuckoo-shrike *Coracina novaehollandiae*
Brush Cuckoo *Cacomantis variolosus*
Buff-rumped Thornbill *Acanthiza reguloides*
Channel-billed Cuckoo *Scythrops novaehollandiae*
Chestnut-rumped Thornbill *Acanthiza uropygialis*
Horsfield's Bronze-Cuckoo *Chrysococcyx basalis*
Inland Thornbill *Acanthiza apicalis*
Pallid Cuckoo *Cuculus pallidus*
Red-browed Pardalote *Pardalotus rubricatus*
Rufous Whistler *Pachycephala rufiventris*
Shining Bronze-Cuckoo *Chrysococcyx lucidus*
Striated Pardalote *Pardalotus striatus*
Weebill *Smicrornis brevirostris*
Western Gerygone *Gerygone fusca*
White-bellied Cuckoo-Shrike *Coracina papuensis*
White-throated Gerygone *Gerygone olivacea*
Yellow-Rumped Thornbill *Acanthiza chrysorrhoa*

FOLIAGE GLEANER/SALLIER (LS)
Grey Shrike-Thrush *Colluricincla harmonica*
Olive-backed Oriole *Oriolus sagittatus*
Spotted Bowerbird *Chlamydera maculata*
White-winged Triller *Lalage sueurii*

NECTARIVORE (N)
Brown Honeyeater *Lichmera indistincta*
Little Friarbird *Philemon citreogularis*
Noisy Friarbird *Philemon corniculatus*
Rainbow Lorikeet *Trichoglossus haematodus*
Varied Lorikeet *Psitteuteles versicolor*
White-plumed Honeyeater *Lichenostomus penicillatus*
White-throated Honeyeater *Melithreptus albogularis*

NECTARIVORE/GLEANER (NL)
Black-chinned Honeyeater *Melithreptus gularis*
Blue-faced Honeyeater *Entomyzon cyanotis*
Grey-fronted Honeyeater *Lichenostomus plumulus*
Rufous-throated Honeyeater *Conopophila rufogularis*
Singing Honeyeater *Lichenostomus virescens*
Spiny-cheeked Honeyeater *Acanthagenys rufogularis*
Striped Honeyeater *Plectorhyncha lanceolata*

POUNCING INSECTIVORE (PI)
Hooded Robin *Melanodryas cucullata*
Tawny Frogmouth *Podargus strigoides*

RAPTOR (R)
Australian Hobby *Falco longipennis*
Black-breasted Buzzard *Hamirostra melanosternon*
Brown Goshawk *Accipiter fasciatus*
Collared Sparrowhawk *Accipiter cirrhocephalus*

SALLIER (S)
Australian Owlet-nightjar *Aegotheles cristatus*
Grey Fantail *Rhipidura fuliginosa*
Jacky Winter *Microeca fascinans*
Rainbow Bee-eater *Merops ornatus*
Restless Flycatcher *Myiagra inquieta*
Spotted Nightjar *Eurostopodus argus*
White-throated Nightjar *Eurostopodus mystacalis*
Willie Wagtail *Rhipidura leucophrys*

TRUNK GLEANER (T)
Brown Treecreeper *Climacteris picumnus*
Varied Sittella *Daphoenositta chrysoptera*

TERRESTRIAL INSECTIVORE (TI)
Grey-crowned Babbler *Pomatostomus temporalis*
Red-backed Fairy-wren *Malurus melanocephalus*
Rufous Songlark *Cincloramphus mathewsi*
Spinifexbird *Eremiornis carteri*
Variegated Fairy-wren *Malurus lamberti*
White-winged Fairy-wren *Malurus leucopterus*

TERRESTRIAL OMNIVORE (TO)
Apostlebird *Struthidea cinerea*
Australian Bustard *Ardeotis australis*
Australian Magpie *Gymnorhina tibicen*
Australian Raven *Corvus coronoides*
Banded Lapwing *Vanellus tricolor*
Barn Owl *Tyto alba*
Black Kite *Milvus migrans*
Black-shouldered Kite *Elanus axillaris*
Blue-winged Kookaburra *Dacelo leachii*
Brown Falcon *Falco berigora*
Bush Stone-Curlew *Burhinus grallarius*
Crested Bellbird *Oreoica gutturalis*
Emu *Dromaius novaehollandiae*
Forest Kingfisher *Todiramphus macleayii*
Grey Butcherbird *Cracticus torquatus*
Ground Cuckoo-shrike *Coracina maxima*
Laughing Kookaburra *Dacelo novaeguineae*

Little Eagle *Hieraaetus morphnoides*
Magpie-Lark *Grallina cyanoleuca*
Masked Lapwing *Vanellus miles*
Nankeen Kestrel *Falco cenchroides*
Noisy Miner *Manorina melanocephala*
Pheasant Coucal *Centropus phasianinus*
Pied Butcherbird *Cracticus nigrogularis*
Pied Currawong *Strepera graculina*
Red-backed Kingfisher *Todiramphus pyrrhopygia*
Richard's Pipit *Anthus novaeseelandiae*
Sacred Kingfisher *Todiramphus sanctus*
Southern Boobook *Ninox novaeseelandiae*
Spotted Harrier *Circus assimilis*
Torresian Crow *Corvus orru*
Wedge-tailed Eagle *Aquila audax*
Whistling Kite *Haliastur sphenurus*
Yellow-throated Miner *Manorina flavigula*

<u>WETLAND (W)</u>
Brolga *Grus rubicunda*
Magpie Goose *Anseranas semipalmata*

<u>DASYURIDAE (DA)</u>
Planigale ingrami
Planigale maculata
Planigale tenuirostris
Sminthopsis douglasi
Sminthopsis macroura
Sminthopsis murina

<u>MACROPODIDAE (MA)</u>
Lagorchestes conspicillatus
Macropus dorsalis
Macropus giganteus
Macropus robustus
Macropus rufus

<u>MURIDAE (MU)</u>
Leggadina forresti
Leggadina lakedownensis
Pseudomys delicatulus
Pseudomys desertor
Pseudomys patrius
Rattus sordidus
Rattus villosissimus

<u>PETAURIDAE (PE)</u>
Petaurus breviceps

<u>PHALANGERIDAE (PH)</u>
Trichosurus vulpecula

<u>POTOROIDAE (PO)</u>
Aepyprymnus rufescens

<u>TACHYGLOSSIDAE (TA)</u>
Tachyglossus aculeatus

<u>AGAMIDAE (AG)</u>
Amphibolurus burnsi
Amphibolurus gilberti
Amphibolurus nobbi
Chlamydosaurus kingii
Ctenophorus nuchalis
Diporiphora australis
Diporiphora winneckei
Pogona barbata
Pogona vitticeps
Tympanocryptis lineata

<u>BOIDAE (BO)</u>
Aspidites melanocephalus

<u>COLUBRIDAE (CO)</u>
Boiga irregularis

<u>ELAPIDAE (EL)</u>
Demansia atra
Demansia psammophis
Denisonia devisi
Furina diadema
Pseudonaja nuchalis
Pseudonaja textilis
Rhinoplocephalus boschmai
Simoselaps australis
Simoselaps warro
Suta suta

<u>GEKKONIDAE (GE)</u>
Diplodactylus ciliaris
Diplodactylus conspicillatus
Diplodactylus steindachneri
Diplodactylus tessellatus
Diplodactylus vittatus
Diplodactylus williamsi
Gehyra catenata
Gehyra dubia
Gehyra variegata
Heteronotia binoei
Nephrurus asper
Oedura castelnaui
Oedura marmorata
Oedura rhombifer
Rhynchoedura ornata

<u>PYGOPODIDAE (PY)</u>
Delma tincta
Lialis burtonis
Paradelma orientalis
Pygopus nigriceps

<u>SCINCIDAE (SC)</u>
Carlia munda
Carlia pectoralis
Carlia schmeltzii
Cryptoblepharus carnabyi
Cryptoblepharus plagiocephalus
Ctenotus capricorni
Ctenotus hebetior
Ctenotus ingrami
Ctenotus pantherinus
Ctenotus robustus
Ctenotus rosarium
Ctenotus spaldingi
Ctenotus strauchii
Egernia striolata
Eulamprus sokosoma
Glaphyromorphus punctulatus
Lerista sp nov
Lerista muelleri
Lerista punctatovittata
Lerista wilkinsi
Lygisaurus foliorum
Menetia greyii

Menetia timlowi
Morethia boulengeri
Morethia taeniopleura
Proablepharus tenuis
Tiliqua multifasciata
Tiliqua scincoides

TYPHLOPIDAE (TY)
Ramphotyphlops ligatus
Ramphotyphlops sp
Ramphotyphlops unguirostris

VARANIDAE (VA)
Varanus gouldii
Varanus panoptes
Varanus tristis

Chapter 4. Regional ecosystems and other surrogates of vertebrate fauna diversity

Introduction

The protection of the variety of Australia's biota and landscapes in their most natural and robust state is a universally accepted goal for all land managers, be they pastoral (Ash *et al.* 1997; Landsberg *et al.* 1998), indigenous (Yibarbuk *et al.* 2001) or conservation (Woinarski 1999b). However what constitutes natural or appropriate can vary according to the land steward's perceptions (see papers in Hale *et al.* 2000). One facet of land management is the explicit protection of land for nature conservation purposes alone, and in the past this has been the primary realm of National Park selection and management (Recher and Lim 1990; Pressey and Nicholls 1991). National Parks have been gazetted as early as the nineteenth century in Australia (e.g. Mount Buffalo, Wilson's Promontory, Houghton 1998), though as much for scenic amenity as for biological values. However in the current era there is recognition that National Parks alone are insufficient for continent-wide biodiversity protection. There is a continuing, seemingly unrelenting decline in many native animal species and guilds (Burbidge and McKenzie 1989; Franklin 1999) even within well-protected conservation reserves (Woinarski *et al.* 2001b). Though National Parks are still the conservation cornerstone, management of off-park landscapes for multiple purposes, including nature conservation also has more current government focus (e.g. Binning and Young 1999). The accent is now on management by the gamut of land stewards using a variety of techniques that enhance biodiversity maintenance (e.g. fire, livestock, weed, feral animals, revegetation, see papers in Hale and Lamb 1997). As such, there are two subtly alternate approaches to planning. Firstly, in highly fragmented environments, financial constraints dictate that careful choice is exercised in selecting what to add to an unbalanced or unrepresentative reserve network (Pressey and Taffs 2001a, b). Secondly, in intact environments where there is strong impetus for intensive agricultural or resource development, planning emphasises decision-making on what and how much to keep, and the imperative to manage the remaining landscape-scale values outside reserved areas (JANIS 1997; Woinarski *et al*. 2000c).

Approaches to the process of conservation planning, that is the selection of areas for reservation and protection (hereafter reserves), have been widely reviewed and debated (Pressey *et al.* 1993; Ferrier and Watson 1997; Prendergast *et al.* 1999; Pressey and Cowling 2001; Margules and Pressey 2000). There are two major paradigms, which focus respectively on design characteristics and location criteria. Design involves questions of size and shape, and is strongly rooted in the theories of island biogeographic and species-area relationships (Diamond 1975; Margules *et al.* 1982). Approaches relying on planning in this manner have been discounted as less valuable for targeted protection of biodiversity (Lombard 1995). Realistically there is little luxury of design when faced with remnant landscapes and cadastral boundaries. The current emphasis, particularly in Australia, is on reserve location. This is largely due to a pragmatic need to maximise biodiversity protection in systems with limited land area available, the constraints of funding and previous poor planning through expediency (Pressey and Tully 1994). Underpinning this is the explicit government policy of comprehensiveness, adequacy and representativeness of the reserve system (JANIS 1997). However area targets are often below what is considered adequate to prevent continued species relaxation or extinction debt (James and Saunders 2001).

The effective selection of the reserve location is a fundamental planning activity. There are three broad approaches:

- *ad hoc* selection in response to aesthetics, availability and political-will, which characterises the early approach to conservation planning (Pressey and Tully 1994);
- species-based approaches that focus on identifying areas of high species richness, endemism or rarity (Williams *et al.* 1996a; Prendergast *et al.* 1993; Reid 1998); and
- approaches that focus on representativeness of the reserve system so that it contains examples of as many elements of biodiversity as possible. This involves exploration of the concept of complementarity, and the process of selecting minimum areas for reserves to maximise representativeness of biota and landscapes (Vane-Wright *et al.* 1991; Pressey *et al.* 1993).

Apart from *ad hoc* approaches, the focus on reservation of areas of high species richness is the most simple, and is pre-eminent outside Australia (Prendergast *et al.* 1998). Locations can be chosen as areas of high species or taxonomic richness or a high richness of rare, threatened or endemic species (Prendergast *et al.* 1993; Williams *et al.* 1996a; Reid 1998). These then become priorities for reservation. Some examples exist in Australia, such as the accumulation of biodiversity data preceding the proclamation of the Wet Tropics World Heritage Area (Keto and Scott 1986). Another is the identification of areas of high conservation value on Cape York Peninsula for a regional land use strategy (Abrahams *et al.* 1995; Winter and Lethbridge 1995).

Reserve selection techniques based on complementarity analysis have received greatest attention and have undergone their primary development in Australia (Margules *et al.* 1988; Bedward *et al.* 1992; Pressey *et al.* 1993). This in part reflects a goal of maximising diversity protection first and foremost (Margules *et al.* 1988). In general the process involves the selection of a minimum sub-set of sites or areas that represents the greatest number of species or landscapes (Bedward *et al.* 1992; Pressey *et al.* 1993). These techniques have evolved from simple scoring procedures (Purdie *et al.* 1986; Pressey and Nicholls 1989a, b) to heuristic (iterative, rule-based) algorithms (Margules *et al.* 1988). Further refinement has included the incorporation of location and cost factors, geographic isolation, phylogenetic diversity and more explicit concepts of irreplaceability (Bedward *et al.* 1992; Nicholls and Margules 1993; Woinarski *et al.* 1996; Ferrier *et al.* 2000). There has been debate regarding the value, use and applicability of the use of reserve selection algorithms (Pressey *et al.* 1996; Prendergast *et al.* 1999; Pressey and Cowley 2000), though their incorporation as one facet of systematic conservation planning is well accepted (Margules and Pressey 2000).

However, where reliable and comprehensive data are not available, there is increasing interest in the value of surrogates or indicator species (Flather *et al.* 1997). The premise is that patterns in species richness, distribution, composition and rarity for well-studied taxa are concordant with similar patterns in other unmeasured and under-studied taxa (Landres *et al.* 1988), so that intensive (and expensive) surveys for all groups are not necessary. The hope, therefore, is that reservation of an area of high richness for one species or group will also reserve an area of high richness for other taxa (Williams *et al.* 1996a). This extends to notions of assemblage fidelity or the possibility that one taxon or an environmental domain can represent the patterns of diversity of other taxa (Faith and Walker 1996; Ferrier and Watson 1997).

The evidence for these expectations and assumptions is mixed. Prendergast *et al.* (1993) examined a range of vertebrate and invertebrate taxon hotspots in Britain and found little concordance, except for ecologically similar taxa (butterflies and dragonflies), and perversely between sites of low and high richness for different taxa. Conversely Ricketts *et al.* (2001) found no relationship between species richness of butterflies (a well known taxon), and moths (a poorly known taxon), and concluded that a habitat-based approach would be more suitable for conserving moths. Finally Lombard (1995) identified generally good concordance between some vertebrate groups (frogs and birds), but not so for many other taxa combinations. There are many more equivocal examples (see reviews Landres *et al.* 1988; Flather *et al.* 1997; Prendergast *et al.* 1998).

In Australia, studies have had similarly equivocal results. In a series of papers examining the relationship between distribution of forest types, vascular plants and lower plant taxa in eastern Australian mixed-use forests a number of patterns were identified. Fern richness was found to be a good predictor of bryophyte and lichen richness (Pharo *et al.* 1999), and vascular plants overall were a useful surrogate for reservation of bryophytes and lichens, despite not all significant sites being captured (Pharo *et al.* 2000). Refined categories of forest management type performed consistently well in predicting total species composition and turnover for all plant taxa, more so than environmental variables (Pharo and Beattie 2001). In an exhaustive study of surrogate evaluation techniques, and the use of biotic data and environmental domains, Ferrier and Watson (1997) also found idiosyncratic patterning. Despite performance similarities for plants and animals, invertebrate assemblage fidelity was poor in relation to other taxa and mapped landscape predictors and abiotic surrogates. Moritz *et al.* (2002) examined concordance in the species and endemic-rich wet tropical rainforest. They detected correlations in the patterns of richness and complementarity between invertebrates, plants and vertebrates, but concluded that diverse, restricted distribution invertebrates such as snails were the best predictors of conservation priorities for higher order taxa. Notably, the relationships were not reciprocal. More recently, detailed pattern analysis of Mitchell Grass Downs also indicated low correspondence between sites of high species richness for various taxa, and higher assemblage fidelity between ants and plants, than those for vertebrates and ants or plants (Fisher 2001a).

The lack of concordance between spatial patterns of species richness in different taxonomic has been attributed to the consequence of scale, as some lower-order taxa may be responding to fine-scale environmental patterns different to those for higher taxa, an effect amplified over geographic distance (Ferrier and Watson 1997). One solution suggested is to use higher taxon levels than species or genera, though the results of doing this have still been mixed (Williams and Gaston 1994). Balmford (1998) and Howard *et al.* (1998) argue that low spatial congruence in patterns of species richness in different groups between sites of high richness of indicator groups does not necessarily mean they have no value in conservation planning. In a detailed survey of Uganda's forest estate, correspondence between species richness in many forest areas was poor, but a proposed reserve system using analogous sites for a single target taxon captured the diversity of other taxa equally well (Howard *et al.* 1998). Common biogeographic patterns between many taxa in these heterogeneous environments were considered to be the cause of their substitutability in conservation planning (Howard *et al.* 1998).

Land classifications are commonly used as the foundation for reserve selection (Pressey 1994a). This is generally due to the widespread availability of historical land system mapping derived for agricultural land capability assessment and the relative ease of mapping and extrapolating vegetation and landscape data from aerial photography and remote images (Accard *et al.* 2001). However the value of land classifications as a surrogate for spatial patterns of biodiversity is uncertain, with few studies examining the direct relationship of fauna distribution to *a priori* classifications (Pressey 1994a). Woinarski *et al.* (1988) identified some correspondence between pre-defined vegetation communities and bird species composition and density in the Northern Territory, though most particularly with the most distinct types (mangroves, closed forest). Subsequent surveys emphasised the significant temporal variation in these woodland bird communities (Woinarski *et al.* 1991; Woinarski *et al.* 1992c), which creates a further variant to the conservation planning process (Woinarski 1999b). Braithwaite *et al.* (1988) also identified variation in density of arboreal species cross different eastern Australian forest types, and as indicated earlier, Pharo and Beattie (2001) concluded that forest types performed well as surrogates in predicting spatial variation in species composition of vascular plants ferns, bryophytes and lichens. Ferrier and Watson

(1997) examined a range of abiotic environmental data and vegetation units as surrogates for fauna, and concluded that mapping of forest types performed the best. Pressey (1994a) suggested that planning based on land classification alone would be enhanced via better examination of its relationship with fauna distribution. However this should not exclude more traditional approaches that target rare and threatened species and critical resources (Pressey 1994a).

A system of land classification fundamentally underpins much of the conservation planning in Queensland (Sattler and Williams 1999). Regional ecosystems and their conservation status (see chapter 1) are used in a legislative capacity for assessing and managing statewide tree-clearing and vegetation management (Neldner *et al.* 2002; Queensland Government 2001). These are also the base unit for prioritising nature conservation efforts either for National Park or off-reserve planning (Sattler and Williams 1999; Neldner *et al.* 2002). Recently a Biodiversity Assessment and Mapping Methodology have been developed to complement the regional ecosystem planning approach (Environmental Protection Agency 2002). Though this still uses the land classification system as the base unit, it explicitly focuses on flora and fauna and supplementary diagnostic criteria that are more relevant to biota. However two disadvantages remain: the inherent and inescapable derivation of methodologies that focus on remnant landscapes, which are poorly applicable to intact areas; and the spectacular lack of primary fauna data across much of northern and western Queensland (see chapter 2). Therefore there is a continued reliance on land classification as a surrogate for capturing all biodiversity, with little evidence that it does this successfully.

Rare and threatened species themselves often carry substantial weight in land-use and reservation decision-making, not the least due to Australia being signatory to international conventions that oblige governments to protect such species (Male 1996). In many cases species of conservation significance partly guide agendas for reserve acquisition (Pressey and Cowling 2001), with those species extremely restricted or threatened being the primary impetus (e.g. Northern Hairy-nosed Wombat *Lasiorhinus krefftii*, Horsup 1996). Federal and state legislation ranks in priority the species for protection or recovery action (e.g. Environment Protection and Biodiversity Conservation Act 1999), and this controls the allocation of scarce funding for conservation programs (Burgman 2000). On the other hand, the protection of threatened species may take precedence in reserve planning over other objective criteria such as representativeness of land types or maximising species diversity (Pressey *et al.* 1994). The irony is that often species considered rare and threatened may be so only due to the lack of data, or natural patterns of restriction, thus channelling resources into biota not necessarily threatened (Burgman 2000). Conversely the protection of charismatic, higher-order species can sometimes have broader biodiversity benefit by ensuring the protection of habitats and suites of species not otherwise afforded protection. Prime examples include agriculturally productive and valuable landscapes, where there may otherwise be little political stimulus for protection (e.g. Mahogany Glider *Petaurus gracilis*, Queensland Government 1995). Unfortunately it is often the case that the urgency to protect threatened landscapes and species can supersede a more balanced approach to plan comprehensive and representative reserves (Burgman 2000; Pressey and Cowling 2001), though the value of this opportunism in protecting wider species assemblages is rarely examined.

In previous chapters I examined aspects of the regional and local patterns of the vertebrate fauna composition and distribution of the Desert Uplands. The inventory of the bioregion's fauna indicated an assemblage that has been shaped by its geographic position, zoogeographical barriers and neighbouring bioregions. There is a pattern of species turnover across the bioregion, dictated by sub-regional affiliation to wet coastal and arid inland bioregions, but also a broad connectivity with other tropical savanna bioregions where open woodlands predominate (chapter 2). It was also identified that where structural and floristic features of the habitat were distinct, the vertebrate fauna composition was similarly characteristic. Conversely, in vegetation types where there was structural and floristic continuity, the vertebrate fauna became less well defined, with subtle environmental variation causing shifts in species abundance and composition (chapter 3). Underpinning the stratification of the sampling was the concept of regional ecosystems, the base land classification unit for Queensland conservation planning (chapter 1). There was evidence that some regional ecosystems have discrete fauna communities, whereas others do not (chapter 3). In this chapter I examine more closely the question of assemblage fidelity between land classification and the biota recorded within them, and the extent to which underlying patterns in the distribution and diversity of vertebrates and plant taxa are represented by the classification of landscapes into distinct regional ecosystems. Using simple reservation scenarios I also investigate the implications of these results for conservation planning in the Desert Uplands. More specifically the questions asked are:

- given regional ecosystems are the primary classification used for conservation planning in the Desert Uplands, do they act as adequate surrogates for vertebrate fauna composition and distribution?;
- following from the above, as greatest planning emphasis is given to the reservation and protection of regional ecosystems of significant status, does this also protect sites of high species richness or vertebrate fauna of conservation significance?;
- apart from *a priori* land classifications, is there assemblage fidelity in the species-richness, distribution and composition of plant and vertebrate taxa, and therefore can some groups be used as adequate surrogates for others?; and
- is there compositional complementarity between species recorded at the quadrat-level? This also allows further investigation of the value of regional ecosystems as a surrogate for diversity of vertebrate fauna, by examining the weighting of regional ecosystems types in each of the minimum sets of quadrats chosen.

I investigate these four primary questions through a series of analyses that include:

- examination of the correspondence between a series of pre-existing land classifications and plant and animal composition using analysis of similarity, and the pattern of ordination of quadrats in respect to regional ecosystem types;
- examination of the fidelity of vertebrate fauna species to regional ecosystem types using a measure of habitat breadth for each species, and the frequency of occurrence of species in each regional ecosystem and the total quadrat sample pool. These data are used to identify species either widespread or restricted to particular regional ecosystem types, and the general patterns for each taxa in regards to habitat breadth;
- examination of the similarities and difference in fauna species richness and habitat breadth between regional ecosystems using analysis of variance;
- examination of the correspondence between significant species richness and abundance with regional ecosystems of conservation significance, also via analysis of variance;

- examination of the variation between vertebrate fauna and plant species assemblages richness and composition using Mantel tests, Spearman rank correlation and hotspot analysis for species richness; and
- examination of the level of complementarity between regional ecosystems, vertebrate fauna and plant taxa using quadrat samples, firstly by comparison of the species richness captured by random selected quadrats against a set constrained to select from the range of regional ecosystems, and then using a simple algorithm, derive a range minimum sets of quadrat sites to capture the diversity of a range of plant and animal taxa. These results are used to assess how representative a set of sites for taxa will be for another. These analyses are also used to examine the relative value of regional ecosystem types in representing the range of species within the bioregion.

Methods

Species data

This chapter utilises the abundance data for the 158 wet season quadrats. Location and sampling methods are as previously described in Chapters 1 and 3. Data used include all vertebrate species and sub-sets of birds, reptiles, mammals, and species of conservation significance, all plant species, plants in the upper strata (>1.5 m in height) and those in the lower strata (<1.5 m in height). Amphibians, microchiropteran bats and introduced species are excluded.

Vertebrate species of conservation significance (EVRs) include those listed under a number of sources. These include:

- the Queensland Nature Conservation Legislation Amendment Regulation (No. 2) 1997;
- the Commonwealth Environmental Protection and Biodiversity Conservation Act 1999;

- the National Action Plans for marsupials and monotremes (Maxwell *et al.* 1996), reptiles (Cogger *et al.* 1993), shorebirds (Watkins 1993), birds (Garnett and Crowley 2000), rodents (Lee 1995), frogs (Tyler 1997) and bats (Duncan *et al.* 1999); and
- species considered being of biogeographic conservation significance in the Desert Uplands bioregion (Morgan *et al.* 2002).

Land classification as a surrogate

Analysis of similarity (ANOSIM, see chapter 3) was used to examine how well a range of classifications (including regional ecosystems), either based on the species composition, conservation status, location, vegetation characteristics and land capability assessment, performed as *a priori* categorisations of species composition. Nine classifications were examined against composition of quadrats by the plant and animal groupings identified above:

- EPA Biodiversity status: conservation status of regional ecosystem as recognised by the Queensland Environmental Protection Agency (Sattler and Williams 1999);
- Land management unit: LMUs categories of land use capability derived from landform, soil and pasture characteristics that determine susceptibility to soil erosion and other forms of land degradation (Morgan *et al.* 2002);
- Landzone: see Chapter 1 (Sattler and Williams 1999);
- Plant groups: these were defined from species cover abundance data for 158 wet season sites, using hierarchical agglomerative clustering produced by the flexible UPGMA routine in PATN (Belbin 1995) and the Bray-Curtis association measures. Thirteen groups were defined from the resultant dendrogram;
- Property: property on which the quadrat was sampled;
- Regional ecosystem: see Chapter 1 (Sattler and Williams 1999);
- Sub-region (Province): see Chapter 1 (Sattler and Williams 1999);
- Vertebrate groups: as derived in Chapter 3; and
- VMA status: conservation status of regional ecosystem as listed in the Queensland Vegetation Management Act 2000.

Vertebrate fauna composition of regional ecosystems

Vertebrate species composition of the quadrats was examined by ordination using semi-strong hybrid multi-dimensional scaling derived from Bray-Curtis association (dissimilarity) indices (Belbin 1995). Ordinations used range-transformed vertebrate abundance data, and only species recorded in more than one quadrat were used. Each quadrat was labelled with regional ecosystem type, and a mean ordination score and standard error (for both axes) was calculated for each regional ecosystem. The group centroid and standard error whiskers are presented in the ordination space to indicate the patterns of overlap and distinctiveness of the fauna composition of the quadrats of each regional ecosystem type.

For species recorded in three or more quadrats, I tabulated the total number of quadrats and number of regional ecosystems in which it was recorded. A measure of the range of use of regional ecosystem types (habitat breath) was also calculated for each species using the following equation:

$$B(x) = 1/\Sigma p_i^2$$

where B is the habitat breadth of species x and p_i is the proportion of the species found in regional ecosystem i (Levins 1968). A low habitat breadth score indicates that a species was recorded in high abundances in one or very few of the regional ecosystem types, and a high score indicate a species recorded equally across a wide range of types. The distribution of habitat breadth scores for each vertebrate taxon (all vertebrates [= verts], birds, mammals [=mamm] and reptiles [=rept]) was plotted for nine categories: species with a score of B=1, indicating restriction to a single regional ecosystem type; through to species where B>10 indicating a widespread species.

The pattern of restricted and widespread species was further illustrated by plotting for each taxon (birds, reptiles and mammals), the relationship between the number of regional ecosystems and the number of quadrats for each species recorded, and identifying the line of best fit. Labelling selected species on the resultant scatter-plot indicates those species recorded frequently and in a wide or small range of regional ecosystems, and those recorded less frequently, again either being widespread or restricted in regional ecosystems preference. As the number of quadrats sampled is much higher than the number of regional ecosystems sampled, one would expect a logarithmic relationship. Species recorded in only a single regional ecosystem irrespective of the number of quadrats they were recorded were tabulated separately.

As a supplementary measure of habitat fidelity, the distribution of species in three broad habitat groups (*Eucalypt*, *Acacia* and grasslands) was examined. The sum of abundance for each species within each group was calculated, and then divided by the total abundance to give a relative association with habitat type.

The variation in average habitat breadth scores and species richness of vertebrates, birds, reptiles, mammals and EVR species for each regional ecosystems was examined using parametric one-way analysis of variance. Those groups significantly different were identified using a *post hoc* test (Student- Kuels-Newman, SKN), and these results were used to order regional ecosystems in ascending mean richness and habitat breadth.

Correspondence between regional ecosystems and species of conservation significance

There exist three categories of status for regional ecosystems: not of concern (>30% of its pre-clearing extent remaining); of concern (10-30% of its pre-clearing extent remaining); and endangered (<10% of its pre-clearing extent remaining). There are two differing interpretations of status. Firstly those as recognised by the Queensland Environmental Protection Agency that includes additional criteria such as threatening processes (e.g. clearing), susceptibility to land degradation as well as simple areal extent (Sattler and Williams 1999). Secondly, those as listed in the Queensland Vegetation Management Act 2000, in which conservation status is purely a factor of percentage of area remaining. The abundance of species of conservation significance within the three categories of regional ecosystem conservation status was compared using Kruskal-Wallis tests, though only species recorded in three or more quadrats were analysed. Variability of total species richness of vertebrates, birds, reptiles, mammals and EVR species in these categories was examined using parametric analysis of variance and *post hoc* tests. The intention was to examine whether there was any correspondence between regional ecosystems of high conservation value, which are generally a priority for protection, and both vertebrate species of high conservation value (EVRs) and quadrats of high species richness.

Correspondence between site species richness

Spearman rank correlations were calculated between quadrat richness of vertebrates, birds, reptiles, mammals, EVR species, all plants, upper strata plants and ground strata plants to examine simply how well species richness for different taxa at each site correspond. A low correlation between quadrat richness of different taxa across all sample sites may hide the fact that a small number of species-rich sites are shared (Fisher 2001a). In this case, the top 20 species rich sites for each taxon were also identified, and the number of species-rich quadrats in common for each pair of taxa was tabulated as a frequency. The relationship between total EVR and vertebrate species richness was also examined via correlation.

Correspondence between site species composition

The correspondence between plant and fauna composition was examined via Mantel type permutation tests (Legendre and Legendre 1998) using RELATE in Primer, (Clarke and Gorley 2001). Standardised Bray-Curtis dissimilarity matrices derived from abundance data were used, and the significance of the rank correlation coefficient was tested by permutation (n=999) of the matching coefficients (see Chapter 3). A high correlation indicates a high level of assemblage fidelity. Comparisons were made between vertebrates, birds, reptiles, mammals, EVRs, all plants, upper and groundcover species. The correlation coefficients were tabulated as an association matrix for a simple 2-dimensional ordination (MDS in Primer), and the distance between taxa represents the level of fidelity between taxa. It should be noted that for species poor groups (e.g EVR, mammals, reptiles), there are a number of quadrats in the array that have no target species recorded within them, and therefore a dissimilarity matrix could not be derived. As a solution, an additional "species" was added to the array (e.g. No EVRs present), and the quadrat was scored as "1" for this column.

Complementarity: regional ecosystems versus random selection

The strength of regional ecosystems as a surrogate for vertebrate fauna composition and species richness was further tested using a simple selection procedure that chooses a sub-set of quadrats from the entire pool of sites by two methods: at random; and a selection also at random, but constrained to sample the entire range of regional ecosystem types. If regional ecosystem area is a useful surrogate for species composition, selecting sites using this classification system should provide a more representative sample of the regional species pool than if sites were selected at random.

As some regional ecosystems were sampled more frequently than others, these types may be over-represented in the random sampling, and hence the random sample may result in having fewer species selected. Therefore all over-represented regional ecosystems were reduced in the number of quadrats to a maximum of six (all other regional ecosystems already having between two and six quadrats sampled). Therefore four trials were undertaken for comparison:

1. selection of 28 quadrats (as there are 28 regional ecosystems sampled) at random (note that random selections are made without replacement - that is they couldn't include the same quadrat twice in any selected set);
2. selection of 28 sites constrained to be one from each regional ecosystem, but randomly within regional ecosystems;
3. selection of 56 sites at random; and
4. selection of 56 sites constrained to be two from each regional ecosystem, but randomly within regional ecosystems.

Each trial was run a total of 50 times, and from these results the mean number (and standard error) of species represented in the selected set was calculated and plotted. Trials were conducted for all plant and animal species combined, all vertebrates, birds, mammals, reptiles, all plants, upper storey plants and ground cover plants.

Complementarity: minimum sets for sites

The concept of minimum set analysis generally involves the derivation of the smallest number of sites (quadrats) that contain a specified number of replicates of all species (Margules *et al.* 1988). This process was undertaken using an iterative, heuristic algorithm based on rarity (Margules *et al.* 1988; Fisher 2000), rather than one based on site richness, as rarity-based algorithms are considered more efficient (Csuti *et al.* 1997). Though these heuristic algorithms are thought less valuable than linear programming methods in that they may not guarantee an optimal result, they have the advantages of simplicity and efficiency (Belbin 1993, 1995; Fisher 2001a).

Initially the frequency of each species in the entire set of quadrat sites was calculated. The process of selecting sites via iteration then began with the site containing the species with the lowest frequency (the rarest) of unreserved species. All species represented in this site were considered “reserved” and were removed from the sites remaining in the data set. The frequency of each remaining species was recalculated and the selection process repeated. Iterations continued until all taxa were “reserved”. The cumulative number of species reserved at each step was recorded. A hierarchical set of rules was used to resolve ties in the selection process:

1. select the site with the lowest frequency (rare) unreserved species;
2. select the site with the greatest number of lowest frequency (rare) unreserved species;
3. select the site with the greatest number of lowest frequency (rare) unreserved species of recorded conservation significance;
4. select the site with the largest number of (rare) unreserved species;
5. select the first site in the list.

The selection process was repeated to select minimum sets of sites that represented all vertebrates, birds, reptiles, mammals, all plants, upper strata plants and ground strata plants. In each case the accumulation of all other taxa was monitored so representation of any taxa at any target level (e.g. 50%) could be assessed. Minimum sets were developed using all sites and comparisons of reservation of other taxa with target taxa at the 100% selection level only are tabulated. Species accumulation curves for minimum set selection for birds, reptiles, mammals, species of conservation significance, upper strata plants and ground strata plants are presented, including the corresponding accumulation of other taxa.

The relative importance of regional ecosystem types in the minimum set selection for each species was examined by identifying the sites selected by their classification. From this the percentage of sites that were from that regional ecosystem type was calculated.

Results

Species data

A total of 227 vertebrate fauna species comprising 119 birds, 22 mammals, 75 reptiles and 11 amphibians were recorded from the 158 wet season samples (Table 4.15). The numbers of quadrats in which each species was recorded and the mean quadrat abundance per regional ecosystem are also presented in Table 4.15. Twenty-three species were of conservation significance (EVRs): nine birds, seven mammals and seven reptiles (Table 4.1). Furthermore a total of 364 plant species were identified from the quadrats, comprising 101 upper strata species and 263 ground strata species (species not tabulated).

Table 4.1 Species conservation significance comprising the EVR data set. Status sources: EPBC = Commonwealth Environment Protection and Biodiversity Conservation Act 1999, QNC = Queensland Nature Conservation Act (Wildlife) 1994, AP = Environment Australia Action Plans, QM = Queensland Museum status (Ingram and Raven 1991), DEU = considered to be of bioregional significance. Status codes are: E = Endangered, V = Vulnerable, R = Rare, RK = rare or insufficiently known, NT = near threatened, B = bioregional significance (Morgan *et al.* 2002).

Species	EPBC	QNC	AP	QM	DEU
Birds					
Australian Bustard			NT		
Black-chinned Honeyeater		R	NT		
Black-throated Finch		V	V	R	
Brown Treecreeper			NT		
Bush Stone-Curlew			NT		
Grey-crowned Babbler			NT		B
Hooded Robin			NT		
Spinifexbird					B
Squatter Pigeon		V	NT		
Mammals					
Aepyprymnus rufescens			NT		
Lagorchestes conspicillatus			NT		
Leggadina lakedownensis				RK	
Pseudomys desertor			RK		B
Pseudomys patrius				RK	
Sminthopsis douglasi	E	E	E	RK	
Trichosurus vulpecula			NT		
Reptiles					
Ctenotus capricorni		R	RK	RK	
Ctenotus rosarium					B
Lerista sp nov					B
Lerista wilkinsi		R	RK	RK	
Paradelma orientalis		V	V	V	
Simoselaps warro		R	RK	RK	
Tiliqua multifasciata					B

Land classification as a surrogate

Almost all land classifications identified significant differences in the vertebrate and plant assemblage compositions (Table 4.2). The strongest relationships were between regional ecosystem categories and vertebrates, birds, reptiles, plants, upper strata and ground strata ($r>0.6$), and naturally for the plant and vertebrate groups derived from the hierarchical clustering (plant and vertebrate groups and vertebrate, bird, reptile, plants, upper and ground strata all $r>0.5$). Both land zones (which represent broad geomorphic and geological features), and sub-regions (which reflect broad geographic location), performed poorly in distinguishing assemblage differences, whereas property location identified strong assemblage fidelity. Land management units, which are an amalgam of regional ecosystems, predicted plant assemblage differences well. No classification system identified a strong relationship with mammals or EVR species (all $r<0.4$) and both the EPA and VMA conservation status categories performed extremely poorly (all $r<0.2$ and generally not significant), other than for the plant groups.

Table 4.2 Analysis of similarity between land classifications and vertebrate fauna taxa and plant groups. n = the number of classes in the classification. Data represents the Global R statistic. Probability levels are *$p<0.05$, **$p<0.01$, ***$p<0.001$, ns = not significant.

Classification	n	Verts	Bird	Mamm	Rept	EVR	Plants	Upper	Ground
EPA status	3	0.189***	0.184***	0.05 ns	0.203***	0.002 ns	0.407***	0.406***	0.162***
LMU	15	0.476***	0.455***	0.265***	0.41***	0.225***	0.622***	0.56***	0.522***
Landzone	5	0.156***	0.143***	0.148***	0.151***	0.158***	0.279***	0.274***	0.194***
Plant groups	13	0.601***	0.567***	0.39***	0.561***	0.31*	0.893***	0.808***	0.649***
Property	14	0.577***	0.422***	0.356***	0.432***	0.245***	0.6***	0.578***	0.407***
Regional ecosystem	28	0.716***	0.629***	0.384***	0.603***	0.366***	0.902***	0.809***	0.778***
Sub-region	3	0.149***	0.105**	0.114**	0.102**	0.041**	0.069**	0.028 ns	0.108***
Vert groups	13	0.726***	0.728***	0.343***	0.496***	0.219***	0.71***	0.641***	0.532***
VMA status	3	0.111 ns	0.152*	0.1*	0.06 ns	-0.008 ns	0.344***	0.286***	0.136*

Vertebrate fauna composition of regional ecosystems

The ordination of all quadrats by vertebrate species composition identified a moderate degree of group definition when illustrated with regional ecosystem type. There is high degree of overlap for open woodland vegetation communities, in the central ordination space (Figure 4.1), and the inter-connectivity and the subtle variation and turnover in vertebrate species composition in these types has been discussed in chapter 3. However many of these groups are still tightly defined as evidenced by the low standard error.

Other groups, which are generally structurally more simple (grasslands and heath regional ecosystems 37, 322, 329, 77, 323, see descriptions in Table 4.3) and species-poor, are clearly more disparate and unique in composition, though this is partly an artefact of variation within quadrats with very few species.

Figure 4.1 Two-dimensional ordination of quadrats by fauna composition. Ordination used semi-strong hybrid multi-dimensional scaling (stress = 0.32), and Bray-Curtis dissimilarity indices. Data were standardised and species recorded in only one quadrat were removed from the analysis. Number indicates regional ecosystem group centroid and whiskers the standard error.

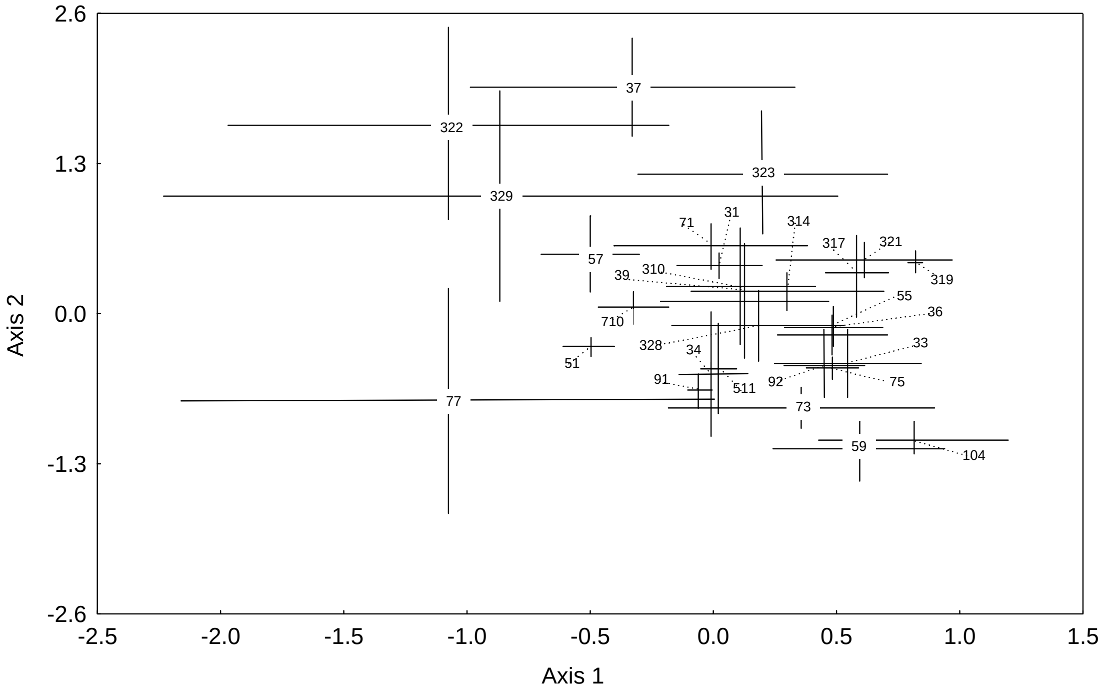


Table 4.3 Regional ecosystem codes and short descriptions. Information derived from Sattler and Williams (1999).

Code	Description
104	*Corymbia leichhardtii*, *E. exilipes,* or *C. lamprophylla* on sandy soils.
31	*Acacia argyrodendron* woodland on clays
310	*Corymbia dallachiana* and/or *Corymbia plena* on sandy alluvial soil.
314	*Eucalyptus coolabah* and *E. camaldulensis* on alluvial soils.
317	*Acacia excelsa* and *Grevillea striata*. on weathered sand dunes.
319	*Acacia cambagei* on duplex soils on lake-fringing dunes.
321	*Acacia salicina* and *Grevillea striata* on weathered sand dunes.
322	Shrubland of *Lawrencia buchananensis*, *Halosarcia* spp on alluvial flats and old dunes.
323	Shrubland *Halosarcia* spp or *Acacia stenophylla* on alluvial flats and clays
328	*Eucalyptus melanophloia* on yellow earths.
329	Hummock grassland of *Triodia longiceps*.
33	*Eucalyptus cambageana*, *Acacia harpophylla* or *A. argyrodendron* woodland on clays
34	*Acacia cambagei* woodland on clays.
36	*Eucalyptus brownii* on alluvial plains.
37	Tussock grassland on gravelly clays.
39	*Eucalyptus whitei* on sandy alluvial soil.
51	*Eucalyptus similis* usually with *Corymbia brachycarpa* on deep red sands.
511	*Eucalyptus whitei* on red sandy soil.
55	*Eucalyptus melanophloia* on loam to sandy clay soils.
57	*Grevillea striata*, *G. parallela* and *Acacia coriacea* on sandplains.
59	*Eucalyptus quadricostata* and usually *Corymbia erythrophloia* on red sands.
71	*Eucalyptus whitei* and *Corymbia dallachiana* on shallow gravelly sandy soil.
710	*Eucalyptus whitei* and *Corymbia setosa* on shallow gravelly sandy soil.
73	*Acacia shirleyi* or *A. catenulata* on skeletal sandstone soils.
75	*Eucalyptus thozetiana* on colluvial fans and slopes.
77	Shrubland of *Melaleuca* spp, *Acacia* spp and *Thryptomene parviflora* on shallow soils.
91	*Acacia argyrodendron* on clays.
92	*Acacia cambagei* +/- *Eucalyptus thozetiana* or *E. cambageana* on clays.

Table 4.4 lists all fauna species recorded in more than one quadrat, and the number of quadrats and regional ecosystems in which each of these species was recorded, as well as its habitat breadth. Seven species that were recorded from three or more quadrats were restricted to one regional ecosystem (B=1): Hooded Robin (RE 51); Spinifexbird (RE 329); Rufous-throated Honeyeater (RE 710); *Rattus villosissimus* (RE 37); *Sminthopsis douglasi* (RE 37); *Delma tincta* (RE 37); and *Diplodactylus tessellatus* (RE 31). Most of these regional ecosystems are the species-poor and structurally simple grassland types, but also include the widespread woodlands on deep red earths (RE 51 and 710).

Other species were also less catholic in their habitat (1<B>3), and many of these could be loosely grouped into functional guilds linked to particular resources or substrates provided by a regional ecosystem type, as follows:

- hummock and tussock grasslands (RE’s 37, 329, 323 and Australian Bustard, Red-chested Button-Quail, White-winged Fairy-wren, Richard's Pipit, *Tympanocryptis lineata*);

- deep, sandy soils (RE's 51, 710 and *Simoselaps australis*, *Ctenotus rosarium*);
- communities with sparse ground cover and outcropping rock (RE's 73, 104 and *Pseudomys patrius*, *Nephrurus asper*);
- communities with trees that have ample exfoliating bark (RE's 36, 91, 92, 317, 73 and *Gehyra dubia*, *Gehyra variegata*, *Oedura marmorata*);
- communities with large hollow-bearing trees (RE's 314, 36 and *Trichosurus vulpecula*, *Petaurus breviceps*); and
- communities with high ground cover (RE's 39, 71 and *Lagorchestes conspicillatus*).

Conversely, fauna that were recorded from a broad habitat range (B>10) were represented by ubiquitous species with extensive northern Australian distributions. Most of these species are nominally disturbance-tolerant or increaser species (Landsberg *et al.* 1997; Fisher 2001a), and common also in semi-rural and urban environments. These species typically have simple habitat requirements and examples include reptiles (*Heteronotia binoei*, *Diplodactylus steindachneri* and *Menetia greyii*), mammals (*Macropus rufus*), and birds (Crested Pigeon, Willie Wagtail, Little Friarbird, Australian Raven, Yellow-throated Miner, Jacky Winter, Rufous Whistler, Magpie-Lark, Grey Shrike-Thrush, Weebill, Black-faced Cuckoo-shrike, Australian Owlet-nightjar, Australian Magpie and Pied Butcherbird).

Table 4.4 Habitat breadth of vertebrate fauna from at least three quadrats. The table also shows the total number of quadrats and the total number of regional ecosystems in which the species was recorded. Frequency of species recorded in three broad habitat groups (Eucalypt %E, Acacia %A and grassland %G) regional ecosystems is also tabulated.

Species	No. quadrats	No. reg. eco.	B	%A	%E	%G
n of quadrats and % of total				38 (24%)	102 (65%)	18 (11%)
BIRDS						
Apostlebird	25	13	8.9	63.8	32.1	4.1
Australian Bustard	5	4	2.2	0	25.0	75.0
Australian Magpie	87	25	17.2	50.2	42.7	7.2
Australian Owlet-nightjar	99	20	16.8	41.0	59.0	0
Australian Raven	43	18	11.0	25.5	54.9	19.6
Barn Owl	10	4	3.6	33.3	66.7	0
Black-faced Cuckoo-shrike	74	23	16.7	43.8	51.5	4.7
Blue-faced Honeyeater	8	8	6.1	81.9	6.0	12.1
Black-faced Woodswallow	22	7	5.4	15.2	74.1	10.7
Black-shouldered Kite	3	2	1.7	0	100.0	0
Blue-winged Kookaburra	14	8	5.6	56.6	43.4	0
Brown Falcon	20	9	7.4	73.1	21.2	5.8
Brown Goshawk	4	4	3.5	66.7	33.3	0
Brown Honeyeater	19	11	5.5	29.9	68.3	1.8
Brown Quail	4	2	1.6	0	100.0	0
Brown Treecreeper	16	7	4.6	28.6	71.4	0

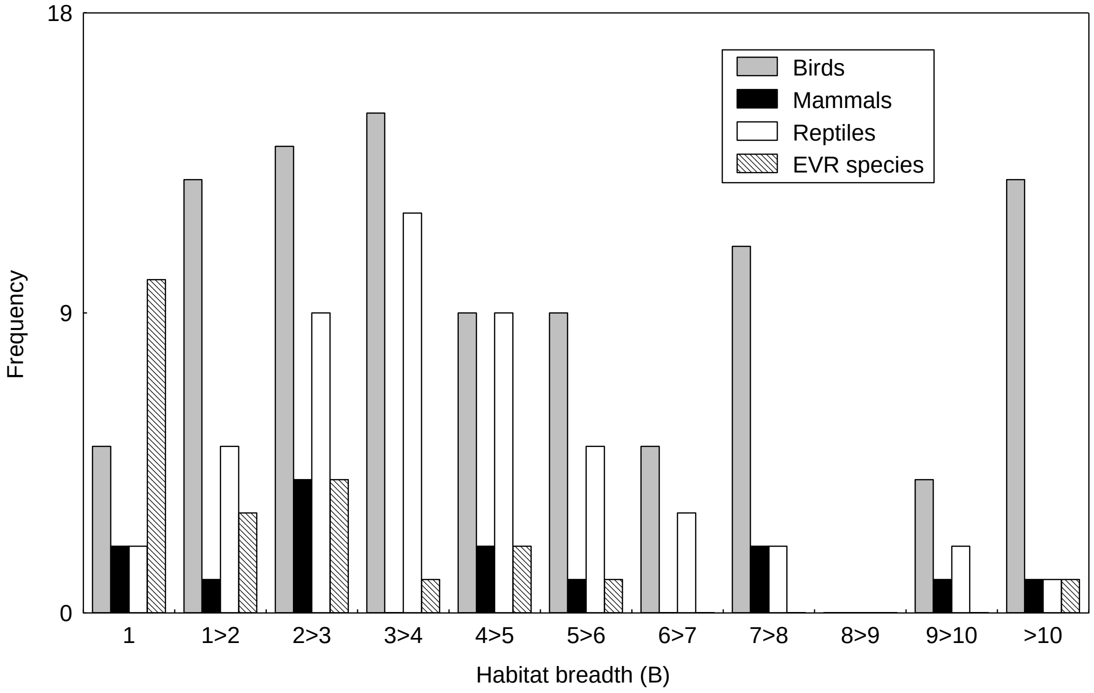
Species	No. quadrats	No. reg. eco.	B	%A	%E	%G
Buff-rumped Thornbill	7	6	4.8	75.6	24.4	0
Channel-billed Cuckoo	7	5	3.1	12.5	87.5	0
Chestnut-rumped Thornbill	4	3	1.6	19.7	80.3	0
Cockatiel	22	12	7.4	63.6	25.9	10.5
Collared Sparrowhawk	3	2	1.7	100.0	0	0
Common Bronzewing	31	12	6.3	35.4	64.6	0
Crested Bellbird	65	14	7.5	13.3	86.7	0
Crested Pigeon	36	15	10.7	53.4	41.5	5.2
Diamond Dove	15	8	4.9	24.2	75.8	0
Double-barred Finch	9	7	4.1	28.7	71.3	0
Dollarbird	7	3	1.8	14.3	85.7	0
Emu	16	12	6.6	56.5	29.4	14.1
Galah	39	19	9.3	31.8	54.3	13.9
Grey-crowned Babbler	49	20	12.8	48.7	46.9	4.4
Grey Butcherbird	63	21	14.0	49.2	49.6	1.3
Grey Fantail	3	3	2.8	40.0	60.0	0
Grey Shrike-Thrush	59	18	13.3	45.7	54.3	0
Grey-fronted Honeyeater	4	3	1.6	0	100.0	0
Ground Cuckoo-shrike	6	6	5.2	20.3	32.8	46.9
Hooded Robin	6	1	1.0	0	100.0	0
Horsfield's Bronze-Cuckoo	26	7	5.5	20.7	79.3	0
Jacky Winter	66	15	11.7	36.6	63.5	0
Laughing Kookaburra	8	7	4.5	79.3	20.8	0
Little Button-Quail	7	4	3.6	0	46.7	53.3
Little Friarbird	55	19	10.4	52.4	47.6	0
Little Woodswallow	16	4	3.1	0	100.0	0
Magpie-Lark	55	19	13.1	62.4	30.4	7.2
Masked Woodswallow	5	2	1.1	0	100.0	0
Mistletoebird	32	13	7.0	76.9	15.4	7.7
Nankeen Kestrel	12	9	5.2	34.0	6.4	59.6
Noisy Friarbird	50	16	9.5	35.7	58.8	5.5
Olive-backed Oriole	17	10	7.7	34.7	65.3	0
Pale-headed Rosella	26	14	8.5	48.4	51.6	0
Painted Button-Quail	6	3	2.5	46.7	53.3	0
Pallid Cuckoo	29	7	3.7	10.0	90.0	0
Peaceful Dove	37	12	8.7	41.7	56.1	2.2
Pheasant Coucal	9	6	3.7	44.4	44.4	11.1
Pied Butcherbird	110	24	19.4	43.6	53.4	3.0
Pied Currawong	8	4	3.1	50.0	50.0	0.0
Rainbow Bee-eater	25	9	7.1	11.5	88.5	0.0
Rainbow Lorikeet	7	6	3.4	24.3	54.3	21.4
Red-backed Fairy-wren	13	6	4.1	20.8	68.8	10.4
Red-backed Kingfisher	19	6	5.2	0	100.0	0
Red-browed Pardalote	13	3	2.7	0	100.0	0
Red-chested Button-Quail	5	3	2.4	10.0	40.0	50.0
Red-tailed Black-Cockatoo	3	3	1.2	0	100.0	0
Red-winged Parrot	30	16	9.0	57.8	40.6	1.6
Richard's Pipit	7	3	2.0	0	0	100.0
Rufous Songlark	4	4	3.2	38.1	61.9	0
Rufous Whistler	94	20	12.9	28.0	71.3	0.7
Rufous-throated Honeyeater	3	1	1.0	0	100.0	0
Sacred Kingfisher	17	11	6.4	15.5	79.3	5.2
Shining Bronze-Cuckoo	4	4	3.4	0.0	100.0	0.0
Singing Honeyeater	62	15	9.8	42.0	58.1	0.0
Southern Boobook	36	15	8.9	42.0	58.0	0.0
Spiny-cheeked Honeyeater	28	13	9.2	19.3	67.0	13.8
Spinifexbird	4	1	1.0	0.0	0.0	100.0
Spotted Bowerbird	14	10	5.6	35.6	64.4	0.0
Spotted Nightjar	16	8	6.6	24.1	55.2	20.7

Species	No. quadrats	No. reg. eco.	B	%A	%E	%G
Squatter Pigeon	7	5	3.8	20.4	79.6	0
Striped Honeyeater	44	15	8.9	62.8	37.2	0
Striated Pardalote	50	16	9.0	44.6	55.4	0
Sulphur-crested Cockatoo	11	7	3.5	25.5	29.4	45.1
Tawny Frogmouth	20	11	7.7	48.8	51.2	0
Torresian Crow	20	10	7.6	40.9	38.0	21.1
Variegated Fairy-wren	25	12	7.4	45.8	51.0	3.2
Varied Sittella	9	5	4.0	35.1	64.9	0
Weebill	51	18	13.9	27.4	72.6	0
Western Gerygone	10	4	3.7	0	100.0	0
Wedge-tailed Eagle	6	4	3.8	0	78.6	21.4
White-bellied Cuckoo-Shrike	5	4	2.3	33.3	66.7	0.0
Whistling Kite	3	3	2.9	37.5	37.5	25.0
White-plumed Honeyeater	5	2	1.2	0	100.0	0
White-throated Gerygone	3	3	1.6	0	100.0	0
White-throated Honeyeater	6	2	1.1	0	100.0	0
White-winged Fairy-wren	3	3	2.6	0	0	100.0
White-winged Triller	12	3	2.7	0	100.0	0
Willie Wagtail	58	18	10.3	55.5	38.7	5.8
Yellow-Rumped Thornbill	26	11	8.2	42.9	57.1	0.0
Yellow-throated Miner	63	20	11.5	47.5	51.1	1.4
Zebra Finch	3	2	1.9	0.0	100.0	0.0
MAMMALS						
Lagorchestes conspicillatus	4	3	2.6	0	100.0	0
Macropus giganteus	79	17	9.8	43.9	38.2	17.9
Macropus robustus	50	14	7.9	67.3	32.7	0
Macropus rufus	56	20	10.8	49.5	38.6	11.9
Petaurus breviceps	3	3	2.6	42.9	57.1	0
Planigale maculata	5	3	2.8	21.4	78.6	0
Pseudomys delicatulus	41	13	4.9	5.3	92.4	2.3
Pseudomys desertor	46	13	4.7	14.1	63.5	22.4
Pseudomys patrius	5	3	2.7	50.0	50.0	0
Rattus villosissimus	3	1	1.0	0	0	100.0
Sminthopsis douglasi	3	1	1.0	0	0	100.0
Sminthopsis macroura	39	13	7.5	23.9	52.1	23.9
Tachyglossus aculeatus	28	8	5.2	36.7	63.3	0
Trichosurus vulpecula	6	3	1.7	0	100.0	0
REPTILES						
Amphibolurus gilberti	7	5	3.6	60.0	40.0	0
Amphibolurus nobbi	31	9	6.0	40.3	59.7	0
Carlia munda	24	9	3.7	2.4	93.9	3.7
Carlia pectoralis	3	2	2.0	100.0	0	0
Carlia schmeltzii	3	2	1.4	0	100.0	0
Cryptoblepharus carnabyi	14	8	4.0	13.0	87.0	0
Cryptoblepharus plagiocephalus	15	9	3.2	87.6	4.1	8.3
Ctenotus capricorni	25	2	2.0	0	100.0	0
Ctenotus hebetior	54	13	5.8	54.2	43.8	2.0
Ctenotus ingrami	4	4	3.6	33.3	66.7	0
Ctenophorus nuchalis	19	9	7.2	37.1	31.4	31.4
Ctenotus pantherinus	28	8	5.3	20.3	64.1	15.6
Ctenotus robustus	13	6	4.0	0	66.7	33.3
Ctenotus rosarium sp nov	14	2	1.3	0	100.0	0
Ctenotus spaldingi	14	6	4.2	5.4	94.6	0
Ctenotus strauchii	17	10	5.5	27.3	72.7	0
Delma tincta	3	1	1.0	0	0	100.0
Demansia psammophis	4	3	2.3	60.0	40.0	0
Diplodactylus ciliaris	5	3	2.3	41.7	58.3	0
Diplodactylus conspicillatus	21	9	4.1	17.3	82.7	0
Diplodactylus steindachneri	49	17	11.5	37.5	60.7	1.8

Species	No. quadrats	No. reg. eco.	B	%A	%E	%G
Diplodactylus tessellatus	3	1	1.0	100.0	0.0	0.0
Diplodactylus vittatus	5	3	3.0	61.1	38.9	0.0
Diplodactylus williamsi	15	7	4.8	8.8	82.4	8.8
Diporiphora australis	11	3	2.0	0	100.0	0
Egernia striolata	14	7	3.0	96.6	3.5	0
Gehyra catenata	28	12	7.2	92.3	3.1	4.6
Gehyra dubia	14	4	2.3	71.4	28.6	0
Gehyra variegata	11	7	2.8	85.6	14.4	0
Heteronotia binoei	52	19	10.5	49.7	50.3	0
Lerista muelleri	14	8	4.6	63.8	36.2	0
Lerista punctatovittata	13	7	4.4	35.0	65.0	0
Lialis burtonis	16	6	5.1	0	100.0	0
Menetia greyii	52	13	10.7	12.8	77.4	9.8
Menetia timlowi	6	4	3.3	50.0	50.0	0.0
Morethia boulengeri	12	8	4.8	82.2	11.0	6.9
Morethia taeniopleura	6	2	1.6	75.0	25.0	0
Nephrurus asper	4	3	2.7	56.3	43.8	0
Oedura castelnaui	8	6	4.8	34.3	65.7	0
Oedura marmorata	5	2	2.0	50.0	50.0	0
Oedura rhombifer	4	4	3.3	0	100.0	0
Pogona barbata	36	16	9.6	60.0	40.0	0
Proablepharus tenuis	24	11	6.2	2.5	97.5	0
Pseudonaja nuchalis	4	4	3.4	81.3	18.8	0
Pygopus nigriceps	15	9	6.5	51.6	48.4	0
Rhynchoedura ornata	17	4	3.1	0	100.0	0
Simoselaps australis	4	2	1.6	0	100.0	0
Suta suta	10	6	5.1	38.9	16.7	44.4
Tiliqua scincoides	5	4	3.3	42.9	57.1	0
Tympanocryptis lineata	5	2	1.6	0	0	100.0
Varanus gouldii	7	4	3.3	0	57.1	42.9
Varanus tristis	33	12	9.9	22.8	77.2	0

The pattern of frequency of species in eleven habitat breadth categories indicated a variation in pattern across taxa, though generally a slightly right-skewed relationship with highest number of species within the intermediate categories where B>1 but < 8 (Figure 4.2). Birds have some peaks in the lower (B=1-4) and higher habitat breadth categories (B=7-8, B>10). The pattern for reptiles is approximately normal with a clear peak between B=2-5, whereas mammals demonstrate the least consistency, with equal numbers of species in the low, intermediate and high categories. The EVR counts included all species rather than just those recorded in three or more quadrats, and identifies a very strong right skew. Though it is recognised that a single quadrat result is possibly not ideal for assessing habitat breadth, the presumption is made that EVR species are by nature uncommon and infrequently recorded. As such the pattern does have some ecological standing in that EVR species are often restricted to specific habitat types, and therefore a habitat breadth tending to the lower scores.

Figure 4.2 Frequency distribution of habitat breadths for all vertebrate taxa. Columns represent the number of species in each habitat breadth (B) group. 1>2 indicates B > 1, but < 2, 2>3 indicates B is >= 2, but < 3 and so on. Only species recorded in three or more quadrats are included, except for EVR species, which includes all species.



As a supplementary measure of habitat breadth, the degree of fidelity to three broad habitat types (*Acacia*, *Eucalyptus* and grassland) was calculated by identifying the proportion of species in regional ecosystems within these categories, compared to the total abundance (Table 4.3). A total of 38 *Acacia*, 102 *Eucalyptus* and 18 grassland quadrats were sampled, representing 24%, 65% and 11% respectively of the total sampled. This provides an indication whether a species, if restricted for example to *Eucalyptus* woodlands, is either widespread (high habitat breadth score) or restricted (low habitat breadth score) within this group. As may have been expected, there is a range of species strongly affiliated to these habitat types. For example of the quadrats in which Collared Sparrowhawk, Blue-faced Honeyeater, *Carlia pectoralis*, *Cryptoblepharus plagiocephalus*, *Diplodactylus tessellatus*, *Gehyra catenata*, *Egernia striolata* were recorded, greater than 80% were *Acacia* sites. Hooded Robin, Grey-fronted Honeyeater, Red-backed Kingfisher, Red-browed Pardalote, Pallid Cuckoo, White-winged Triller, *Lagorchestes conspicillatus*, *Trichosurus vulpecula*, *Carlia munda*, *Lialis burtoni* and *Rhynchoedura ornata* occurred exclusively in *Eucalypt* quadrats. A similar situation occurred for Richards Pipit, Spinifexbird, White-winged Fairy-wren, *Rattus villosissimus*, *Sminthopsis douglasi*, *Delma tincta* and

Tympanocryptis lineata in grassland habitats. Only three out of 124 species (2% of total) were recorded only from the *Acacia* quadrats, whereas 27 out of 153 species (18%) were recorded in *Eucalyptus* communities and seven out of 64 species (11%) only in grassland communities.

A number of species were equally distributed across two groups. The following species, Australian Owlet-nightjar, Pied Butcherbird, Crested Pigeon, Grey-crowned Babbler, Yellow-throated Miner, *Petaurus breviceps*, *Amphibolurus nobbi*, *Ctenotus hebetior*, *Diplodactylus ciliaris, Pygopus nigriceps* and *Tiliqua scincoides*, occurred in similar frequency in *Acacia* and *Eucalypt* quadrats. Very few animals ranged equitably across all types (e.g. Sulphur-crested Cockatoo, *Macropus giganteus*, *M. rufus*, *Sminthopsis macroura*, *Suta suta*). Furthermore, some species with a high fidelity to a broad habitat group ranged widely across regional ecosystems (*Gehyra catenata*, 12 REs, 92% *Acacia*, *Proablepharus tenuis* 11 REs, 97% *Eucalypt*), whereas others were more restricted (*Egernia striolata*, 7 REs, 96% *Acacia*; *Lialis burtoni*, 6 REs, 100% *Eucalypt*).

The relationship between the number of regional ecosystems and the number of quadrats a species was recorded in illustrates a consistent logarithmic pattern for all three taxa (Figure 4.3a-d). Generally there are more birds recorded frequently across a wide range of regional ecosystems, while for reptiles, species have a greater tendency to be recorded frequently, but in fewer regional ecosystems. This suggests stricter habitat association. The relationship for mammals is intermediate between birds and reptiles.

The patterns for individual species reinforce those described for habitat breadth, but also neatly illustrate those species that are frequently recorded and wide-ranging across many regional ecosystems (typically above the fitted curve), and those wide-ranging but consistently recorded in fewer regional ecosystems (below the fitted curve). Examples in the former category are species such as Australian Magpie, Yellow-throated Miner, Galah, *Macropus giganteus*, *Pogona barbata*, *Ctenotus hebetior*, and in the latter group Singing Honeyeater, Australian Owlet-nightjar, *Pseudomys desertor*, and *Amphibolurus nobbi*. These graphs also highlight that many species that are prevalent in tropical savanna woodlands across northern Australia are neither overtly widespread nor restricted to particular regional ecosystem types. Examples include Apostlebird, Yellow-rumped Thornbill, Peaceful Dove, Varied Fairy-wren, *Sminthopsis macroura*, *Pseudomys delicatulus*, *Tachyglossus aculeatus*, *Morethia boulengeri*, *Pygopus nigriceps*, *Ctenophorus nuchalis* and *Gehyra dubia*. These species typically occur in open woodlands, but are associated with particular microhabitat features that vary between different *Eucalypt* and *Acacia* woodland types (see chapter 3).

Figure 4.3 (a-d). The relationship between the number of regional ecosystems and the number of quadrats for birds, mammals and reptiles. For the sake of graph clarity all points are shown, but only a representative set of species are labelled. No species recorded in fewer than 3 quadrats are identified.

Figure 4.3(a) The general relationship for birds, mammals and reptiles combined.

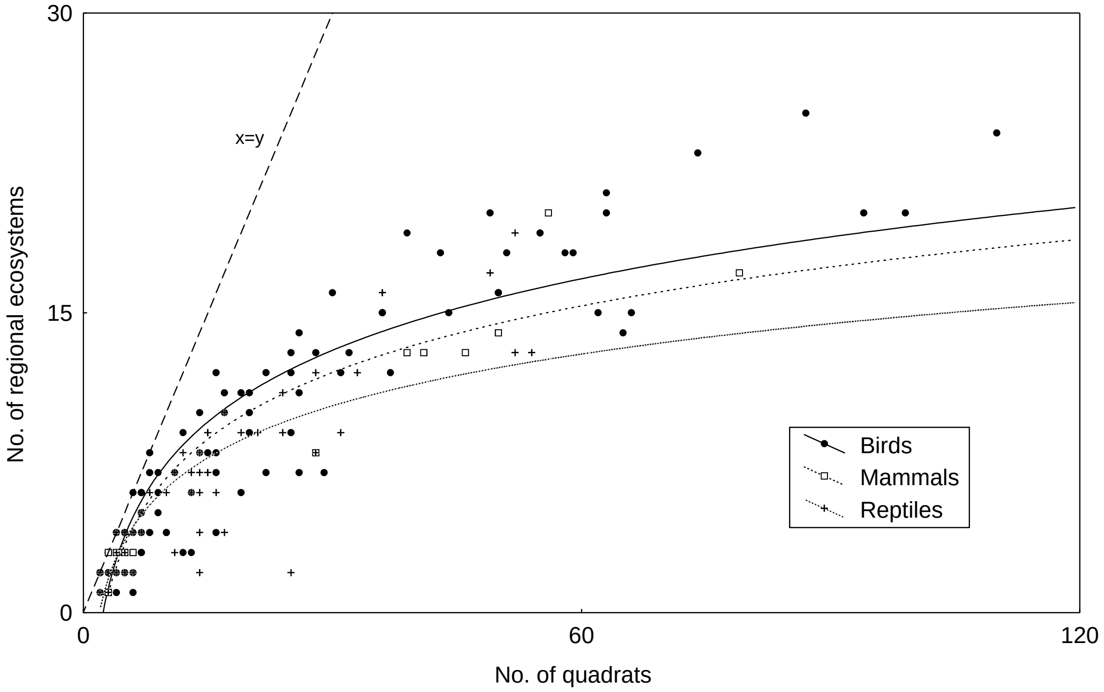


Figure 4.3(b) The relationship for birds, with selected species illustrated.

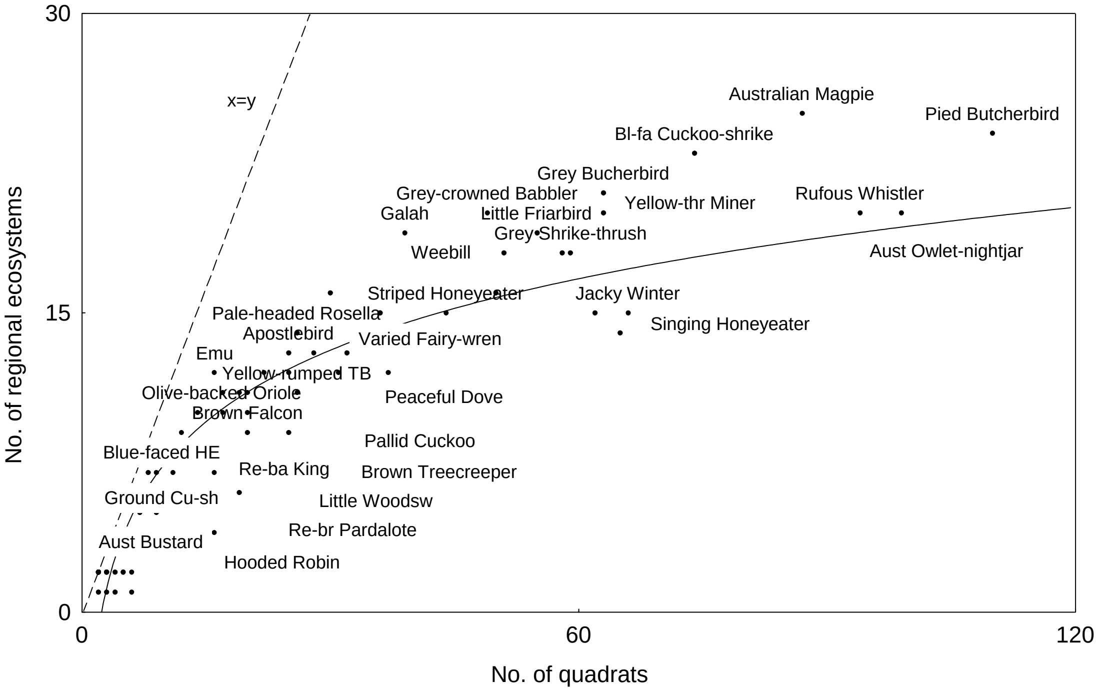


Figure 4.3(c) The relationship for mammals, with selected species illustrated.

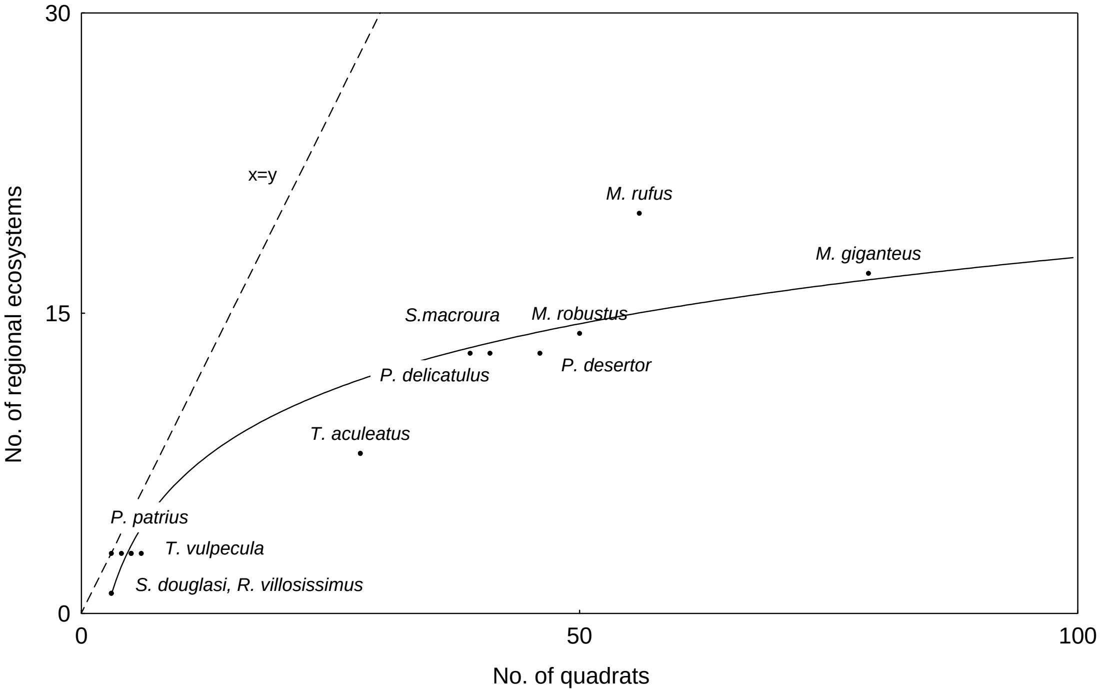
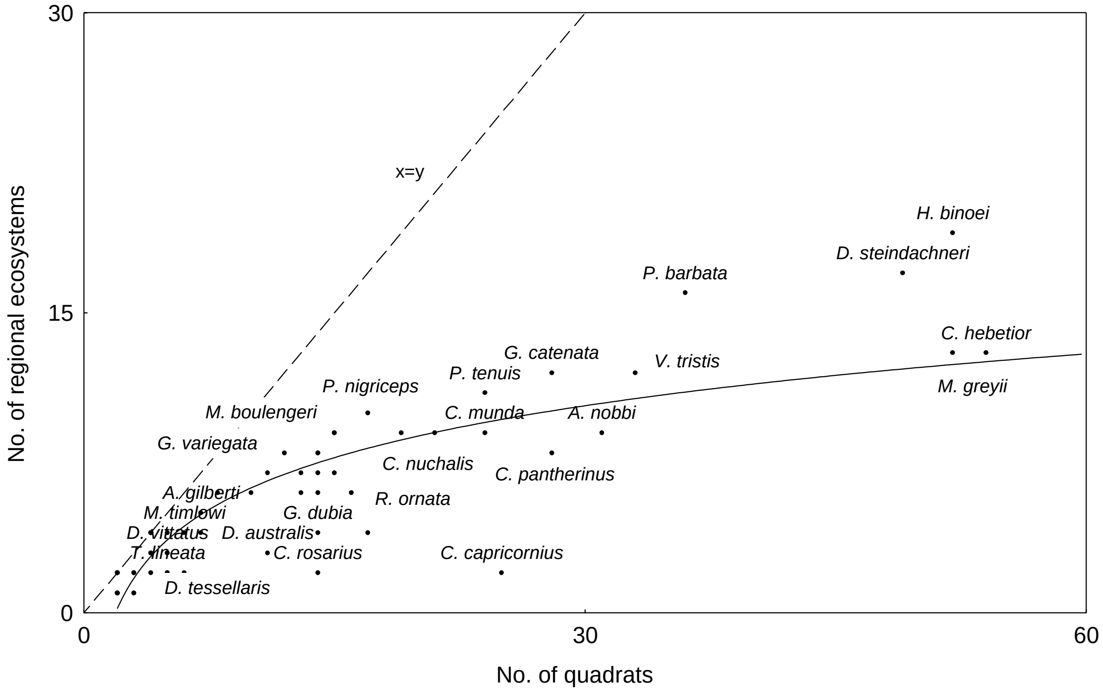


Figure 4.3(d) The relationship for reptiles, with selected species illustrated.



Forty-nine species were recorded from only one regional ecosystem, and of these, 36 were recorded in only a single quadrat, six in two and seven in three or more (Table 4.5). Of these ten were EVR species, which accounts for almost half of the total EVR species recorded over the entire sample. This tends to re-emphasise that species of conservation significance are by nature rare and uncommonly recorded. Of those recorded exclusively but multiple times in a single regional ecosystem, three are birds (Spinifexbird, Hooded Robin, and Rufous-throated Honeyeater), two are reptiles (*Delma tincta*, *Diplodactylus tessellaris*), and two are mammals (*Rattus villosissimus*, *Sminthopsis douglasi*). Most have a known strong habitat association (see chapter 3), though the Rufous-throated Honeyeater is highly nomadic and follows nectar. Though it is difficult to draw any conclusions about species recorded only at a single locality, a number of species are cryptic (*Lerista* sp nov and *Glaphyromorphus punctulatus*), trap-shy (e.g. *Planigale ingrami*, *Leggadina lakedownensis* and *Sminthopsis murina*), or naturally occur in very low abundances (e.g. Little Eagle, Spotted Harrier and *Aepyprymnus rufescens*).

Table 4.5 List of the vertebrate fauna species recorded only in one regional ecosystem. RE = regional ecosystem. q = the total number of quadrats sampled in that regional ecosystem. n = the total number of species unique to that regional ecosystem. The number in parentheses after the species indicates the number of quadrats it was recorded in. * indicates the species is of conservation significance.

RE	q	n	Birds	Mammals	Reptiles
31	5	3			*Amphibolurus burnsi* (2) *Diplodactylus tessellatus* (3) *Pogona vitticeps* (1)
33	2	0			
34	4	0			
36	17	3	Restless Flycatcher (2)	*Rattus sordidus* (1)	*Aspidites melanocephalus* (1)
37	6	8	Magpie Goose (1) Spotted Harrier (1)	*Leggadina forresti* (1) *Planigale ingrami* (1) *Rattus villosissimus* (3) *Sminthopsis douglasi* (3)*	*Denisonia devisi* (1) *Delma tincta* (3)
39	4	1		*Aepyprymnus rufescens* (1)*	
51	36	4	Black-chinned Honeyeater (1)* Hooded Robin (6)*		*Lerista* sp nov (1)* *Simoselaps warro* (1)*
55	13	3			*Boiga irregularis* (1) *Demansia atra* (1) *Rhinoplocephalus boschmai* (2)
57	3	0			
59	5	2		Noisy Miner (1)	*Glaphyromorphus punctulatus* (1) *Lygisaurus foliorum* (2)
71	4	0			
73	7	2		*Macropus dorsalis* (1) *Sminthopsis murina* (1)	
75	2	0			
77	3	1			*Eulamprus sokosoma* (1)
91	2	2		*Planigale tenuirostris* (1)	*Liasis stimsoni* (1)
92	4	1			*Paradelma orientalis* (2)
104	3	3	Brown Thornbill (1)* White-throated Nightjar (1)		*Lerista wilkinsi* (1)*
310	5	1			*Ramphotyphlops unguirostris* (2)
314	4	4	Black-breasted Buzzard (1) Little Eagle (1) Varied Lorikeet (1)		*Furina diadema* (1)
317	3	1			*Varanus panoptes* (1)
319	2	1			*Pseudonaja textilis* (1)
321	3	1	Black Kite (1)		
322	4	3	Banded Lapwing (1) Brolga (1) Masked Lapwing (1)		
323	4	0			
328	3	0			
329	4	3	Spinifexbird (4)*	*Leggadina lakedownensis* (1)*	*Diporiphora winneckei* (1)
511	2	0			
710	6	1	Rufous-throated Honeyeater (3)		

There was significant variation in species richness between regional ecosystems for all taxa (Table 4.6). The greatest contrasts in species richness per quadrat were between the grassland (tussock, hummock, chenopod) regional ecosystems (RE's 322, 37, 329, 323: 7.7-12.2 species) and the *Acacia* and *Eucalyptus* woodland types (RE's 310, 39, 314, 710, 31.6-32.1 species). However the pattern varied somewhat between taxa, with the order of regional ecosystems not fully coincident. Bird species richness followed the general trend of species richness increasing with increasing complexity of the vegetation type: low in the grasslands (e.g. 4.5 in RE 37 tussock grasslands and 5.7 in RE 77 heaths); intermediate in low open woodlands (e.g. 13.6 in RE 73 *Acacia shirleyi* and 13.6 in mixed *Acacia* and *Grevillea* on sands); and high in *Eucalypt* woodlands (e.g. 23.0 in RE 314 riparian woodlands and 21.5 in RE 39 ironbark woodlands). The pattern for mammals and reptiles was more idiosyncratic and reflective of different habitat requirements. Species richness was lowest for mammals in some of the more widespread and complex woodland types (RE 55 and RE 36, box-ironbark woodland associations with 1.0-1.1 species), low in chenopod and lake dune *Acacia* woodlands (RE’s 319, 317, 321, 323 with 0.5-1.3 species), but quite high in habitats such as the tussock and hummock grasslands (REs 37, 329 with 2.3-3.0 species). The highest numbers of mammal species were recorded in ironbark woodlands on sandy and shallow soils (RE’s 511, 39, 71 with 4.0-4.8 species). Reptile diversity was more typically lowest in grassland ecosystems and increasing in more complex environments, though species richness was again low in some of the more widespread woodland types (RE’s 55, 36, 314), including riparian woodlands, which were high in mammal and bird numbers. Highest species richness was associated with regional ecosystems with hummock grass understorey (RE’s 511, 710, 51) or woodlands with very sandy soils (RE’s 310, 317).

There was no significant variation in mean habitat breadth between regional ecosystems for mammals and EVR species, and only a weak relationship for all vertebrates, birds, and reptiles (Table 4.7). Habitat breadth for birds was generally high (5.9-11.2), indicating that a majority of bird species utilised a range of regional ecosystem. Regional ecosystems with species with the lowest niche breadth included grasslands (RE’s 322, 37, 329) and the three most widespread and species-rich woodland types (RE’s 51, 36, 55). Conversely *Acacia* dominated woodlands supported bird communities that were well spread across other regional ecosystems (seven of the ten highest habitat breadth scores). The pattern for reptiles was more variable. Habitat breadth measures were lower in range (2.6-8.8), with the most restricted communities being tussock and hummock grasslands again (RE’s 37, 329), but also a mixture of *Eucalypt* and *Acacia* woodland types. Regional ecosystems with high average habitat breadth score for reptiles included lake edge *Acacia* communities and a mixture of sandy woodland types.

Table 4.6 Mean species richness per quadrat for fauna taxa within each regional ecosystem type. Significance in variation tested via analysis of variance. F-ratio = test statistic. d.f. = degrees of freedom. Probability levels are *p<0.5, **p<0.01, ***p<0.001, ns = not significant. Letters join regional ecosystem groups that are not significantly different (SNK test). RE = regional ecosystem.

RE	Verts	RE	Birds	RE	Mamm	RE	Rept	RE	EVR
322	7.8 a	322	4.3 a	319	0.5 a	37	1.5 a	91	0 a
37	9.3 ab	37	4.5 a	317	0.7 a	322	1.8 ab	322	0a
329	11.3 abc	329	5.5 ab	55	1.1 abc	323	2.3 abc	75	0.5 ab
323	12.3 abcd	77	5.7 abc	36	1.0 ab	329	3.5 abcd	59	0.6 ab
77	12.7 abcd	323	8.8 abce	321	1.0 abc	55	3.8 abcd	57	0.7 ab
59	17.4 abcde	59	9.6 abcef	323	1.3 abc	91	4.0 abcd	321	0.7 ab
319	17.5 abcdef	319	10.5 abcefg	104	1.3 abc	57	4.3 abcd	73	0.7 ab
55	19.0 abcdef	104	11.3 abcefgh	328	1.3 abc	77	4.3 abcd	34	0.8 ab
104	19.0 abcdef	71	11.5 abcefg	33	1.5 abc	75	4.5 abcd	36	0.8 ab
57	20.3 abcdef	57	13.7 abcefgh	75	1.5 abc	31	5.0 abcd	55	0.9 ab
321	20.3 bcdef	321	13.7 abcefgh	322	1.5 abc	73	5.0 abcd	33	1.0 ab
73	20.8 bcdef	55	13.7 abcefgh	34	1.8 abcd	314	5.0 abcd	104	1.0 ab
75	21.0 bcdef	73	13.6 abcefgh	59	2.0 abcde	36	5.4 abcd	317	1.0 ab
71	21.8 bcdef	317	14.3 abcefgh	92	2.3 abcde	92	5.5 abcd	319	1.0 ab
317	22.3 bcdef	75	15.0 abcefgh	329	2.3 abcde	33	5.5 abcd	323	1.0 ab
91	23.5 cdef	511	15.0 abcefgh	73	2.2 abcde	71	5.5 abcd	37	1.2 ab
92	24.2 cdef	51	16.2 bcefgh	57	2.3 abcde	321	5.7 abcd	77	1.3 ab
36	24.3 cdef	92	16.5 cefgh	91	2.5 abcde	328	5.7 abcd	328	1.3 ab
328	25.0 def	31	16.8 efgh	77	2.7 abcde	39	5.8 abcd	710	1.3 ab
31	25.2 def	91	17.0 efgh	37	3.0 abcde	59	5.8 abcd	31	1.4 ab
51	26.5 ef	36	17.6 efgh	310	3.0 abcde	319	6.0 abcd	92	1.5 ab
33	27.0 ef	328	17.7 efgh	51	3.3 abcde	104	6.3 abcd	511	1.5 ab
511	27.5 ef	310	20.6 fgh	710	3.3 abcde	34	6.5 abcd	314	1.7 ab
34	29.5 ef	33	20.0 efgh	31	3.4 abcde	317	6.7 bcd	310	1.8 ab
310	31.6 f	34	21.3 gh	314	3.8 bcde	51	7.0 cd	39	2.0a b
39	31.8 f	39	21.5 gh	511	4.0 cde	710	7.3 cd	71	2.3 ab
314	31.8 f	710	21.5 gh	39	4.5 de	310	8.0 d	51	2.3 ab
710	32.2f	314	23.0 h	71	4.8 e	511	8.5 d	329	2.8 b
d.f.	27, 130	d.f.	27, 130	d.f.	27, 130	d.f.	27, 130	d.f.	27, 130
F-ratio	8.15	*F*-ratio	6.98	*F*-ratio	5.93	*F*-ratio	4.38	*F*-ratio	3.56
p	***	*p*	***	*p*	***	*p*	***	*p*	***

Table 4.7 Mean habitat breadth per quadrat of all fauna taxa recorded within each regional ecosystem type. Significance in variation tested via analysis of variance. F-ratio = test statistic. d.f. = degrees of freedom. Probability levels are *p<0.5, **p<0.01, ***p<0.001, ns = not significant. Letters join regional ecosystem groups that are not significantly different (SNK test). RE = regional ecosystem.

RE	Verts	RE	Bird	RE	Mamm	RE	Rept	RE	EVR
37	6.1 a	322	5.9 ab	59	4.1	37	2.5 a	91	0
51	6.6 ab	37	6.8 ab	104	5.2	329	3.6 ab	104	2.7
329	6.7 abc	51	7.2 ab	73	5.2	92	3.9 abc	59	3.0
36	6.8 abc	36	7.4 ab	55	5.4	59	4.3 abc	329	3.2
59	6.8 abc	55	8.0 ab	75	5.4	314	4.7 abc	75	3.8
322	7.0 abc	329	8.2 ab	314	6.0	31	4.9 abc	51	4.4
77	7.1 abc	710	8.3 ab	37	6.0	104	5.0 abc	55	4.6
104	7.3 abc	310	8.4 ab	77	6.1	51	5.1 abc	511	4.7
55	7.3 abc	39	8.5 ab	310	6.4	36	5.2 abc	77	5.0
310	7.4 abc	314	8.7 ab	51	6.7	33	5.4 abc	323	5.3
314	7.6 abc	34	8.7 ab	511	6.7	77	5.4 abc	37	5.7
73	7.7 abc	77	8.7 ab	39	6.7	73	5.4 abc	71	5.8
710	7.7 abc	104	8.9 ab	317	6.7	310	5.5 abc	39	6.5
39	7.8 abc	59	8.9 ab	36	7.0	71	5.6 abc	314	6.5
71	7.9 abc	73	8.9 ab	710	7.2	55	5.7 abc	310	7.1
92	7.9 abc	71	9.0 ab	71	7.2	91	5.8 abc	322	7.5
34	8.0 abc	323	9.1 ab	329	7.3	323	5.8 abc	328	7.5
57	8.3 abc	57	9.1 ab	31	7.6	34	5.9 abc	710	7.6
511	8.4 abc	92	9.2 ab	322	7.7	317	5.9 abc	73	7.8
323	8.4 abc	328	9.3 ab	57	8.3	75	6.0 abc	92	8.1
31	8.6 abc	33	9.6 ab	34	8.4	511	6.1 abc	36	8.3
33	8.6 abc	31	9.7 ab	92	9.0	57	6.1 abc	31	8.4
317	8.7 abc	321	9.8 a	323	9.2	710	6.4 abc	33	8.7
321	8.7 abc	511	10.1 ab	33	9.4	39	6.5 abc	57	8.8
328	8.8 abc	317	10.2 ab	91	10.3	321	6.8 abc	317	9.0
75	9.2 abc	75	10.7 b	328	10.3	328	7.2 abc	34	12.8
91	10.0 bc	91	10.8 b	319	10.8	319	8.0 b	319	12.8
319	10.1 c	319	11.2 b	321	10.8	322	8.8 bc	321	12.8
d.f.	27, 1339	d.f.	27, 874	d.f.	27, 87	d.f.	27, 322	d.f.	26, 60
F-ratio	2.05	*F*-ratio	1.69	*F*-ratio	0.95	*F*-ratio	1.34	*F*-ratio	0.83
p	**	*p*	*	*p*	ns	*p*	*	*p*	ns

Correspondence between regional ecosystems and species of conservation significance

The correspondence between regional ecosystems and vertebrates of conservation significance was examined using ANOSIM and analysis of variance. Twenty-four species of known conservation significance were recorded across all sites. The ANOSIM indicated that both the EPA (R=0.002) and VMA (R=-0.008) categories for conservation status of regional ecosystem types failed to demonstrate any relationship with the composition of EVR species across all sites (Table 4.2).

The relationship between species richness for all taxa and subsets with regional ecosystem categories of significance was also examined with analysis of variance

(Table 4.8). In reference to the categories of conservation significance, species richness of the ground strata were highest in the "of concern" EPA category, and reptiles ("endangered"), EVR and ground strata ("of concern") in the VMA categories, but none of these were significantly so. Significant variation was identified for vertebrates, birds, mammals and EVRs using the EPA categories, with the "not of concern" and "of concern" groups being higher than the "endangered" group in each case. Only mammals and upper strata plant richness significantly varied using the VMA categories, again the "not of concern" category with the highest species richness.

Table 4.8 Mean richness for vertebrate and plant taxa, within each regional ecosystem category of conservation significance. Categories are O = of concern, N = not of concern and E = endangered. Significance in variation tested via analysis of variance. F-ratio = test statistic. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant. Letters join regional ecosystem groups that are not significantly different (SKN test).

	EPA					VMA				
Species	E	O	N	F-ratio	*p*	E	O	N	F-ratio	*p*
Verts	16.17	22.73a	23.6a	5.04	**	17.5	19.29	23.28	2.12	ns
Bird	10.17	15.21a	15.3a	4.02	**	10.5	12.29	15.21	2.0	ns
Rept	4.67	5.03	5.68	1.70	ns	6.0	5.21	5.49	0.13	ns
Mamm	1.0	2.48a	2.5a	5.87	**	0.5ab	1.64b	2.48a	3.71	*
EVR	0.58b	1.21ab	1.54a	5.17	**	1.0	1.57	1.39	0.32	ns
Plants	14.17	17.73	18.22	2.25	ns	13.0	15.86	18.07	1.36	ns
Upper	3.58	4.97	5.73	2.79	ns	3.5ab	3.43b	5.63a	3.36	*
Ground	11.5	13.61	12.88	0.73	ns	10.0	13.0	12.96	0.31	ns

Examination of EVR species richness in each of the two sets of conservation categories showed that most were recorded at highest abundances in regional ecosystem category "not of concern" (Table 4.9). Of the 23 species identified, only seven were recorded at highest abundances in the "of concern" and "endangered" categories under the EPA listing (Grey-crowned Babbler, Spinifexbird, Squatter Pigeon, *Leggadina lakedownensis*, *Trichosurus vulpecula*, *Tiliqua multifasciata* and *Paradelma orientalis*). The Spinifexbird and Squatter Pigeon was recorded in significantly higher abundances in "of concern" regional ecosystems, while *Pseudomys desertor, Ctenotus capricorni, C. rosarium* were significantly higher in regional ecosystems "not of concern". Again of the 23, seven species were recorded at highest abundances in the "of concern" and "endangered" categories under the VMA listing (the same set as the EPA list, except *P. desertor* replaces *T. vulpecula*), with only the Grey-crowned Babbler significantly so in " endangered" regional ecosystems.

Table 4.9 Mean abundance for vertebrate EVR species within each regional ecosystem category of conservation significance. Significance in variation tested via Kruskal-Wallis one-way analysis of variance by ranks. H= test statistic. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant. Only species recorded in three or more quadrats were tested. Categories are O = of concern, N = not of concern and E = endangered. Figures in bold indicate the highest abundance.

	EPA					VMA				
Species	E	O	N	H	*p*	E	O	N	H	*p*
BIRDS										
Australian Bustard	0	0	**0.12**	2.05	ns	0	0	**0.09**	0.58	ns
Black-chinned Honeyeater	0	0	**0.03**			0	0	**0.02**		
Black-throated Finch	0	0	**0.05**			0	0	**0.04**		
Brown Treecreeper	0	0.12	**0.54**	4.41	ns	0	0	**0.46**	2.01	ns
Bush Stone-curlew	0	0	0.04			0	0	**0.03**		
Grey-crowned Babbler	**2.33**	2.0	1.64	3.14	ns	**6.0**	1.93	1.69	5.67	**
Hooded Robin	0	0	**0.17**	2.48	ns	0	0	**0.13**	0.71	ns
Spinifexbird	0	**0.52**	0	15.5	***	0	**1.21**	0	42.4	***
Squatter Pigeon	0	**0.30**	0.11	6.01	**	0	**0.29**	0.13	3.58	ns
MAMMALS										
Aepyprymnus rufescens	0	0	**0.01**			0	0	**0.01**		
Lagorchestes conspicillatus	0	0	**0.08**	1.63	ns	0	0	**0.06**	0.46	ns
Leggadina lakedownensis	0	0.06	0			0	0.14	0		
Pseudomys desertor	0	1.06	**2.07**	5.36	*	0	**2.0**	1.70	0.84	ns
Pseudomys patrius	0	0	**0.08**	2.06	ns	0	0	**0.06**	0.58	ns
Sminthopsis douglasi	0	0	**0.05**	1.22	ns	0	0	**0.04**	0.34	ns
Trichosurus vulpecula	0	**0.39**	0.06	3.41	ns	0	0	**0.14**	0.71	ns
REPTILES										
Ctenotus capricorni	0	0	**0.53**	11.8	***	0	0	**0.42**	3.34	ns
Ctenotus rosarium sp nov	0	0.03	**0.43**	8.79	**	0	0	**0.35**	3.34	ns
Lerista sp nov	0	0	**0.03**			0	0	**0.02**		
Lerista wilkinsi	0	0	**0.01**			0	0	**0.01**		
Paradelma orientalis	0	**0.06**	0			0	**0.14**	0		
Simoselaps warro	0	0	**0.01**			0	0	0.01		
Tiliqua multifasciata	0	**0.03**	0.01			0	**0.07**	0.01		

Correspondence between site species richness

The correlation between vertebrate and plant quadrat species richness is presented in Table 4.10. There was strongest correlation (r>0.5) between site richness of major taxa and their subsets of those taxa, namely vertebrates and birds, vertebrates and mammals, plants, ground strata and upper strata (Table 4.10). Significant but weaker correlations (r=0.4-0.5) were between reptiles and EVR species, and across taxa between upper strata plant species, reptiles and mammals. The remainder of the comparisons were significant, but weakly so, with interesting non-significant results between ground strata plants and mammals and reptile richness, two predominantly terrestrial groups. The richness hotspot analysis generally supports the correlations, with vertebrates, birds and reptiles, birds and reptiles, EVR species and reptiles and all plants and ground strata plants having more than 50% of their richest sites in common.

Table 4.10 Relationship between vertebrate and plant quadrat species richness. In the lower left of the array, the data indicates the spearman rank correlation coefficient and significance level for comparisons between all groups. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant. In the upper right of the array the data indicates the proportion of the top 20 species rich sites that correspond between groups. Spearman rank correlation between site richness for all vertebrate groups and site richness for EVR species.

Taxa	Verts	Bird	Rept	Mamm	EVR	Plants	Upper	Ground
Verts		0.9	0.6	0.3	0.25	0.35	0.35	0.25
Bird	0.93***		0.5	0.25	0.2	0.35	0.3	0.35
Rept	0.49***	0.31***		0.45	0.6	0.35	0.25	0.25
Mamm	0.64***	0.38***	0.29***		0.45	0.15	0.3	0.1
EVR	0.36***	0.26***	0.44***	0.28***		0.05	0.25	0.05
Plants	0.35***	0.37***	-0.03 ns	0.23***	-0.02 ns		0.45	0.7
Upper	0.42***	0.32***	0.20*	0.47***	0.21*	0.56***		0.1
Ground	0.19***	0.26***	-0.14 ns	0.01 ns	-0.17 ns	0.85***	0.08 ns	

The correlations between vertebrate species richness for major taxonomic groups and the EVR richness within those groups (Table 4.11) not unexpectedly indicated the strongest relationship between like-groups (birds and EVR birds, mammals and EVR mammals, reptiles and EVR reptiles). Vertebrate site species richness was also generally linked to high EVR richness for birds and reptiles. There was no significant or even strong correlation between site richness for EVRs of different taxa.

Table 4.11 Relationship between vertebrate and EVR quadrat species richness. The data indicates the spearman rank correlation coefficient and significance level for comparisons between vertebrate and EVR groups. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant.

Taxa	EVR Bird	EVR Mamm	EVR Rept
Verts	0.3***	0.05 ns	0.21**
Birds	0.39***	-0.09 ns	0.07 ns
Mamm	-0.001 ns	0.51***	0.26**
Rept	0.04 ns	0.08 ns	0.35***
EVR Bird	-	-0.11 ns	-0.15 ns
EVR Mamm	-	-	0.11 ns

Correspondence between site species composition

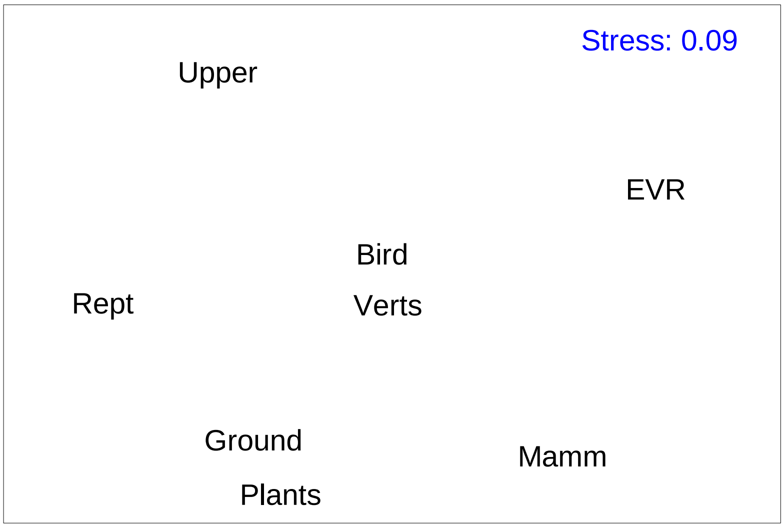
The correlations between composition of sites using the Mantel tests and dissimilarity matrices derived from abundance data were significant for all comparisons (Table 4.12). However in the majority of cases the rank correlation or Mantel coefficient (ρ) was less than 0.5, indicating only partial fidelity between plant and animal assemblages. Comparisons between vertebrates, birds and reptiles, and all plants, upper and ground strata, identified the strongest correlations (r>0.5), as did the cross-taxon data sets vertebrates, all plants and upper strata, and birds, all plants and upper strata. These taxa demonstrate a high degree of assemblage fidelity. Other pairings demonstrated a moderate level of correlation (r=0.4-0.5), including vertebrates and mammals, ground strata with vertebrates, birds and reptiles, and all plants with reptiles. There was generally a poor correspondence between all vertebrate and plant taxa and EVR species, mammals and all other taxa (except vertebrates themselves).

Table 4.12 Results of Mantel tests estimating correlations between composition of vertebrates and plants. Data indicates rank correlation coefficient using standardised Bray-Curtis dissimilarity matrices derived from abundance. Significance identified via permutation. Probability levels are *p<0.05, **p<0.01, ***p<0.001.

Taxa	Bird	Rept	Mamm	EVR	Plants	Upper	Ground
Verts	0.925***	0.557***	0.406***	0.295***	0.566***	0.504***	0.483***
Bird		0.33***	0.197***	0.23***	0.51***	0.502***	0.415***
Rept			0.153***	0.182***	0.451***	0.303***	0.418***
Mamm				0.244***	0.165***	0.088**	0.171***
EVR					0.176***	0.152***	0.157***
Plants						0.587***	0.902***
Upper							0.388***

Ordination of these correlation scores illustrates well the degree of inter- and intra-taxa assemblage fidelity (Figure 4.4). Vertebrates and birds, and plants and ground strata are quite closely related, probably due to the predominance of both birds and ground strata plant species in the total composition of vertebrates and plants respectively. Conversely mammals, reptiles and EVRs are generally equidistant from each other, whereas upper strata plants identify a moderate and equal fidelity to birds/verts, as do reptiles in comparison to ground strata/all plant species.

Figure 4.4 Two-dimensional ordination using multi-dimensional scaling indicating the extent of assemblage fidelity between the vertebrate and plant taxa. Ordination derived from Mantel test scores in Table 4.11. Position in space indicates the relative similarity (closest) and dissimilarity (distance).



Complementarity: regional ecosystems versus random selection

There was no significant difference in the total species-richness of vertebrate fauna in the set of quadrats selected at random compared to the set constrained to select from the range of regional ecosystems (Figure 4.5). However for plants there was clearly an advantage in selecting quadrats based on regional ecosystems, as these always resulted in a highest richness in the final total pool. This pattern remained consistent between sets selected from 28 and 56 quadrats. For all species (plants and vertebrate fauna combined), there were also significant differences for the regional ecosystem sets, though this is presumably due to the predominance of plants in the total species pool.

Figure 4.5 (a-b) Random quadrat selection versus selection via regional ecosystems. Data in columns indicates the mean species richness and standard deviation from 50 random selections. (a) selection of 28 quadrats at random versus selection constrained to be one quadrat from each regional ecosystem. (b) selection of 56 quadrats at random versus selection constrained to be two quadrat from each regional ecosystem.

Figure 4.5 (a) Selection of 28 quadrats only.

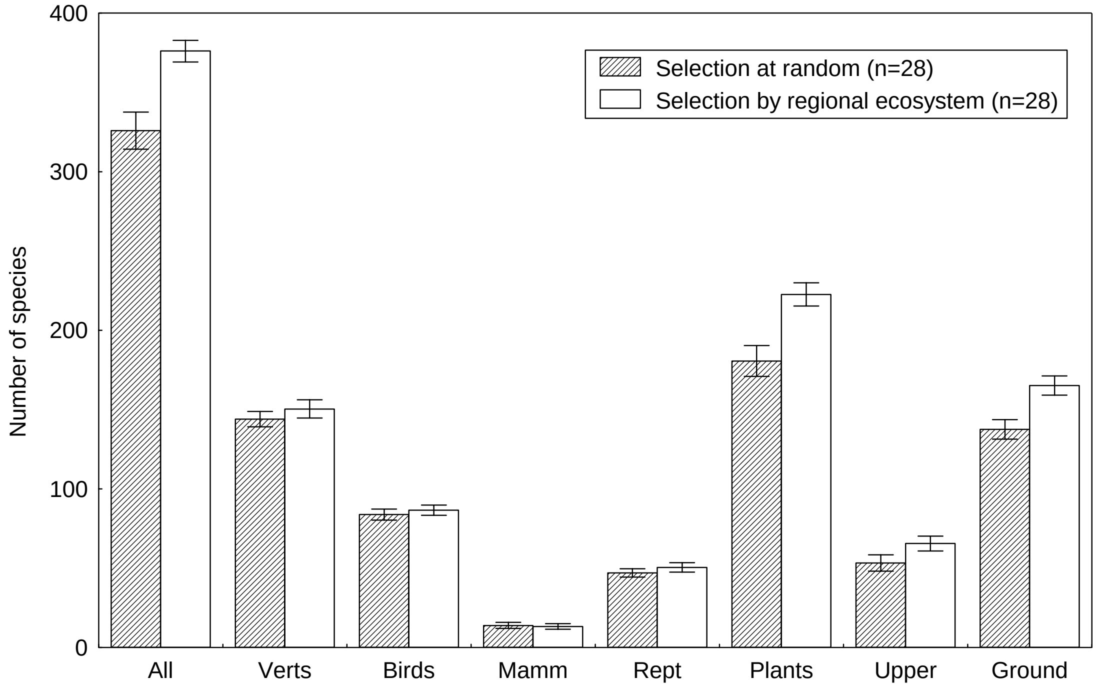
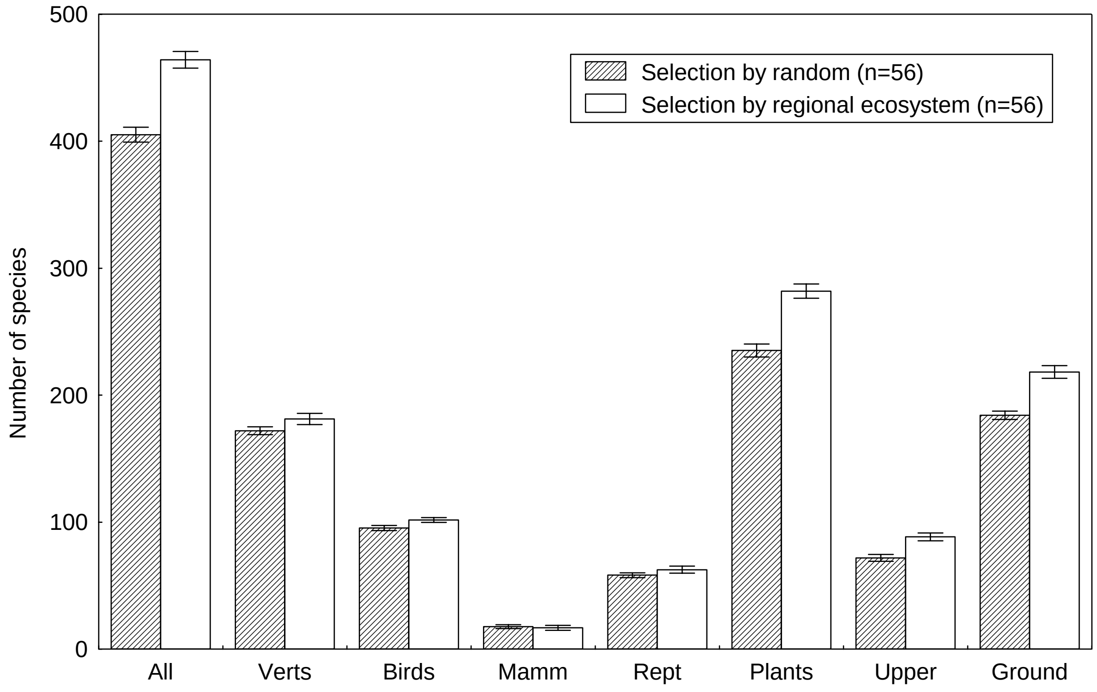


Figure 4.5 (b) Selection of 56 quadrats only.



Complementarity: minimum sets for sites

The minimum-set algorithm identified substantial disparity in the number of sites required to represent all species: 48 for vertebrates, 26 for birds, 28 for reptiles, 10 for mammals, 13 for EVRs, 71 for plants, 29 for upper strata plants, 62 for ground strata and 85 for all plants and animals. This ranged from only 6% of all available 158 sites for mammals to 77% to represent all species (plants and animals), with vertebrates, birds, reptiles, EVRs and upper strata requiring <50% of sites, and plants and ground strata requiring >50% (Table 4.13). Forty-seven sample sites were not utilised in the minimum-sets for all taxa. In regards to the relative complementarity of reservation of 100% of one taxon to other taxonomic groups, the results were also mixed with only the most closely related taxa showing high congruence. Selection for all bird species captured between 58% (reptiles) to 88% (EVR) of fauna, 54% of the ground and 67% of the upper strata, and 66% of all species. Reptiles similarly captured between 59% (mammals) and 72% (EVR) of fauna and 59% (upper) to 73% (ground) of plants, and 68% of all species. Mammals generally captured <50% of all other species diversity, as did EVRs for plants, but more adequately (50-60%) for reptiles, mammals and birds. Upper and ground strata plants were not particularly complementary, though both performed adequately for the species-rich fauna taxa (birds and reptiles) and less well for the species poor groups (mammals and EVR). In general, using all plants captured most of the species (95%) and performed as a better surrogate for vertebrate taxa (68-95%), than vertebrates did for plant taxa (74-79%).

Table 4.13 Results of the minimum-set algorithm to select sets of sites that contain 100% of the target taxon (verts, bird, rept, mamm, EVR, plants, upper, ground and all species). Data indicates the number of sites, the percentage of the total sites available and the percentage of the total sites used in all analysis). Data also indicate the complementarity that is the percentage captured of other taxa in the minimum-set after 100% of the target taxon is reserved.

	n	Verts	Bird	Rept	Mamm	EVRs	Plants	Upper	Ground	All spp
No. of sites		48	26	28	10	13	71	29	62	85
% total sites	158	30	16	18	6	8	45	18	39	54
Verts	217	100	100	100	100	100	76	74	79	85
Bird	119	82	100	58	77	88	58	67	54	66
Rept	76	79	70	100	59	72	61	59	73	68
Mamm	22	55	58	38	100	48	25	24	25	36
EVR	24	61	66	51	68	100	36	34	37	46
Plants	364	87	91	85	68	80	100	100	100	95
Upper	101	71	73	71	55	44	68	100	55	69
Ground	263	83	88	82	63	68	91	69	100	91

Species accumulation curves further identify the degree of complementarity between the taxa, with the relationship between birds, reptiles, mammals, EVRs, upper and ground strata plants examined (Figures 4.6 a-f). A total of 50% of the bird richness is accounted for by the selection of five sites, which captures 45% of the mammals and EVR species also, but <30% of the other taxa. A further 10 sites account for 80% of the bird species, but only 40-65% of all other taxa. A similar pattern occurs for reptiles with six sites capturing 50% of reptile species, as well similar proportions of EVRs and birds, while a further 11 sites account for 80% reptiles, but <60% of all other taxa. The pattern here is a moderate complementarity in the early phase of site selection, which declines as more sites are chosen to specifically accumulate the species richness of the target taxa. This suggests that for birds and reptiles, there are a small number of sites, which are broadly complementary in the patterns of species composition, but many that are not.

The pattern for the species-poor taxa (mammals and EVR) indicates a generally low level of complementarity between these and other taxa. A very small set of sites will account for all of the target taxa (n=10 for mammals, n=13 for EVR), yet this accounts for generally <70% for other taxa. In some cases, the relationship is extremely weak. Selection of the 80% mammal species only accounts for <40% of all reptiles and approximately 20% of the upper and ground strata plants, while selection of 80% EVR species is similarly inefficient for these taxa. An equivalent reciprocity exists for upper strata plants. Five sites will select 50% of the richness, but these sites account for <40% of the species for all other taxa, while 17 sites select 80% of the target taxa, but at best 60% of reptiles and birds and <50% of the others. Within the species rich ground strata taxa, 10 sites select 50% of the species, unlike the pattern for all other examples, 60% of bird species, and 40% and 50% of mammals and reptiles respectively. Forty sites account for 80% of the ground strata plants and equally high numbers of bird and reptile species, and over 50% of the other taxa except EVRs. A few general patterns are evident in all these cases. A small proportion (<5%) of sites will generally capture 50% of the target taxa species richness, and similar levels of a few concordant taxa. However the capture of a further 30% of the target taxa species requires up to twice as many sites as to reach the 50% level, and the other taxa in this period show less or little complementarity. The capture of the final 20% of species for any target taxa supplies the weakest complementarity for all taxa, whereas for species-poor target taxa (mammals, EVRs), richness can be captured in very few sites but with low correspondence to other taxa. Finally for the most species rich taxa (ground strata) there is strong complementarity for other species-rich taxa (reptiles, birds) and, though still poor, moderate complementarity for other taxa (>50% richness covered).

Evaluation of the proportion of regional ecosystems types chosen for each taxon also reveals the varying significance of these in representing any taxon in a minimum-set (Table 4.14). For vertebrates only a maximum of 59% of the regional ecosystems available are chosen for birds and reptiles and 28% for the species-poor groups, mammals and EVRs. Three regional ecosystems are not used in the minimum-set at all, and only two (RE 37 tussock grasslands and RE 329 hummock grasslands) are used by all taxa. Reptiles utilise the most regional ecosystems uniquely (six types of mainly *Acacia* woodlands), followed by birds (four types of open woodlands and lake communities). The highest percentage of sites for birds, reptiles and EVRs come from the most species-rich and EVR rich regional ecosystem (RE 51 *Eucalyptus similis* woodlands), though no sites are selected from this group for mammals. Instead 25% of the mammal sites are selected from the species-poor, EVR rich community (RE 37 tussock grasslands) which has a high proportion of restricted mammals. Apart from the high proportion selected from a few particular regional ecosystem types, the proportion of sites selected from the range of remaining regional ecosystems is generally low, and did not seem to target species-rich or EVR rich types. In regards to plants, only 45% of the regional ecosystems were required for a minimum-set for upper strata species, whereas 86% were required for the ground strata. Again quadrats in a few particular regional ecosystem type were selected most frequently (RE's 51, 104, 314 for upper strata, RE's 51, 36, 55 for ground strata), and these represented the most species-rich types for each group. The remainder of quadrats selected was spread evenly across the regional ecosystems chosen.

Table 4.14 The level of representation of each regional ecosystem in the minimum-set analysis that captures 100% of the vertebrate and plant species. Data is the percentage of sites in each regional ecosystem (= RE) in each minimum-set. n = the number of sampled quadrats of the RE available and the number of sites chosen for each taxon. The proportion of RE's utilised is listed at the bottom. In the right hand side of the table the total richness of each RE and the number of EVR species is also listed. * = RE of conservation significance.

	Taxa	Verts	Bird	Rept	Mamm	EVR	No. spp	No. EVR	Plants	Upper	Ground	All
RE	n	48	26	28	10	13	217	24	71	29	62	85
31*	5	5.0		7.7			49	3	4.3	3.7	5.0	3.5
33*	2			3.8			44	0	1.4	3.7		1.2
34*	4			3.8			61	0	4.3		3.3	3.5
36	17	2.5	3.8	3.8	11.1		101	2	8.7	7.4	8.3	8.2
37	6	7.5	7.7	7.7	22.2	8.3	30	8	2.9		3.3	4.7
39	4	1	3.8		11.1	8.3	71	1	5.8	3.7	5.0	4.7
51	36	12.5	15.4	15.4		25.0	113	5	18.8	18.5	16.7	18.8
55	13	5.0	3.8	7.7			82	3	5.8	3.7	8.3	7.1
57*	3	2.5		7.7			41	0	2.9	3.7	3.3	1.2
59*	5	2.5	7.7	3.8			41	3	5.8	7.4	6.7	4.7
71	4						44	0	1.4	3.7	1.7	1.2
73	5	2.5	7.7		11.1		69	2				3.5
75*	2						29	0	1.4		1.7	1.2
77	3	2.5		3.8	11.1		31	1	1.4	3.7	1.7	1.2
91*	2	5.0		3.8	11.1		29	2	1.4		1.7	2.4
92*	4	2.5		3.8		8.3	49	1	4.3		5.0	3.5
104	3	5.0	3.8	7.7		8.3	41	3	4.3	11.1	1.7	3.5
310	5	2.5	3.8				82	0	1.4	7.4	1.7	1.2
314*	4	5.0	7.7		11.1	8.3	71	3	4.3	11.1	6.7	4.7
317*	3	2.5		3.8			38	1	1.4		1.7	2.4
319*	2	2.5		3.8			23	1	1.4		1.7	1.2
321*	3	2.5	3.8				36	1	4.3	7.4	1.7	3.5
322*	4	5.0	7.7				18	3	2.9		3.3	3.5
323	4	2.5	7.7			16.7	31	0	4.3		5.0	3.5
328	3	2.5	3.8				47	0				1.2
329*	4	5.0	3.8	3.8	11.1	16.7	31	3	1.4		1.7	3.5
511	2						44	0	1.4	3.7		
710	6	5.0	7.7	7.7			67	1	1.4		3.3	1.2
No. RE%	100	83	59	59	28	28			93	45	86	97

Figure 4.6 (a-f) Results of the minimum-set algorithm indicating the relative species accumulation curves rate against number of sites chosen, and therefore the complementarity between target and non-target taxon. Taxa used to indicate patterns are (a) birds, (b) reptiles, (c) mammals, (d) EVR, (e) upper strata plants and (f) ground strata plants.

Figure 4.6 (a) Selection using bird species.

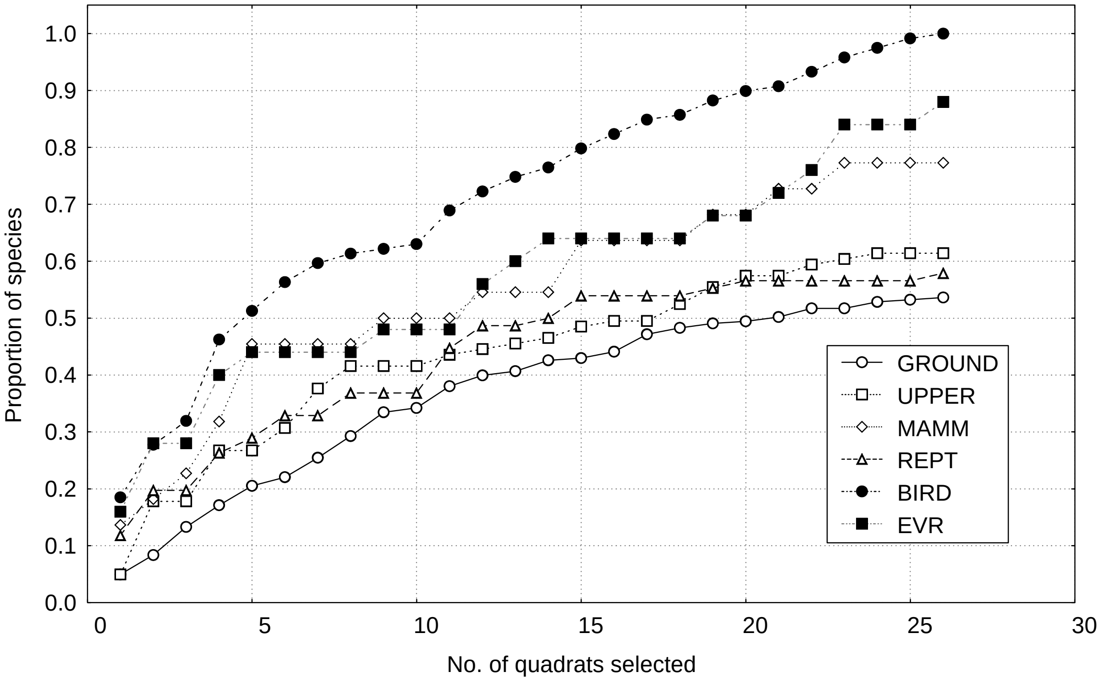


Figure 4.7 (b) Selection using reptile species.

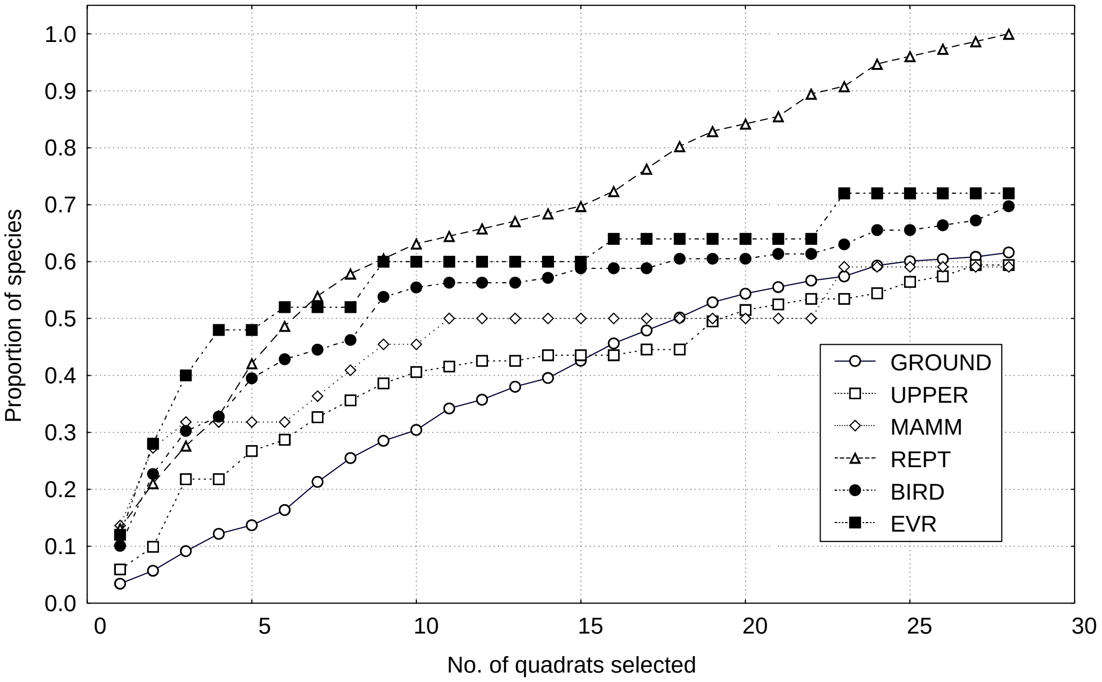


Figure 4.6 (c) Selection using mammal species.

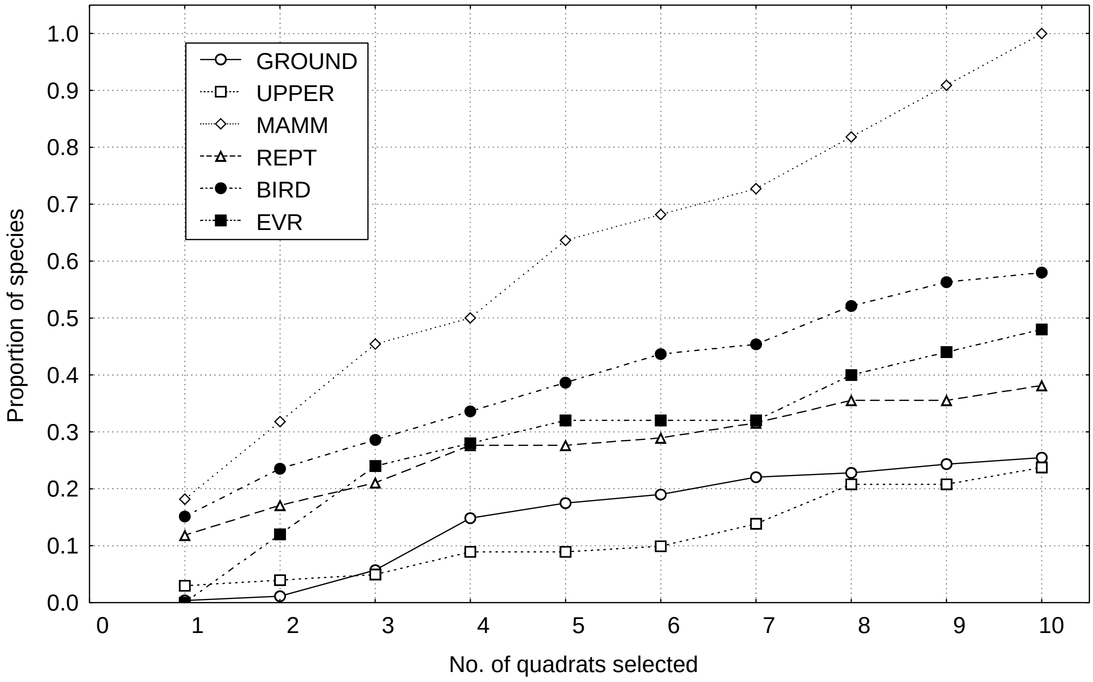


Figure 4.6 (d) Selection using EVR species.

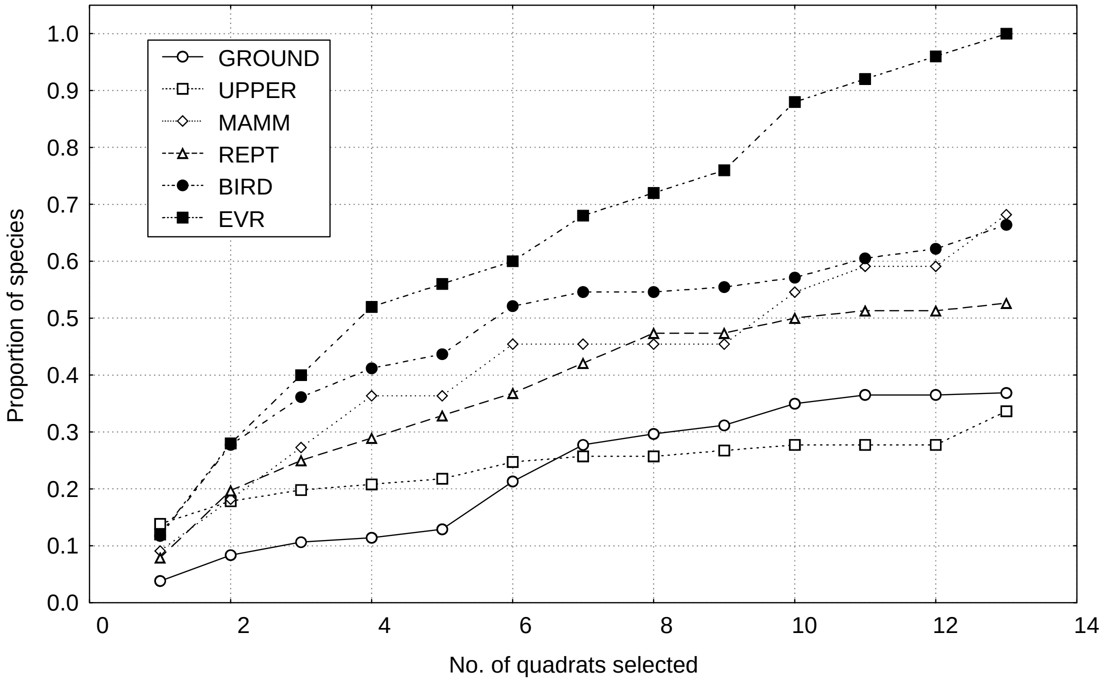


Figure 4.6 (e) Selection using upper strata plant species.

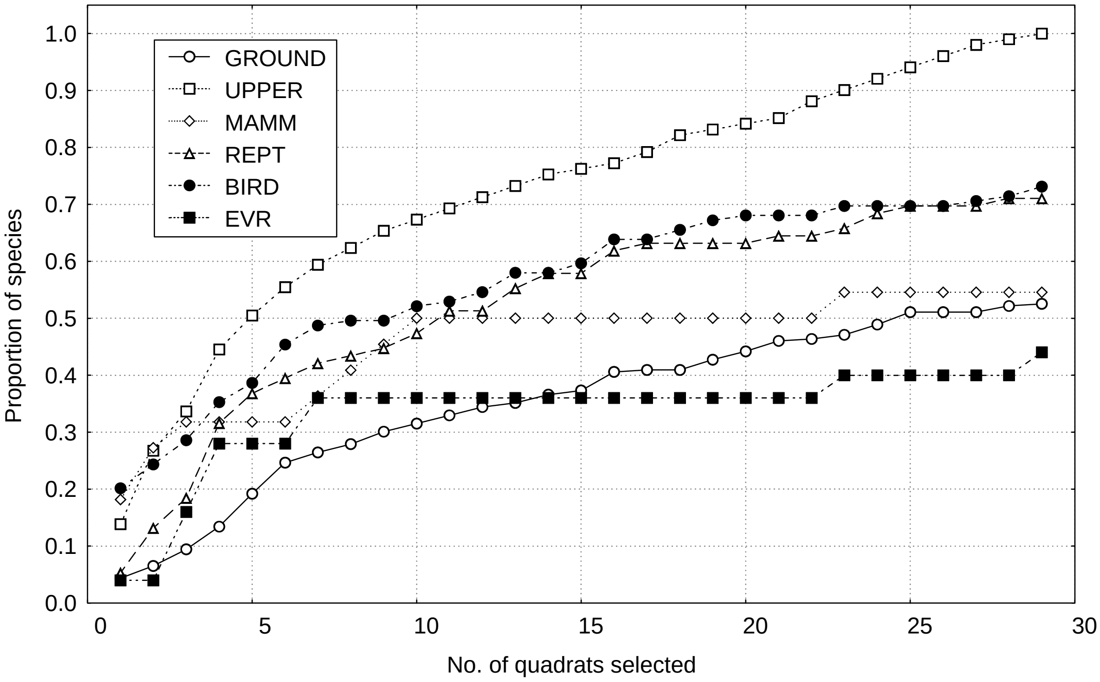
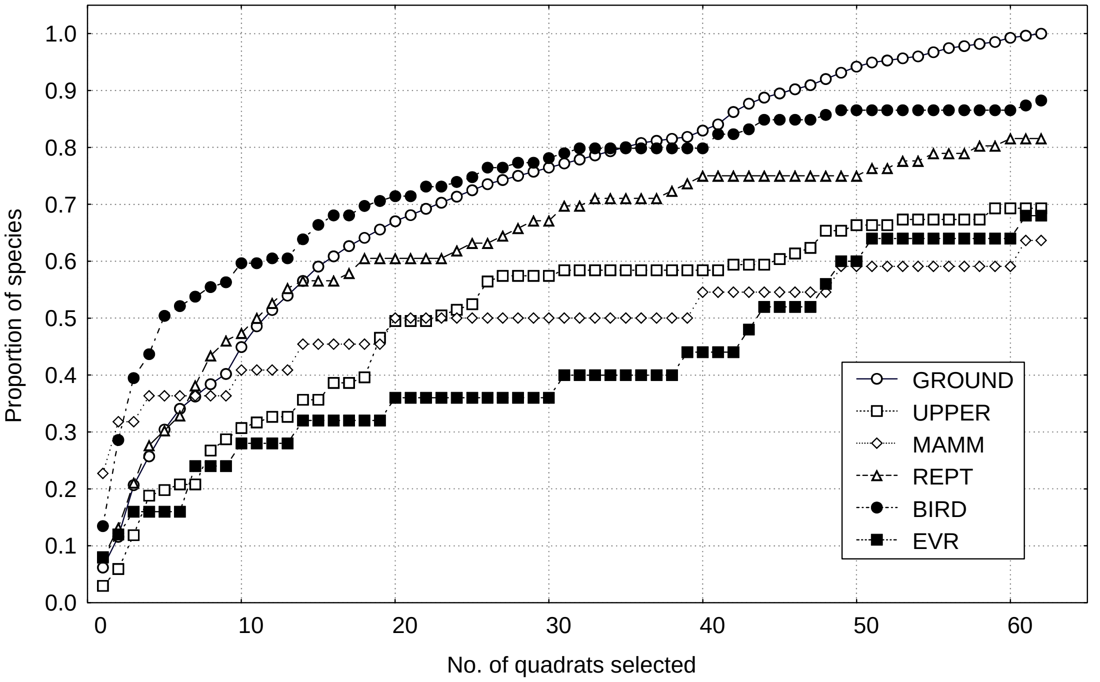


Figure 4.6 (f) Selection using ground strata plant species.



Discussion

Land classifications as surrogates

The efficacy of land classifications in characterising measured species composition varied between types. Those based on biotic features were the most successful. Correlations with species poor groups (mammals and EVRs) were universally the weakest indicating that both distribution and abundance of these were idiosyncratic and independent of larger patterns in vegetation and landform, or that species were equally spread across all forms of land classification. A high proportion of these species also occurred in few quadrats, hence were unlikely to be selected. In general those classifications that worked best for fauna also worked well for flora (regional ecosystems, plant and fauna groups), indicating interrelatedness of patterns of composition. Previous chapters have highlighted the broad coincidence of vegetation structural characteristics and fauna assemblage. There was a strong relationship between regional ecosystems and composition of entire fauna and flora assemblages, which is in keeping with previous studies. Pharo *et al.* (2000) reported that groups derived from vascular plant composition and an even simpler categorisation using over-storey species alone was useful in predicting bryophyte and lichen diversity.

Regional ecosystems are defined using both floristic and soil characteristics, which in part may explain their reasonable fidelity to some fauna groups. In tropical savannas both broad structural characteristics and underlying substrate have been identified as strong predictors for vertebrate fauna composition, more so than floristic variation (Woinarski *et al.* 1991; Gambold and Woinarski 1991; Trainor and Woinarski 1992). Conversely Pharo and Beattie (2001) found that broad forest type was a better surrogate for vascular plant richness than other environmental variables, though one would expect the relationship between closely related taxa (plants) must typically be strong. In widespread uniform *Eucalyptus* woodlands, patterns of species richness and composition can vary spatially and temporally (Woinarski *et al.* 1988; Woinarski *et al.* 1999a, b). Preliminary investigations, not reported in this thesis, indicate that across the range of widespread regional ecosystem types, significant variation in fauna composition is accounted for by the distance between sites, a result also found for some taxa in Mitchell Grass Downs (Fisher 2001a) and eastern Australian wet forests (Ferrier *et al.* 1999). The implication is that though regional ecosystems can be shown to adequately represent variation in fauna composition, unless variation across the range of regional ecosystem is identified, each reserve selection using this classification will be sub-optimal.

Property characterised most biota moderately well, and this suggests some spatial autocorrelation between neighbouring sites. There is inescapable bias in site selection in that surveys are conducted on a property-level (which are often are dominated by a few regional ecosystem types), resulting in the clumping of quadrats that sample similar habitats. This emphasises one of the problems of reserve selection constrained by cadastral boundaries. Reserves based on properties only ever capture a subset of flora and fauna, and therefore many properties are required to capture the diversity of a region.

Vertebrate fauna composition of regional ecosystems

It is axiomatic that landscape classification is designed to simplify complex underlying environmental patterns, for both ease of conservation planning and human interpretation. However, the prevalent use of vegetation (i.e. dominant plant species) and geological and soil parameters is due to the widespread availability of data primarily derived from assessment of agricultural potential (e.g. Turner *et al.* 1993), and aerial-photo and satellite imagery for remote interpretation of these patterns (Burrough and McDonnell 1998). There is little definite expectation that they provide an adequate surrogate for patterns within all biotic systems; instead their use is purely pragmatic (Pressey and Nicholls 1991). Identification of the environmental determinants of biological patterns is commonplace (e.g. in tropical savannas, see Woinarski *et al.* 1992a; Fisher 2001a), though assessments of the relationship between *a priori* mapped landscape categories and their ability to predict patterns in other systems are few (Pressey 1994b).

In this study there was a clear partition in species composition between the more distinctive regional ecosystem types (e.g. grasslands versus woodlands), and blurring between types that were structurally similar but which varied in diagnostic over-storey species. Over half the species recorded varied significantly in abundance between regional ecosystems, but these were predominantly mammals and reptiles. Birds were more catholic in distribution, recorded more frequently in higher abundances and across a broader range of regional ecosystems. Species strongly associated with one or very few regional ecosystem types were:

- habitat specialists (e.g. Spinifexbird, *Rattus villosissimus, Pseudomys patrius* and *Trichosurus vulpecula*);
- geographically restricted (e.g. *Ctenotus rosarium* and *Lygisaurus foliorum*);
- migratory or irruptive (e.g. Painted Button-quail);
- potentially associated with temporal or seasonal resources (e.g. White-throated Honeyeater and White-plumed Honeyeater); or
- simply rare (e.g. *Paradelma orientalis* and *Ramphotyphlops unguirostris*).

Widespread species, of course, typically had more universal habitat requirements. Simple structural features common to many vegetation types predict these species' occurrence. This includes features such as open ground (e.g. Australian Magpie, *Macropus rufus* and *Ctenophorus nuchalis*), canopy and mid-storey vegetation (e.g. Pied Butcherbird, Weebill and Grey Shrike-thrush), litter and fallen timber (e.g. *Menetia greyii*, *Heteronotia binoei*), sandy soils (e.g. *Diplodactylus steindachneri*) or ground cover (e.g. *Pseudomys desertor*).

Species richness varied significantly between regional ecosystems for all taxa considered, though the pattern differed between taxa quite markedly. With birds, there was a clear association of increasing richness with increasing complexity of vegetation structure, a pattern with ample precedent (low in tussock grasslands, Fisher 2001a; intermediate in *Acacia* woodlands, Woinarski and Fisher 1995a; high in riparian systems Woinarski *et al.* 2000a; also see Chapter 3). Patterns for mammals and reptiles corresponded to key habitat and structural features deterministic of these taxa. For mammals, richness was highest in regional ecosystems with good ground cover, notably tussock grasslands (RE 37) and woodlands with hummock grass under-storey (RE's 71, 511, 51, 710) though riparian communities are included (RE 314), as they are important sources of large and hollow-forming trees for arboreal species. The surprising lack of mammal diversity in some structurally diverse and widespread woodland box and ironbark associations (RE 55, 36) is possibly related to grazing pressure, reducing ground cover (Ludwig *et al.* 2000). This is particularly problematic in that there is inescapable difficulty in trying to find patterns within the shards of a formerly more substantial fauna (e.g. Krefft 1866; Finlayson 1934). For all taxa there was a central core of regional ecosystems that did not vary in species richness. Additionally there were few common species-rich and species-poor regional ecosystems for each taxon, suggesting some independence in factors determining species diversity within regional ecosystem types.

Patterns of mean habitat breadth (Levins 1968) indicated that the species assemblages recorded for regional ecosystems were, by and large, composites of generalists and specialists. Species in all taxa were most frequently recorded in low to intermediate habitat breadth categories with birds having a peak of widespread generalists. The lack of significant variation in habitat breadth between most regional ecosystem types suggests that though some bird and reptile assemblages are nominally restricted to a specific type (e.g. tussock and hummock grasslands RE's 37, 329), the majority demonstrated little fidelity. Regional ecosystems with high mean habitat breadth that varied significantly from other type, including communities that were of intermediate to simple structural complexity (lake dune, skeletal soil woodland types), already shown to be depauperate (see chapter 3). This pattern has been recorded in other indistinct woodland communities (e.g. *Acacia shirleyi*, Woinarski and Fisher 1995b).

Two ends of a spectrum represented the greatest concordance between bird communities and vegetation types: the grasslands (as expected) and, curiously, the structurally diverse and most widespread woodlands (RE's 36, 55, 51). This reinforces the pattern for bird species found in these environments, specialists occur in more distinct environments, but suggests woodlands themselves have an evenly spread, equally abundant diagnostic group. This corresponds to the patterns recorded previously (chapter 3) where the extensive open woodlands were characterised by a core suite of species that varied only in relative abundance. The high number of bird species recorded at high abundances of the generic woodland types reinforces that there is a species pool that is associated with broad structural type, but if de-constructed and simplified (e.g. *Acacia* complexes), the composition becomes more indistinct. However within woodland structural types, regional ecosystems characterised neither fauna community nor richness. Woinarski *et al.* (1988) concluded similarly that tangible differences occurred between discrete vegetation units (e.g. vine-thicket or swamps), which disappeared within floristically variant *Eucalyptus* types. Rapid temporal and spatial variation in tropical woodland bird communities further blurs attempts to partition vegetation types with assemblages (Woinarski and Tidemann 1991).

The implication for use of regional ecosystems as surrogates or planning units for vertebrate fauna is clear. Particular regional ecosystem types have high richness and distinct fauna composition, but regional ecosystems vary a great deal in their extent, internal variability, and the distinctiveness of their fauna assemblages. Protection of the entire variety of these units at a set minimum level (e.g. 30%), may fail to capture the complete vertebrate fauna assemblages of the bioregion adequately. Some geographically widespread regional ecosystems may need greater areal protection to capture the variation of composition, whereas some small and restricted units with indistinct assemblages may have little value for protecting fauna biodiversity. Conversely some small units with discrete and restricted fauna need explicit reservation. The implications of existence of redundant land units for complete biodiversity protection have been identified previously (Pharo and Beattie 2001), though this counters expectations of representative reserve systems that capture a minimum amount of all landscapes (JANIS 1997; Sattler and Williams 1999). Inclusion of habitat and resources that directly reflect fauna needs and variation (e.g. hummock grass ground cover, number of logs or hollows, flowering period) into land classification systems is one solution (Woinarski *et al.* 1988), though this defeats the purpose of a simplified vegetation mapping system. However single taxon resource maps have been successfully designed using honeyeater communities in the Northern Territory (Woinarski *et al.* 2000b). The simple message is that developing a strategy for fauna species representation and conservation using regional ecosystems isa reasonable foundation but, as a stand-alone, is not enough.

Correspondence between regional ecosystems and species of conservation significance

Identifying the conservation significance of vegetation types is a fundamental means of protecting and regulating vegetation clearing, choosing areas for addition to existing reserves, or targeting areas for off-park management (Sattler and Williams 1999).

Concerns relating to vertebrate fauna are often secondary, not the least due to lack of data, or expectations of coincidence of biodiversity of plant and animal taxa (Stanton and Morgan 1977; Queensland Government 2001). In this study, there was no significant relationship between regional ecosystem categories of conservation status and composition of EVR species and no significant variation in the richness of EVR species between regional ecosystem types. Vertebrate and plant species richness was seldom notably different between the three conservation classifications, though species richness was consistently lower in endangered types. The low species richness in “endangered” and “of concern “regional ecosystems is possibly a reflection of reduced size (<10-30% of their former extent). However, this means that the high emphasis on this category for protection above all others (Sattler and Williams 1999) does not translate to protection of sites of high species richness. Similarly only a maximum of two threatened species were significantly more abundant in regional ecosystems of high conservation significance. The simple reality is that the protection of regional ecosystems of conservation significance will not protect species-rich regional ecosystems or sites with high abundances of significant vertebrate species. The naturally low abundances of species that are of conservation significance further complicates the problems of targeting appropriate areas of habitat for these species. This supports the contention that any investigation of the relationship between land classification and fauna distribution should not be to the exclusion of more traditional approaches that target rare and threatened species and critical resources (Pressey 1994a).

It may be unreasonable to expect that this simple triplet of categories (endangered, of concern, not of concern) will match a sparsely distributed, disparate and biologically unrelated fauna assemblage. However primary regulatory weight is placed upon such classifications (Queensland Government 2000). Ancillary means to protect other habitats of high conservation value for fauna are rarely enacted (e.g. Queensland Government 1995). There is also some generic expectation that threatened vegetation types may similarly protect threatened species (Stanton and Morgan 1977; Sattler 1993), and certain targets for native vegetation protection are adequate for representing and maintaining species biodiversity (JANIS 1997; James and Saunders 2001). These contentions are both true and false, and dependent on geography. In highly fragmented landscapes where the area of remnant native vegetation is very low, the coincidence of diverse assemblages and significant fauna quite often exists by default, the remnants being the only habitat for many species (Robinson and Traill 1996; Reid 2000). Conversely, starting from a palette of intact vegetation, the clearing of large proportions of habitat results in loss in species and abundance, and some differential increase for disturbance-tolerant species (Landsberg *et al.* 1997; James and Saunders 2001; Ludwig *et al.* 2000). In Australia there is a substantial literature on the values and management of networks of remnant and production landscapes (see Saunders *et al.* 1996; Craig *et al.* 2000).

The problem with the predominance of a conservation ethos based on fragmented landscapes is the creation of an expectation that significant or remnant vegetation adequately protects biodiversity (JANIS 1997). The positive spin on the value of small patches (e.g. Barrett 2000; Fischer and Lindenmayer 2002), while appropriate in systems already fractured, enforces a belief that small investments in conservation reserves are satisfactory. It is clear that riparian and wetland areas support distinct and diverse fauna assemblages (Blackman *et al.* 1999; Woinarski *et al.* 2000a). However overt focus on these systems creates a belief that these can be a panacea of biodiversity protection (Breckwoldt 1990). Practically narrow linear areas can be easily protected with the minor loss of arable land (Breckwoldt 1990; Arthington *et al.* 1995), but despite the biodiversity virtues of riparian systems, these areas can in fact be degraded, heavily invaded by weeds and as a result be depauperate in terrestrial fauna (Kutt and Skull 1995). There is evidence that wildlife corridors coupled with low protection targets may in reality be conservation capital of very low value (Simberloff *et al.* 1991; Saunders and James 2001).

In this study, fauna of high conservation value were found in a wide variety of environments and situations. Examples of this variety are the recording of rare and threatened species in widespread habitat (e.g. *Sminthopsis douglasi* in Mitchell Grass Downs), restricted habitat (e.g. Spinifexbird), threatened habitat (e.g. *Paradelma orientalis*), restricted but unthreatened habitat (e.g. *Pseudomys patrius*), widespread habitat (e.g. Bush Stone-curlew, Brown Treecreeper, Grey-crowned Babbler) and uncertain habitat association (e.g. *Lerista* sp nov). Thus any strategy to protect species must be multi-faceted and taxon-orientated. It has already been stated that in tropical savannas, the spatially and temporally heterogenous nature of the biological systems requires schemes that protect widespread, interconnected areas (Woinarski 1999b). Some bird species (e.g. Grey-crowned Babbler, Brown Treecreeper, Hooded Robin) recorded fairly commonly in the intact Desert Upland *Eucalyptus* woodlands have dramatically declined in temperate and sub-tropical woodlands due to fragmentation (Robinson and Traill 1996). This suggests that an approach to conserving these intact northern woodlands should pay heed to obvious errors and miscalculations made in south-eastern Australia.

Correspondence between site species richness

The identification of sites of high species richness satisfies a simple desire of conservation management to prioritise and protect the highest number of species, given limited opportunities to do so (Williams *et al.* 1996a). In part this must derive from common beliefs that areas with many species are inherently more valuable (Keto and Scott 1986), and that an area of high biodiversity for one group (a "hotspot") means high diversity for all taxa (Myers 1988, 1990). The hope is for congruence in patterns of richness of different taxa and the identification of a few indicator species that can be used as a surrogate for all species (Prendergast *et al.* 1993). Most studies have failed to identify satisfactory concordance between richness patterns for different taxonomic groups (Prendergast *et al.* 1993, Williams *et al.* 1996a; Pharo and Beattie 1997; Oliver *et al.* 1998). Even within similar guilds there have been mixed results ranging from reasonable correlation (e.g. ant groups, Fisher 2001a) to very poor relationships (e.g. butterflies and moths, Ricketts *et al.* 2002). The results of this study support previously published data indicating that sites of high richness between taxa are rarely coincident. Correlation in species richness between taxa and their largest subsets (vertebrates and birds, plants and ground cover species) were understandably strongest, though across disparate groups correlations were generally poor. Reptile and EVR species, and mammals and upper storey plant richness were the best, and the latter can at least be explained by the increase in arboreal fauna in the canopy species-rich riparian sites. Marriage between species hotspots was similarly weak suggesting that selection of diverse sites for taxa must be independent. The lack of a common order of regional ecosystem species richness for taxa discussed earlier supports this contention. Of most concern is the lack of any relationship between EVR taxa and other vertebrate groups. This emphasises that functionally unrelated and species-poor groups are idiosyncratic and uncorrelated. For example, where mammal and bird richness was moderately related, mammal and bird EVR species and *vice versa*, were not. High species rich sites for one taxon did however tend to capture EVR rich sites for those taxa.

On ecological grounds there seems to be little reason to expect that areas of high species richness should coincide for different taxa, given that determinants for species and guild abundance must vary markedly. The concept of hotspots was derived from consideration of continental scale patterns (Myer 1988). It has also been predicted that correlations among taxa are more likely in species-rich tropical habitats, which also share a common biogeographical history, high spatial heterogeneity and a high level of endemicity (Howard *et al.* 1998; Pimm and Lawton 1998). In this study, there was a low level of endemicity and species richness compared to coastal bioregions, and a high species association across Desert Uplands Subregions (chapter 2). This may be a cause for low correlation between richness patterns for different taxa. Differential scales of patterning of fauna (e.g. fine-scale for invertebrates) have previously been suggested as a reason for the lack of neat concordance between assemblage composition and richness for different groups (Ferrier *et al.* 1999; Moritz *et al.* 2002). In addition there is a conundrum of high fidelity of some tropical savanna assemblages to some habitats and the unpredictable patterns of others (Woinarski and Tidemann 1991; Woinarski *et al.* 1992c). This suggests sites themselves vary temporally and choosing sites on species richness alone does not guarantee entire community representation. The protection of many sites, which are species-rich, but similar in species composition, is not really a useful strategy for biodiversity conservation (Pressey *et al.* 1993; Margules and Pressey 2000).

Correspondence between site species composition

Methods that examine the spatial fidelity via composition at sites are considered superior and preferable to strategies based purely on species richness (Faith and Walker 1996). This is in part due to consideration of species representation rather than simple richness, and with this, the ability to examine other surrogates for composition and distribution such as environmental variation (Ferrier and Watson 1997). Matrix correlation analysis using Mantel tests is commonly used in other disciplines (see Smouse *et al.* 1986) but has also been applied in ecological examples (Burgman 1987, 1988; Clark and Ainsworth 1993; Ferrier and Watson 1997; Oliver *et al.* 1998; Pharo *et al.* 2000; Fisher 2001a). Most studies have indicated mixed results, with related taxa often best correlated (e.g. vascular and non-vascular plants, Pharo *et al.* 2000), and environmental factors are generally less effective (e.g. soils and vegetation, Burgman 1988), unless the environmental classification was in some way related to the biota being compared (e.g. forest types and plant composition, Pharo and Beattie 2001). Geographical distance has been identified as a significant influence on the effectiveness of using surrogates with the scale of environmental effect being differential on invertebrates in comparison to vertebrates and plants (Ferrier *et al.* 1999). In this study the spatial fidelity between quadrat assemblages was typically varied, but as with species richness, strong within-taxa correlations were identified (e.g. vertebrates with birds and reptiles, plants with upper and ground strata), as was some reasonable cross-taxa correspondence (birds, upper and ground strata, and mammals and upper strata). This pattern has some foundation in previously identified relationships between environmental determinants and species abundance (chapter 3). For example generalised linear modelling of abundance of many birds identified significant relationships with vegetation structure variables (e.g. basal area, bare ground, tussock and hummock grass cover), and in respect to mammals, there were discrete assemblages in floristically different tussock grass, open woodland and riparian communities (chapter 3). This is consistent with previous studies that identify that composition generally alters in a complementary manner along broad environmental gradients (Oliver *et al.* 1998; Pharo *et al.* 2000; Fisher 2001a).

The composition of species-poor groups, such as mammals and EVRs was not well related to other taxa, in particular plants. The lack of correlation may be in part due to less variation in composition of mammals and EVRs across quadrats, due to the depauperate regional species pool. This result may be inconsequential, in that using diverse taxa as a surrogate may easily capture the mammal diversity, despite the lack of relationship (Oliver *et al.* 1998). However, for biologically diverse EVRs, the lack off correlations may reflect genuine lack of pattern affiliation. This further emphasises the likelihood that targeted strategies are needed to capture individual EVR species with variable and diverse habitat requirements, rather than treatment as an entire unified assemblage.

Complementarity and minimum set selection

Reserve selection procedures, such as the simple minimum-set algorithm used here, are designed to detect overlap in quadrats, and capture rare and unique species. Though they are not as informative about the general match of assemblage composition, the patterns of site accumulation provide data that is more in keeping with the process and data requirements of practical reserve planning. That is the setting of targets for protection and assessing how well targets for some taxa are effective for capturing the diversity of other taxa (Pressey *et al.* 1993; Margules and Pressey 2000). Most reserve planning also involves representativeness at high levels (i.e. >50% capture of target taxon), rather than at the low end of the scale (Pressey *et al.* 1993).

The species accumulation curves indicated in general that a small percentage (3-6%) will always capture 50% of the taxa being targeted, but to extend the minimum set to the full complement of species many more sites are needed. In addition the most species-rich taxa will capture over 50% off all other species, yet species-poor taxa will not. This pattern is slightly anomalous to other studies that indicate that minimum-sets based using the most diverse taxa act as good surrogates for others (Pharo *et al.* 2000; Fisher 2001a). However, Pharo *et al.* (2000) examined related taxa with a very wide richness disparity (plants, vascular species n=477, sub-taxa n=44-77), whereas in Fisher (2001a) there was a lower factor of difference in the taxa diversity, but a strong climatic and structural gradients controlling composition. Using comprehensive, species-rich tropical data sets, Howard *et al.* (1998) and Balmford (1998) identified high complementarity. Conversely, in species-poor temperate environments the complementarity of sites for focal taxa is less successful (Ryti *et al.* 1992). The examples above, coupled with the example of minimum-set analysis provided by this study, suggest that in highly interconnected and heterogeneous environments where there is disparity in species richness between taxa being recorded, site complementarity techniques may be inadequate as a singular planning tool.

Other results identified that selection of fauna species using the entire range of regional ecosystems, did not capture significantly more species than a process of selecting quadrats by random. In comparison, selection by regional ecosystems performed significantly better for plant species. Typically, one may expect that a land classification system that is based on floristic features should be more comprehensive in targeting plant diversity. This has been shown to be the case for forest management units and vascular and non-vascular plants (Ferrier and Watson 1997; Pharo and Beattie 2001) though these positive results are only relevant regionally, rather than universally. It is recognised that conservation planning using regional ecosystems is a compromised technique that may not serve as an adequate surrogate all biota such as vertebrate fauna (Sattler and Williams 1999). However, setting retention targets and representativeness using this land classification, and complementary emphasis on only EVR species in Biodiversity Planning Assessments (EPA 2002) will fail to address issues of protection of vertebrate species diversity and viability of remaining conservation landscapes.

Evaluation of the regional ecosystems chosen to select the targets for each taxonomic set further emphasises that inequity between quadrat composition and land classification: many types are not used, and many differences occur in priority for species selection. Certain regional ecosystems capture high levels of species richness; others are significant for restricted and specialised fauna, whereas some, though structurally and floristically different, have fauna assemblages that are indistinct from those of many other regional ecosystems. As such, using a land classification system that aims for equal representativeness and targets those of conservation significance may fail to capture the species composition and diversity of a region. There may be an argument that longer term sampling that results in more comprehensive species lists for sites or regional ecosystems may improve the complementarity and composition correlation between taxa. Conversely the spatial and temporal fluidity of many tropical savanna assemblages has been well documented (see Introduction in Chapter 3). Therefore the selection of minimum-sets of sites to capture the range of species in a region may vary over time. The use of long-term comprehensive data may in fact cause sites or vegetation to assume high importance when it may be only of seasonal value, and the other species-poor sites may be equally valuable in a set of reserves. Most conservation planning is reliant on rapid assessment using inadequate data sets (Pressey *et al.* 1993). Ideal, comprehensive, long-term species-rich data sets are the exception rather then the norm (Howard *et al.* 1998), and in many respects may provide misleading rather than universal strategies for conservation planning. The need for a different conservation approach in tropical savannas that recognises gradual environmental variation over large geographic areas and the inherent, interconnected mosaic of these landscapes with the fauna has been eloquently argued (Woinarski 1999b).

Conclusions

The purpose of this chapter was to test the surrogacy of land classification systems (e.g. regional ecosystems) in characterising variation in the vertebrate fauna assemblage patterns of the Desert Uplands. In general regional ecosystems types have broad fidelity to fauna composition variation, though there was clear partition in species composition between the more distinctive regional ecosystem types (e.g. grasslands versus woodlands), and blurring between types that were structurally similar. The protection of regional ecosystems of conservation significance will not protect species-rich regional ecosystems or sites with high abundances of significant vertebrate species. The correlation between flora and fauna recorded was typically varied, but strongest between ecologically related groups. Tests of complementarity indicated that selecting quadrats to reserve species-rich taxa (ground cover plants, birds) will capture a majority of other species, but does not necessarily guarantee these will fully reserve the complement of rare species. Species rich taxa will perform more adequately as surrogates for species poor groups, though where environments are interconnected and more subtly graded in richness and composition of the biota, site complementarity techniques may be inadequate as a singular planning tool for capturing rare, unusual, seasonal or intangible biotic assemblages.

Though not an exercise in designing an optimal reserve system, the results have implications for conservation planning in the Desert Uplands and elsewhere. That is, bioregional planning must take into account and consider issues such as geographical representation of widespread regional ecosystem types, and targeted planning that includes consideration of species-rich areas, unique but species-poor areas and species conservation significance. The selection of reserve systems must also take into account the nature and impacts of land uses in the region in question. In the next chapter I examine the impacts of fire and grazing on the biota in a single widespread *Eucalyptus* vegetation type.

Table 4.15 Mean abundance per regional ecosystem of all species recorded in all quadrats. n = number of quadrats in which species recorded. Regional ecosystem types listed in Table 3.7

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
Apostlebird	25	6.8		8.0	3.3		5.0		0.5	4.0			0.8				2.8		3.2	1.5	9.0			2.0		2.3			
Australian Bustard	5					1.5			0.1			0.5													0.3				
Australian Hobby	2						0.3						0.2																
Australian Magpie	87	1.4	1.0		1.4	0.3	1.8	0.8	1.8		0.8	1.5	0.8	1.0	0.7	0.5	2.3	0.3	0.8	0.5	2.3	2.0	3.7		1.3	0.3	0.5	1.0	0.5
Australian Owlet-nightjar	99	0.6	0.5	1.3	1.1		1.0	1.3	1.0			0.8	0.6	2.0		1.0	1.8	0.3	0.8	0.8	1.3		1.3			0.3		1.5	1.2
Australian Raven	43	1.2		1.5	0.2		1.8	0.3	0.9	0.3		0.5	0.4	2.5			0.8	1.3	1.4	1.0		1.0			4.0	1.0			0.3
Banded Lapwing	1																							0.5					
Barn Owl	10							0.2						0.5			0.5			0.3									
Black Kite	1																						0.3						
Black-breasted Buzzard	1																			0.3									
Black-chinned Honeyeater	1							0.1																					
Black-eared Cuckoo	2							0.1																		0.7			
Black-faced Cuckoo-shrike	74	2.2	1.5	0.8	1.7		0.5	1.1	1.5	0.3	0.2		0.8	0.5		1.5	0.5	0.3	0.8	2.0	0.7	2.0			0.8	2.0	0.3	0.5	1.0
Blue-faced Honeyeater	8		2.0		0.1					1.3	0.4						1.3				0.7	1.5					1.0		
Black-faced Woodswallow	22					1.2	1.0	1.1	0.6						1.7											3.3			2.3
Black-shouldered Kite	3						0.3					0.8																	
Black-throated Finch	2							0.1	0.3																				
Blue-winged Kookaburra	14	1.0	1.0	0.5	0.1				0.3								0.5		0.4	1.5									
Brolga	1																							0.5					
Brown Falcon	20	0.2	0.5	1.0				0.4					0.4			1.0					0.7			0.3					0.7
Brown Goshawk	4							0.1											0.2		0.3		0.3						
Brown Honeyeater	19		2.0	1.5	0.1		0.8				7.0		0.2		3.7		0.8	7.3		3.5							0.5		
Brown Quail	4													0.5															1.5
Brown Thornbill	1																	0.7											
Brown Treecreeper	16		3.0		1.8		3.0	0.1	0.3											1.0						1.3			
Brush Cuckoo	2			0.8	0.1																								
Buff-rumped Thornbill	7	1.8		3.0							1.6				0.7	3.5		1.3											
Bush Stone-Curlew	2								0.2																0.5				
Channel-billed Cuckoo	7				0.1		0.8		0.3				0.2																0.2
Chestnut-rumped Thornbill	4							0.3		1.3																		5.0	
Cockatiel	22		2.0		1.1			0.7	0.6	2.0		2.5					1.0		0.6		4.7	5.5		2.5					0.7
Collared Sparrowhawk	3												0.2			0.5													
Common Bronzewing	31	0.6		0.3	0.4			0.5		0.3		0.5	0.2				0.3		0.6		0.3		0.3						2.2
Crested Bellbird	65	0.4		0.5	0.7		0.5	3.0	0.5			1.0	0.2		0.3	1.0			1.0							3.7		1.5	3.7
Crested Pigeon	36	3.6		2.0	1.4		1.0	1.0	0.2			0.5								1.0	0.7	2.0	2.0		1.0	0.7		1.5	0.7
Diamond Dove	15	1.2			0.2			0.2		1.0		1.3		1.5						0.5									3.2

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
Double-barred Finch	9	1.4			0.1		1.0			2.7									5.6	2.8									0.7
Dollarbird	7	0.2						0.2											1.0										
Emu	16			1.0	0.3			0.2	0.2	2.7		0.3	1.0				0.5		0.2	0.5							1.3	1.0	
Forest Kingfisher	2				0.1				0.1																				
Galah	39	4.0		0.5	0.6	2.3	1.5	0.1	0.2	0.7		6.0	0.8						6.8	2.3	0.7	1.0	3.3	1.0	0.5		1.0		1.3
Grey-crowned Babbler	49	7.0	1.0	2.3	2.2	1.0	2.3	0.4	1.1	2.0		1.0	1.0				2.8		6.8	1.3	3.3	6.0	2.0		1.5	5.3			6.0
Grey Butcherbird	63	1.8	0.5	2.5	0.6		2.8	0.7	0.2		1.6		0.4	2.0		2.0	2.3	1.0	0.8	0.5	1.0		1.0			0.7	0.3	0.5	0.2
Grey Fantail	3				0.1						0.2		0.2																
Grey Shrike-Thrush	59	1.2	1.5	2.5	0.2		1.0	0.9	0.5		1.0		0.6	0.5	0.3	2.0	1.0	1.3	0.6	2.5						1.0			1.3
Grey-fronted Honeyeater	4								0.5										0.6							3.7			
Ground Cuckoo-shrike	6					1.5						0.8									1.3					1.0	1.5		0.3
Hooded Robin	6							0.5																					
Horsfield's Bronze-Cuckoo	26			0.3	0.1			0.6		0.3								0.3										0.5	0.8
Inland Thornbill	2							0.2					2.4																
Jacky Winter	66	2.0	1.5	1.8	1.5		1.3	2.3	1.6		0.2		0.4			3.0			1.4	1.0						3.3		0.5	2.0
Laughing Kookaburra	8		1.5		0.1		0.3				0.4		1.4				1.3	0.3											
Little Button-Quail	7							0.2																0.3	0.5			0.5	
Little Eagle	1																			0.2									
Little Friarbird	55	4.2		9.0	2.6		3.8	0.5	0.5	6.0	0.6	0.5	1.2	0.5		1.0	3.0	0.3	2.6	3.5			0.3			3.7			3.3
Little Woodswallow	16							0.9	0.1										0.8									0.5	
Magpie Goose	1					1.0																							
Magpie-Lark	55	2.0	2.0	2.0	0.9	0.3	1.8	0.2	0.3	0.7		0.8	0.6				0.8		1.0	1.8	3.0	3.5	1.0		1.5				0.8
Masked Lapwing	1																							0.3					
Masked Woodswallow	5							0.2																					4.7
Mistletoebird	32	0.4	1.0	1.3	0.5			0.3					1.0			4.0	0.3			0.5	1.0	1.0			1.0				0.7
Nankeen Kestrel	12				0.1	0.2				1.0					0.3				0.2				0.3	1.5	0.3		0.8		
Noisy Friarbird	50		9.5		2.0		1.8	0.5	3.8		7.0		4.4	9.0			5.3	1.3	1.2	1.3	0.3					2.7	3.0	1.5	
Noisy Miner	1										1.2																		
Olive-backed Oriole	17	0.4		0.8	0.4		0.8		0.1				0.2						0.8	0.8	0.3					0.3			
Pale-headed Rosella	26	0.2		0.5	0.3		1.3	0.3	0.4	0.7			0.8	1.0					1.2	1.8		3.0	1.0						0.3
Painted Button-Quail	6				0.2														0.6				0.7						
Pallid Cuckoo	29			0.3	0.2		0.3	1.4	0.2										0.4										0.2
Peaceful Dove	37	1.0	1.0	2.5	2.1		2.5	0.5	1.5	2.0						3.0			1.4	4.8					0.5				
Pheasant Coucal	9			0.8	0.1	0.2	0.3	0.1	0.3																				
Pied Butcherbird	110	2.8	3.5	0.8	3.1		1.5	1.7	2.9	0.7	0.2	2.8	1.6	2.5		3.0	1.5		2.4	3.3	3.3	1.0	3.7		0.5	1.7	1.0	2.5	2.2
Pied Currawong	8										0.6		2.2		0.7			2.3											
Rainbow Bee-eater	25			0.5	0.4		1.0	1.1	0.2				0.2						1.2	0.8						0.7			
Rainbow Lorikeet	7							0.2	0.2	1.7									0.4	3.0							1.5		
Red-backed Fairy-wren	13		2.0		3.6			0.1	0.9									2.0									1.0		

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
Red-backed Kingfisher	19				0.7		0.5	0.3	0.5			0.3																	0.2
Red-browed Pardalote	13							0.7																		0.3			0.8
Red-chested Button-Quail	5					1.5											0.3		1.2										
Restless Flycatcher	2				0.1																								
Red-tailed Black-Cockatoo	3				0.2		2.8	0.1																					
Red-winged Parrot	30	0.6		0.5	0.6		0.8	0.2	0.2			1.5	1.0			3.0	2.0		0.4	3.3	0.7		3.3		0.3				0.8
Richard's Pipit	7					0.5																		4.0	1.8				
Rufous Songlark	4			0.8	0.1							0.5																	0.7
Rufous Whistler	94	2.2		3.3	1.6		2.5	4.4	1.8	0.7	1.2		1.2	1.0	0.3	4.0	0.8	0.3	3.4	1.8					0.3	4.0		3.0	6.8
Rufous-throated Honeyeater	3																												4.0
Sacred Kingfisher	17	0.2	0.5		0.7		1.5	0.1	0.1		0.2		0.2						1.0	1.0					0.3				
Shining Bronze-Cuckoo	4						0.5				0.2							0.3	0.2										
Singing Honeyeater	62		2.5	0.8	0.5		2.3	3.9	0.1	1.7		0.8	0.4		2.0		2.5		2.0							0.3		0.5	3.3
Southern Boobook	36		1.0	0.5	0.7		0.3	0.2	0.2				0.4	2.0			0.5	0.3	0.2		0.3		0.7			0.3		0.5	
Spiny-cheeked Honeyeater	28		0.5	0.5	0.6		0.8	0.3		0.3							0.8		0.6	1.0					1.0		0.5	2.0	2.0
Spinifexbird	4																										4.3		
Spotted Bowerbird	14		0.5	1.3			0.3		0.1								0.3		0.4	1.3		0.5				2.3			0.3
Spotted Harrier	1					0.2																							
Spotted Nightjar	16							0.3	0.1			0.5	0.4		0.3										0.3		0.3		0.7
Squatter Pigeon	7								0.6					2.0			1.0		0.8	0.5									
Striped Honeyeater	44	1.2	7.0	5.8	0.6		1.0	0.9	0.5				0.8	1.5		3.0	5.5	0.7	2.4	2.5						3.7			
Striated Pardalote	50		6.5		2.1			0.5	0.9	2.3	1.4		1.0	7.0			4.0	3.0	0.4	2.0	0.3		1.7			1.3		1.0	
Sulphur-crested Cockatoo	11				0.3			0.1	0.1								0.3			1.0			1.0	2.3					
Tawny Frogmouth	20	0.2			0.1		0.3	0.1	0.2			0.5	0.6			1.0				0.5			0.3					0.5	
Torresian Crow	20		0.5		0.8			0.1	0.5				0.4								1.0		1.0			0.3	1.5	1.0	
Variegated Fairy-wren	25			1.0	0.9	0.8	2.5	0.9	0.8				0.4		4.0	5.0	1.0		2.6	5.0									
Varied Lorikeet	1																			0.5									
Varied Sittella	9			1.3	0.1		0.8	0.8	0.7																				
Weebill	51		2.5		2.1		7.3	0.7	1.8	2.7	3.6	1.0	2.8	6.5	4.0	8.5		3.3	7.0	3.5						5.7		5.0	6.7
Western Gerygone	10							0.3	0.2										0.4										0.2
Wedge-tailed Eagle	6					0.3	0.5					0.3								0.3									
White-bellied Cuckoo-Shrike	5		1.0		0.1						0.2							1.7											
White-breasted Woodswallow	2																									2.0			0.3
Whistling Kite	3			0.3		0.2														0.3									
White-plumed Honeyeater	5				0.4															3.5									
White-throated Gerygone	3				0.1			0.1																		0.7			
White-throated Honeyeater	6										4.8							0.3											
White-throated Nightjar	1																	0.3											
White-winged Fairy-wren	3					1.7																			4.5		2.8		

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
White-winged Triller	12				0.6			1.1												0.5									
Willie Wagtail	58	2.6	1.0	1.0	0.6	0.3		0.9	0.8	1.3		0.3	0.4		0.3	4.0			1.0	0.5					0.8	2.0		0.5	0.8
Yellow-rumped Thornbill	26	2.6		2.8	0.9			1.4	0.5	3.3									3.8	0.8						1.0		2.0	1.2
Yellow-throated Miner	63		2.5	1.0	3.0	0.8	8.3	1.5	2.5	4.0		8.5	0.4	6.5					7.0	0.5	11.3	12.5	11.3		0.5	2.7		3.0	2.7
Zebra Finch	3				0.2			0.3																					
Aepyprymnus rufescens	1						0.3																						
Lagorchestes conspicillatus	4						0.5		0.3			0.8																	
Leggadina forresti	1					0.2																							
Leggadina lakedownensis	1																										0.5		
Macropus dorsalis	1												1.8																
Macropus giganteus	28	1.4		0.1	0.1	0.6	0.6	0.5	0.2	1.9		0.4				1.9	0.1		0.3	1.1						0.1	1.6	0.4	1.0
Macropus robustus	19		0.4	1.5			0.1	0.5		0.6		0.6	2.5	0.7	0.7		1.1	0.1	0.1	0.2								1.0	
Macropus rufus	16	2.2	0.3	0.3	0.2	0.7	0.8			0.4		0.2			0.1	0.4	0.2		0.9	1.0	0.2	0.4	0.5	0.4	0.1	0.6			0.2
Petaurus breviceps	3								0.1											0.3	0.3								
Planigale ingrami	1					0.3																							
Planigale maculata	5										0.6			0.5	0.3														
Planigale tenuirostris	1															0.5													
Pseudomys delicatulus	41			0.5	0.3		1.5	1.7	0.1		5.2		0.2					0.7	0.6	0.5				0.3				1.0	0.5
Pseudomys desertor	46	0.4					1.8	4.6	0.2	0.3	0.6	10.8			3.7				0.2	0.3							7.0	1.0	0.3
Pseudomys patrius	5												0.6		0.7			1.3											
Rattus sordidus	1				0.1																								
Rattus villosissimus	3					2.0																							
Sminthopsis douglasi	3					1.0																							
Sminthopsis macroura	39	2.0			0.1	0.7	0.5	0.8	0.4			2.8			0.3		0.5							0.3	1.8			1.0	0.5
Sminthopsis murina	1												0.6																
Tachyglossus aculeatus	28	0.2					0.5	0.4					1.6						0.2	0.3								1.0	0.7
Trichosurus vulpecula	6				0.1														1.2	3.3									
Amphibolurus burnsi	2	0.4																											
Amphibolurus gilberti	7		1.0	0.8	0.1												0.3			1.3									
Amphibolurus nobbi	31		0.5		0.2			1.0		2.0		0.5	0.2	0.5					1.0										0.8
Aspidites melanocephalus	1				0.1																								
Boiga irregularis	1								0.1																				
Carlia munda	24				0.3		0.3	0.1	1.5		0.2	1.8	0.2							3.5							0.3		
Carlia pectoralis	3		2.5														1.8												
Carlia schmeltzii	3										0.2							1.0											
Chlamydosaurus kingii	2				0.1																0.3								
Cryptoblepharus carnabyi	14			0.3	0.1		0.8	0.2		0.3									0.4	2.0								0.5	
Cryptoblepharus plagiocephalus	15		1.5		0.3				0.1								0.8				5.0	0.5	0.7		0.5		0.3		

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
Ctenotus capricorni	25							1.6																				1.5	
Ctenotus hebetior	54				1.5		1.5	2.8	0.1	7.3		0.5			0.3				10.2	0.3	7.0		6.7	0.8		0.3			
Ctenotus ingrami	4												0.2	0.5	0.3					0.5									
Ctenophorus nuchalis	19							0.3	0.2						0.7						0.3		0.3	0.8	0.3	0.3			0.3
Ctenotus pantherinus	28						0.3	1.6							1.3			0.3	0.2								1.0	1.5	0.2
Ctenotus robustus	13				0.2				0.2					1.0						0.3						0.3	1.0		
Ctenotus rosarium	14							1.4			0.2																		
Ctenotus spaldingi	14						0.5					1.5						2.0		0.5			0.3						0.8
Ctenotus strauchii	17			1.8	0.5			0.1	0.2			1.3	1.8	3.5	0.3													4.0	0.8
Delma tincta	3					1.3																							
Demansia atra	1								0.1																				
Demansia psammophis	4							0.1	0.1								0.3												
Denisonia devisi	1					0.2																							
Diplodactylus ciliaris	5			0.5	0.1														0.6										
Diplodactylus conspicillatus	21				0.5		0.8	0.4			0.2	0.8	1.4						0.2									3.5	0.3
Diplodactylus steindachneri	49		0.5	1.5	0.9		1.5	0.9	0.4				0.2	0.5	1.3			0.3	1.4			2.5	0.3	0.3		2.0		0.5	1.8
Diplodactylus tessellatus	3	1.2																											
Diplodactylus vittatus	5												0.6				0.5	0.7											
Diplodactylus williamsi	15							0.3			0.2				0.3			0.3								1.0	0.3	1.0	
Diporiphora australis	11				0.2				0.6		1.6																		
Diporiphora winneckei	1																										0.3		
Egernia striolata	14	2.4		1.3	0.2								1.2			6.0	0.3		0.2										
Eulamprus sokosoma	1														0.3														
Furina diadema	1																			0.3									
Gehyra catenata	28	4.0		3.8	0.3								0.8	0.5		5.5	7.5		0.2		2.3	4.0	2.0		1.5				
Gehyra dubia	14				0.6				0.2												1.7		0.3						
Gehyra variegata	11	4.6			0.1							0.3	0.2			3.5			0.2	0.8									
Glaphyromorphus punctulatus	1										0.2																		
Heteronotia binoei	52	0.6	0.5	0.8	0.6		1.3	0.3	0.8	0.3	0.2		0.8			0.5			0.6	0.5	3.0	0.5	0.3			2.3		0.5	0.3
Lerista sp nov	1							0.1																					
Lerista muelleri	14		1.0					0.1			0.6		0.6				0.3	0.3				2.5						1.5	
Lerista punctatovittata	13			0.5	0.2		0.3			1.3									1.4	2.0	0.3								
Lerista wilkinsi	1																	0.3											
Lialis burtonis	16				0.1			0.3			0.2								0.4									0.5	0.3
Liasis stimsoni	1															0.5													
Lygisaurus foliorum	2										0.4																		
Menetia greyii	52				1.2		2.0	0.7	0.6			1.3						0.3	1.0		0.7		1.0	0.5	0.8	1.7			1.5
Menetia timlowi	6										0.8		0.8		0.3			0.3											
Morethia boulengeri	12	0.4	2.0	1.8	0.1									0.5			1.8		0.2								0.5		

Species	n	31	33	34	36	37	39	51	55	57	59	71	73	75	77	91	92	104	310	314	317	319	321	322	323	328	329	511	710
Morethia taeniopleura	6							0.1							0.3														
Nephrurus asper	4												0.6				0.3	0.7											
Oedura castelnaui	8			0.8			1.0				0.8		0.4					0.3	0.2										
Oedura marmorata	5							0.2					0.2																
Oedura rhombifer	4						0.3				0.6							1.0	0.4										
Paradelma orientalis	2																0.5												
Pogona barbata	36	0.2		0.3	0.4		0.5	0.4	0.1	0.3		0.3	0.2				0.8		0.2		1.7	1.0	0.3			1.0			0.3
Pogona vitticeps	1	0.2																											
Proablepharus tenuis	24						0.3		0.5		0.8	2.3			0.3			0.7	0.6	1.8						0.3		3.5	1.0
Pseudonaja nuchalis	4									0.3		0.3									0.3		0.7						
Pseudonaja textilis	1																					0.5							
Pygopus nigriceps	15		0.5	0.3	0.1			0.1					0.8						0.2	0.3								0.5	0.3
Ramphotyphlops ligatus	2		0.5																							0.3			
Ramphotyphlops sp	2									0.3									0.2										
Ramphotyphlops unguirostris	2																		0.2										
Rhinoplocephalus boschmai	2								0.2																				
Rhynchoedura ornata	17							0.5	0.1										0.2	0.3									
Simoselaps australis	4							0.1																					0.3
Simoselaps warro	1																												
Suta suta	10	0.4		0.3		0.5		0.1											0.2						0.3				
Tiliqua multifasciata	2																								0.3		0.3		
Tiliqua scincoides	5				0.1			0.1															0.3						0.2
Tympanocryptis lineata	5					0.5																					1.5		
Varanus gouldii	7				0.1			0.1																			0.3		0.2
Varanus panoptes	1																				0.3								
Varanus tristis	33				0.3		0.8	0.4	0.2	0.3	0.8		0.2						0.6			0.5	0.3					0.5	0.8

Chapter 5. Effects of grazing and fire on fauna and flora in *Eucalyptus similis* tropical savanna woodland.

"At length, tracing the dry bed of a creek, (Warrigal Creek, from the many Warrigals or dingoes), he crested the forest-clad Main Dividing Range. A curious sight appeared - trees plastered with yellow earth: these trees, called yellowjacks, are soft wood, so white ants enclose them with earth walls and eat the wood out, leaving shells which first strong wind or bush-fire sweeps away. Around these grew gaudy poison-bush."
(p. 49. Bennett 1928).

Introduction

There is little argument that fire has profoundly influenced the historical evolution and current patterns of biota on the Australian continent. This is clear from the predominance of fire-dependent and promoting flora (Kershaw *et al.* 2002). Other indications of the importance of fire include systems of biota inexorably linked to fire age (Williams and Gill 1995), and climatic patterns that result in fierce seasonal electrical storms sparking wildfire (Cook and Heerdegen 2001). There is also strong evidence of a long history of prescribed burning by Aboriginal land managers (Hallam 1985; Crowley and Garnett 2000). However with European settlement, there was a rapid cessation of pre-existing regimes (Bowman 2000; Yibarbuk *et al.* 2001) and a shift to regimes dictated by pastoral land use and human property protection (Crowley and Garnett 2000). There has been vigorous debate on the extent and importance of traditional Aboriginal burning (e.g. Flannery 1994; Benson and Redpath 1997), though there is general acceptance of an impact on biodiversity (Bolton and Latz 1978; Burbidge and McKenzie 1989; Franklin 1999). This has led to recognition of the value of environmental history to inform current land management (Fensham 1999; Crowley and Garnett 2000; Bowman 2001; Vigilante 2001).

Regardless of the detail regarding scale, frequency, season and size of the regime change, a wholesale shift is evident, and at least coarsely, this is coincident with changes in species diversity (Burbidge and McKenzie 1989; Franklin 1999). Many plant and animal populations follow clear trajectories of increase or decline with time since fire (Williams and Gill 1995). It follows from this that fire will promote a change in composition of plant and animal assemblages, and changes in the fire regime may well have effects on species diversity. The post-European shift has been from fine-scale mosaic burning to one of greater extremes (Burbidge and McKenzie 1989), typically involving one or other of the following:

- deliberate fire exclusion to protect property, stock and ground cover;
- secondary exclusion via continuous grazing removing fuel load;
- complete abandonment of burning in more remote areas, resulting in occasional large-scale fires; or
- a greater frequency of hot, extensive fires.

These changes in regime have resulted in homogenisation of plant and animal composition, loss of particular resource dependent species and, in some instances, decline of those species needing a longer time lag between burning (Burbidge and McKenzie 1989; Bowman and Panton 1993; Franklin 1999).

The historical effects of grazing on Australian ecosystems contrast with those of fire, but they may be equally significant. Since the Late Pleistocene extinction of megafauna, Australia has lacked large native herbivores. The disappearance of the megafauna may have been due to human impact, although this is still debated (Flannery 1994; Horton 2000; Bowman 2000), but it appears to have had little impact on Australian ecosystems. Rather, it has been argued that invertebrates (e.g. termites, ants and grasshoppers) are this continent’s significant herbivores, with a diversity and biomass beyond other comparable systems worldwide (Andersen and Lonsdale 1990). However the current regulatory influence of invertebrates on ecosystem function is still far from being understood (Andersen and Lonsdale 1990; Andersen 2000).

The key event regarding grazing impacts is again post-European change and the massive influx of mammalian herbivores, both hard-hoofed ungulates (sheep and cattle) and rabbits (Lunney 2001). Pastoralism is currently the dominant land use across northern Australia, occupying 60% of the total area (Ash *et al.* 1997) and was introduced to Queensland savannas as early as the 1860’s (May 1984). Grazing alone causes only moderate localised change (such as the removal of ground cover or compaction of soil), but the increasing density of artificial water-points (foci for intense grazing activity) exacerbates these impacts markedly (James *et al.* 1995). In intact environments, this creates a patchwork of piospheres (gradients of intensity of livestock grazing) and ultimately an undifferentiated environment of consistent low ground cover and low plant species richness with a preponderance of less palatable and disturbance-tolerant species (Landsberg *et al.* 1997). Refuges of unaffected, heterogeneous resource rich habitat become uncommon as the density of artificial watering points is increased (Landsberg and Gillison 1996). Coupled with more serious transformations of the landscape such as tree clearing for non-native pasture development, remnant vegetation becomes fragmented, degraded and species poor (Barrett 2000; Ford *et al.* 2001). Bird and mammal species that rely on a dense and floristically diverse ground cover have declined under livestock grazing both in Australia and elsewhere (see reviews in Fleischner 1994; James *et al.* 1999; Woinarski *et al.* 2001a).

Unfortunately the potential of tropical savanna woodlands for pastoralism has been notoriously romanticised (Smith 1994), despite frequent failure of early and current pastoral enterprises (Bennet 1928; Holmes 1996; Ash *et al.* 1997). The reports of explorers typically emphasised wet season resource abundance, and ignored the dramatic seasonality of tropical savannas and the key period of scarcity prior to the wet season (Smith 1994). The response of pastoralists to this has been to shift stock type (sheep to English cattle breeds to Brahman cattle breeds), and to consistently try to modify the landscape resources to standardise annual conditions for stock. This has been via the provision of more water points, pasture improvement with introduced grasses, addition of lick to increase use of poor forage, and tree-clearing to promote pasture growth (Gardener *et al.* 1990; Ash *et al.* 1997). Paradoxically this generally creates degradation and a shift from mixed pasture to a monoculture of perennial grasses, and finally ephemeral grasses or unpalatable species, accentuating the end of dry season resource slump (Ash *et al.* 1994; Ludwig *et al.* 1997).

Native fauna are adapted to this pattern of seasonality, and utilise strategies that compensate for climatic uncertainty, such as dispersal and resource tracking, resource switching within a mosaic home range, and localised extinction and contraction to refuges ready for post-rainfall irruption (Woinarski 1999a). Fundamental to this is access to heterogenous habitat, at a variety of scales. There is a clear recognition that economically sustainable rangeland management also equates to ecological sustainability, and that future stewardship of tropical savannas should embrace a philosophy of land management that in fact creates environments conducive for biodiversity conservation (Ash 1996). Ironically, the conditions most suitable for viable cattle grazing in tropical savannas partly mirror requirements for native fauna (Ludwig *et al.* 1997), yet management for "conservation" is anathema to many pastoralists, despite the shared goal of healthy landscapes (Landsberg *et al.* 1998).

Cattle-grazing in the Desert Uplands has a long history and is the dominant land use (Smith 1994; Rolfe *et al.* 2001). However tree clearing for more intensive production is become more widespread, with the south-eastern parts of the bioregion having undergone some of the highest clearing rates in Queensland (Fairfax and Fensham 2000; Rolfe *et al.* 2001; Neldner *et al.* 2002). The largest and central sub-region of the bioregion is the Alice Tableland, dominated by sandstone ranges and deep red sandy soils of intact Tertiary sandsheets (Sattler and Williams 1999). This area is also the least developed in the bioregion, due to low fertility, and therefore has few artesian bores and little other infrastructure, with some parts identified nominally as wilderness (Morgan *et al.* 2002). A single vegetation type - open *E. similis* woodland with *Triodia pungens* ground cover (regional ecosystem 10.5.1 *sensu* Sattler and Williams 1999) - dominates this area and was chosen to examine the effect of grazing and fire on the vertebrates, ants and plants. Despite the aforementioned low fertility, these areas are still actively grazed. This woodland type is also notable in the region in that many properties have long or permanently ungrazed paddocks due to the presence of heartleaf poison bush *Gastrolobium grandiflorum*, which is toxic to cattle. This plant can only be removed by intensive mechanical means, and though many areas have been treated and are grazed by cattle, many paddocks are left unutilised, or at least used only in extreme circumstances such as drought. Additionally the presence of dense and highly flammable *Triodia* ground cover results in intentional and unintentional periodic burning, more regularly than in surrounding woodlands with predominantly tussock grass ground cover.

In previous chapters I demonstrated that the vertebrate fauna composition of the Desert Uplands has been moulded by broad historical and landscape factors. The bioregional species pool is a function of its geographic position on the Great Dividing Range, being at the boundary of a number of zoogeographical barriers (chapter 2). As such there is an intermingling of arid inland and wet coastal species, and turnover between a number of related and sibling fauna species from the east to west of the bioregion (chapter 2). Some patterns of fauna composition within regional ecosystems are defined by the structural and environmental extremes of many vegetation types. Conversely within the more homogenous widespread woodlands, the fauna assemblage is more integrated with subtle habitat factors responsible for changes in species abundance and composition (chapter 3). One of the more distinct fauna assemblages is that of the widespread *Eucalyptus similis* community, demarked by high reptile and small mammal abundance, endemic and disjunct species and habitat features such as hummock grass cover and deep sandy soils. As indicated above, fire and grazing are primary modifiers of many Australian environments. In the *E. similis* regional ecosystem, there are sites that express the range of influence of these impacts. In this chapter I examine the effect of fire patterns and grazing impacts on a unified biotic assemblage. In particular I aim to determine:

- whether fire and grazing have any impact on vertebrate, invertebrate and plants species, guilds or functional groups;
- whether there is variation in the nature of response by different taxa and guilds; and
- whether there is an interacting effect between fire and grazing that causes amplification or muting of any patterns recorded;

In order to address these questions I have undertaken the following analyses:

- examination of the correspondence between *a priori* grazing and fire class categories and the pattern of composition of vertebrates, ants and plants using analysis of similarity and ordination;
- examination of the correlation between changing environmental factors due to the grazing and fire impacts, with the pattern of ordination for vertebrates, ants and plants using principal axis correlation,
- using generalised linear modelling, investigation of which predictor terms (grazing and fire) significantly account for variation in abundance in the most frequently recorded vertebrates and ant species and guilds, and whether there is any interacting effect between grazing and fire; and
- examination of the shift of plant composition at each quadrat site of known fire and grazing history, using weighed mean ordination scores that indicate the relative

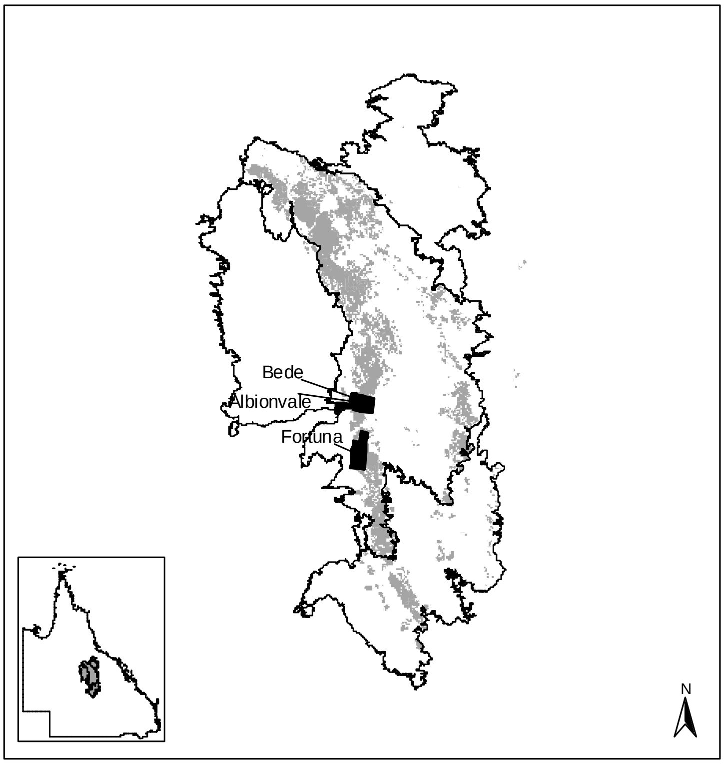
influence of species on the ordination pattern. Individual species variation between sites was investigated using analysis of variance, while the correspondence between floristic and fauna composition was tested using Mantel correlations.

Methods

Study sites

All sampling was conducted on three properties, Fortuna, Bede and Albionvale Stations, which lie between 50-100 km north of Aramac, within the Desert Uplands bioregion (Figure 5.1). The latter two share a boundary while Fortuna is separated by 50 km to the south, though all are situated within the southern end of sub-region 2 within the Desert Uplands bioregion. Four treatment types were identified and sampled: sites actively grazed and burnt recently (within 2 years); sites actively grazed and unburnt (last burnt >2 years ago, but typically at least 5 years prior to sampling); ungrazed sites burnt recently; and ungrazed sites, unburnt. Though landholders could not provide exact stocking figures, discussions indicated that the carrying capacity and hence stocking rate for this type of vegetation is consistent across the region. All sampling sites were situated in typical examples of the vegetation types, and away from features that might have provided confounding influences, such as tracks, water-points and fence lines. An attempt was made to equally spread the treatment types over the two broad property clusters, though there were no grazed and recently burnt (<2 years) sites at Albionvale or Bede. All sampling sites were located within the same regional ecosystem type: *Eucalyptus similis* open woodland on deep red earths of the Tertiary sand-plain, including small areas of *Eucalyptus melanophloia* or *E. whitei* on low rises and *Corymbia brachycarpa* in depressions (Sattler and Williams 1999).

Figure 5.1 Location of Fortuna, Albionvale and Bede Stations where sampling was undertaken. Distribution of *Eucalyptus similis* regional ecosystem (10.5.1) indicated by shading.



Vertebrate sampling

Vertebrate fauna sampling was conducted between late December and early February 1999-2000 (wet season) using the standardised quadrat procedure described in chapter 3. Twenty-nine sites were sampled: six sites actively grazed and burnt recently (within 2 years); eight sites actively grazed and unburnt (last burnt >2 years ago); seven ungrazed sites burnt recently; and eight sites ungrazed and unburnt. Habitat and environmental data for each quadrat was recorded (see chapter 3) for the twenty-nine sites.

Plant sampling

For each quadrat, floristic data was recorded: species presence, cover abundance, height and basal area. Methods for sampling plants are described in chapter 3.

Ant sampling

Ants were sampled in twenty-six quadrats: six sites actively grazed and burnt recently (within 2 years); seven sites actively grazed and unburnt (last burnt >2 years ago); six sites ungrazed and burnt recently; and seven sites ungrazed and unburnt.

Ants were sampled at each site using a line of ten pitfall traps (4 cm diameter) with 2 m spacing, located at the centre of each quadrat. Each trap contained 50 mL of 70% ethanol as a preservative, as well as a small amount of glycerine to reduce evaporation. Traps were operated for a single 48-hour period at each site. The sorting of ant captures was greatly simplified by considering only relatively large (total body length >4 mm) species, as has been successfully done elsewhere in northern Queensland (Andersen *et al.* 2001). Using this threshold, only the following ant taxa (nomenclature follows Andersen 2000) were considered: all spp in the genera *Bothroponera*, *Brachyponera*, *Camponotus*, *Leptogenys*, *Myrmecia*, *Odontomachus*, *Opisthopsis*, *Polyrhachis* and *Rhytidoponera*, as well as the *diversus* group of *Meranoplus*, the *aeneovirens* group of *Melophorus*, the *sjostedti* group of *Tetramorium*, and *Iridomyrmex hartmeyeri*. Many of the species are undescribed, and have been assigned code letters that apply to this study only. Voucher specimens of all species are held at CSIRO’s Tropical Ecosystems Research Centre in Darwin.

Analysis

The composition of species in the quadrats was examined with ordination on two axes using semi-strong hybrid multi-dimensional scaling derived from Bray-Curtis association (dissimilarity) indices (Belbin 1995). Ordinations used abundance data, and were performed on plant cover, vertebrate and ant abundance. Only species recorded in more than one quadrat were used in the ordination, and all abundance data were range transformed.

Analysis of similarity was used to examine the significance of assemblage differences between classes imposed on the sample array Bray-Curtis dissimilarity scores (see chapter 3 for further description, Clarke 1993). In this case the relationship between grazing (2 classes), fire (2 classes) and site location (2 classes) was examined for vertebrates, ants and plants, and sub-groups of these including birds, mammals, reptiles, non-avian families, bird functional groups, ant functional groups, canopy cover, mid-storey cover and ground cover. Species were assigned to bird functional groups after Woinarski and Tidemann (1991) and ant functional groups after Andersen (1995).

Principal axis correlation (PCC) was used to examine the correlation between environmental and habitat measures with the ordination pattern (see chapter 3 for further description, Belbin 1995).

Generalised linear modelling was used to examine the variation in occurrence of vertebrates and ants in relation to four main predictor terms: grazing; fire age; site; and the interaction between grazing and fire age. From these a minimum adequate model was derived using a backwards-stepwise procedure, and a Poisson (log-linear) error distribution, as this provides the best fit to count data that contains many zero values (Crawley 1993). Grazing and site were treated as categorical factors (grazing present or absent, site cluster Bede/Albionvale or Fortuna), and fire as continuous (months since last burn). Mean quadrat abundance and richness, total species and fauna group (as indicated above) abundance were examined, and only vertebrate and ants recorded in more than one quadrat were included in the species analysis.

Plant species responses were not modelled due to the high number of species with low cover abundance, the high number of species recorded in fewer than five quadrats, and the predominant focus on fauna response in this chapter. However as vegetation patterns will often drive the fauna assemblage structure, the general floristic change between quadrats of different grazing and fire history is illustrated by calculating the weighted mean ordination scores for species recorded in more than five quadrats. Weighted mean ordination score is the cover abundance score for each species multiplied by the ordination axis score for each site, averaged over the number of quadrats in which the plant species was recorded. These scores indicate which species most influence the pattern of quadrat placement within the ordination. Mean cover abundance scores were also calculated for these plant species, and non-parametric one-way analysis of variance was used to identify which species varied significantly in cover among quadrats.

The correlation between plant and fauna composition was examined via Mantel type tests using Relate in PRIMER (see chapter 4 for further description, Clarke and Gorley 2001). Comparisons were made between plant, canopy, mid-storey and ground cover abundance with vertebrates, birds, mammals, reptiles, non-avian families, bird functional groups, ants and ant functional groups.

Results

Vertebrate composition

A total of 113 vertebrate species were recorded from all sites, representing 74 birds, 32 reptiles, and seven mammals. Of these, 84 were recorded in more than one quadrat and used to model the response to grazing, fire and site effects. The most abundant species (recorded in >50% of the quadrats) were the Pallid Cuckoo, Rufous Whistler, Singing Honeyeater, Australian Owlet-nightjar, Jacky Winter, Crested Bellbird, Pied Butcherbird, *Macropus giganteus*, *M. robustus*, *Pseudomys delicatulus*, *P. desertor*, *Ctenotus capricorni*, *C. hebetior* and *C. pantherinus*. Thirteen bird foraging guilds and eleven non-avian families were represented by these species, with foliage gleaners (13 species), granivores (14 species), terrestrial omnivores (15 species), geckoes (6 species) and skinks (14 species) being the most species-rich.

Variation among quadrats in species composition is illustrated in Figure 5.2. Although the ordination is not very robust (stress = 0.31), it was not substantially improved in three dimensions, and so only two dimensions are presented. However, as the ANOSIM indicated, the segregation of quadrats showed a highly significant ecological patterning, with especially good correlation with fire class (on axis 2).

Environmental variables significantly associated with the ordination space are also shown in Figure 5.2. Quadrats that were unburnt lie on the upper end of a gradient defined by high hummock grass and total ground cover, and higher foliage projective cover for species between 1-3 m. At the other end of the scale, the recently burnt quadrats are characterised by high bare ground and forb cover, and high ground cover species richness. The variables reflecting cover (percentage total cover and bare ground), both have the highest correlation coefficient (r=0.74 and r=0.76 respectively), and are obviously negatively inter-correlated. However these vectors best illustrate the wholesale change associated with change in fire age; the change in ground cover. The vertebrate composition of the sampled sites is possibly responding to this shift. A vector for canopy height lies parallel with the first ordination axis indicating independence from fire age, some sites being characterised by a higher canopy, but irrespective of time since fire.

The mean scores for those environmental variables, which were significantly correlated to the ordination pattern, are tabulated for the fire and grazing treatments (Table 5.1). These further illustrate the nature of the change between the grazing and fire treatments, and how the interaction between grazing and fire has a compounding or attenuating effect. Analysis of variance indicated the most significant variation was measured for bare ground and forb cover (increasing with either grazing or fire), tussock grass cover (increasing with grazing, but decreasing with fire), and hummock grass and total cover (decreasing with either grazing or fire). However the pattern is more complex in respect to the interacting terms. Bare ground and forb cover is significantly higher in the grazed and burnt sites and substantially higher again in the ungrazed and burnt sites. Tussock grass cover was highest in the grazed and unburnt sites, and at a magnitude of at least four times higher than any other treatment. Finally hummock grass cover is at its lowest level in both burnt and unburnt grazed sites.

Figure 5.2 Two-dimensional ordination of quadrats by vertebrate fauna composition labelled with fire class, including significant environmental vectors. Bare ground cover (GCBARE) r=0.76***, Hummock grass cover (GCHUMM) r=0.51**, Forb cover (GCFORB), r=0.45*, Canopy height (CANHEIGH) r=0.52**, Ground cover plant species richness (GSRICH) 0.53**, Ground cover total (GSCOVER) r=0.74***, Foliage projective cover 1-3m (FPC1-3), r=0.62***. Probability levels are *p<0.05, **p<0.01, ***p<0.001. N=no fire, F=fire.

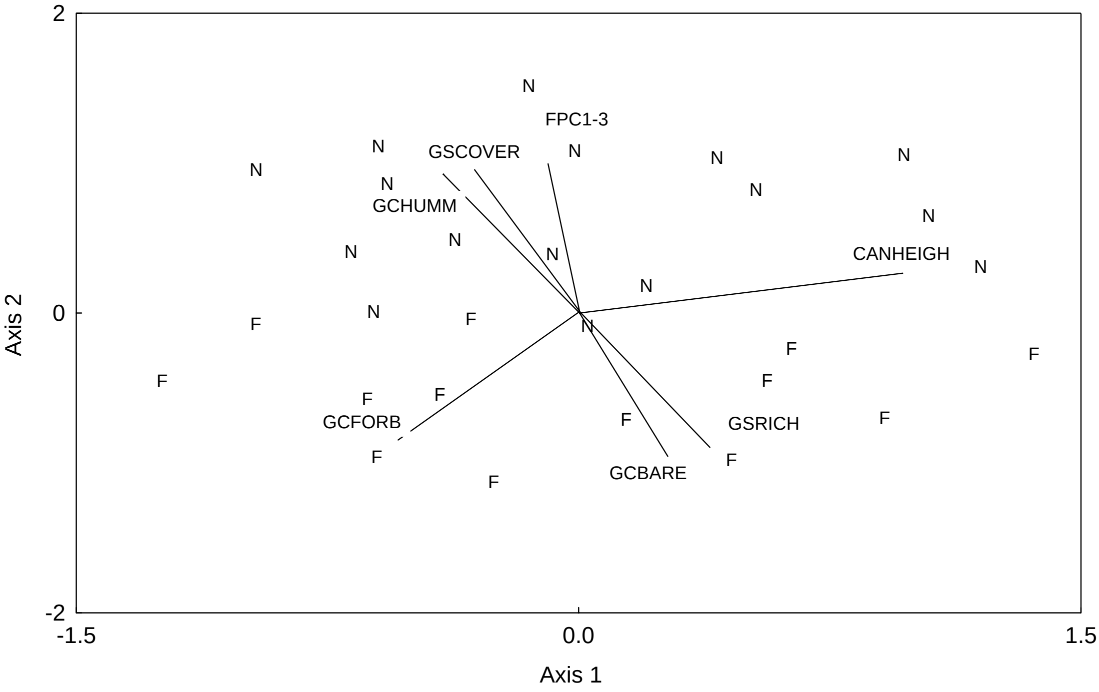


Table 5.1 Mean scores for all habitat measures identified as significant vectors in both the fauna and ant ordinations. Data provided includes both the means for simple fire and grazing treatments, and for the 4 compound treatments of fire and grazing. Kruskal-Wallis ANOVA (H) by ranks undertaken between the four compound treatments only. N=no fire, F=fire, G=grazed, U=ungrazed. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant.

Variable	Fire	No fire	Ungrazed	Grazed	N+G	F+G	N+U	F+U	H	p
Bare ground cover	62.31	32.81	39.33	53.21	40.63	**70.0**	25.0	55.71	22.63	***
Hummock grass cover	21.92	44.06	46.33	21.07	27.50	12.50	**60.63**	30.0	18.57	***
Tussock grass cover	5.08	12.63	5.47	13.29	**20.50**	3.67	4.75	6.29	7.18	*
Forb cover	5.31	3.31	2.87	5.64	3.88	**8.0**	2.75	3.0	8.11	*
Fallen trees diameter >10cm	7.15	5.44	4.80	7.71	6.25	9.67	4.63	5.0	4.99	ns
Modal height of termite mounds	0.24	0.19	0.21	0.21	0.19	0.25	0.20	0.23	1.17	ns
Canopy height	7.38	8.69	7.73	8.50	9.50	7.17	7.88	7.57	5.54	ns
Canopy cover	8.08	12.81	11.0	10.36	13.13	6.67	12.50	9.29	7.43	ns
Ground cover height	0.30	0.58	0.52	0.40	0.54	0.20	**0.63**	0.39	15.86	**
Ground cover plant richness	11.54	7.75	7.87	11.14	9.88	**12.83**	5.63	10.43	11.96	**
Ground cover total	31.92	60.0	54.67	39.64	51.88	23.33	**68.13**	39.29	22.34	***
Foliage projective cover 1-3m	1.23	1.94	1.53	1.71	**2.13**	1.17	1.75	1.29	8.32	*
Foliage projective cover <0.5m	2.62	4.13	4.0	2.86	3.50	2.0	**4.75**	3.14	18.11	***

Vertebrate species and groups

Analysis of similarity indicated that vertebrate assemblages were most strongly segregated by fire treatment, but also varied significantly between the two sites (Table 5.2). Similarity between quadrats as defined by their bird species composition was likewise (but less strongly), associated with differences in fire treatment and, less so, site. Fire was also strongly associated with the similarity between quadrats as defined by their mammal species composition ($p<0.001$), reptile species composition ($p<0.05$), composition of bird functional groups and non-avian families (both $p<0.01$). There was also a strong association between the similarity between quadrats in their reptile species composition and site ($p<0.001$), and grazing ($p<0.001$).

The responses of individual species and ecological/taxonomic groupings of species are described below. In the description of these results, only those bird, mammal and reptile species and groups showing a significant response to the model terms will be listed, though those showing a site effect alone will be discounted from further discussion. Others with grazing, fire or an interacting response will be highlighted, though if also including a site response, it is understood that this may be confounding the grazing and fire effects, but not to the extent to negate the significance of the effect.

In general there are two main fire and grazing responses for biota. Fire or grazing can lead to either an increase in abundance (fire and grazing increaser) or decrease (fire and grazing decreaser). This is often in response to vegetation changes, such as cover or floristic composition. Where the interaction term is significant, the pattern is more complex (see examples within taxonomic group results).

Table 5.2. Analysis of Similarity (ANOSIM) relationships between Bray-Curtis dissimilarity matrices based on abundance, and *a priori* classifications for fire, grazing and site groups. Significance identified via permutation tests. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns=not significant.

Taxon	Fire (n=2)	Site (n=2)	Grazing (n=2)
Vertebrates	0.362***	0.194**	0.059 ns
Birds	0.195**	0.137*	0.03 ns
Mammals	0.533***	0.05 ns	0.008 ns
Reptiles	0.102*	0.291***	0.153**
Non-avian families	0.313**	0.102 ns	-0.008 ns
Bird functional groups	0.173**	0.059 ns	0.001 ns
Ants	-0.044 ns	0.174**	0.164**
Ant functional groups	0.035 ns	-0.06 ns	0.035 ns
Plants	0.274***	0.267**	0.38***
Canopy	0.302***	-0.018 ns	-0.022 ns
Mid-storey	0.134**	0.529***	0.239***
Ground	0.299***	0.154**	0.297***

Bird species and foraging groups

Mean bird abundance was highest in quadrats located in unburnt sites, though mean species richness was constant (Table 5.5). Of the 54 bird species used to model a response to the fire, grazing and site treatments, 11 species and eight foraging groups recorded significant effects. Striped Honeyeater and Pied Butcherbird recorded a significant change in abundance across the two site groups only.

Black-faced Woodswallow, Red-browed Pardalote and Singing Honeyeater recorded a significant response to fire only, the former two being more common in recently burnt areas, and the latter increasing with time since fire (Figure 5.3). The foraging guilds Hawkers and Nectarivore/Gleaners similarly by increasing and decreasing respectively in burnt areas. Hawker species (including Black-faced Woodswallow, Dollarbirds and Little Woodswallows) all increased in abundance at burnt sites, though Black-faced Woodswallows were the most abundant and influential for the pattern in this group. Singing Honeyeaters were the most abundant member of the Nectarivore/Gleaner group and this accounts for the response of this group.

Grey-crowned Babblers increased in abundance in grazed sites, while Cockatiels declined in abundance, though there was a confounding site effect. Foliage gleaners increased in abundance in grazed quadrats, though few individual species indicated any clear pattern to this effect.

Pallid Cuckoos, Jacky Winters, Rufous Whistlers, Rainbow Bee-eaters, Salliers, Granivores and Trunk Gleaners all significantly responded to the interaction of fire and grazing. The modelled relationship is illustrated for the four species (Figure 5.4-5), and two guilds (Figure 5.6) that identify the typical variation. Jacky Winters decreased in abundance with time since fire, but more dramatically when the quadrats were also grazed. Pallid Cuckoos similarly declined in abundance with time since fire, but remained at higher abundances if the quadrats were also grazed. Both Rainbow Bee-eaters and Rufous Whistlers increased rapidly in abundance with increasing fire age in grazed sites, but remained at stable numbers if grazing was absent. The two guilds identified contrary patterns: Granivores decreased in abundance with time since fire (fire increaser), but more notably in grazed environments (grazing decreaser); and Terrestrial Insectivores increased in abundance in quadrats long unburnt (fire decreaser), but more distinctly in the samples that were also grazed (grazing increaser). Terrestrial Insectivores generally increased in abundance with time since fire, a pattern accentuated in grazed environments, perhaps influenced by species such as Magpie-larks and Grey-crowned Babblers.

Figure 5.3 Modelled relationship between abundance of Singing Honeyeater, Black-faced Woodswallow, Red-browed Pardalote, *Ctenophorus nuchalis* and Pygopodidae with increasing time since fire. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.

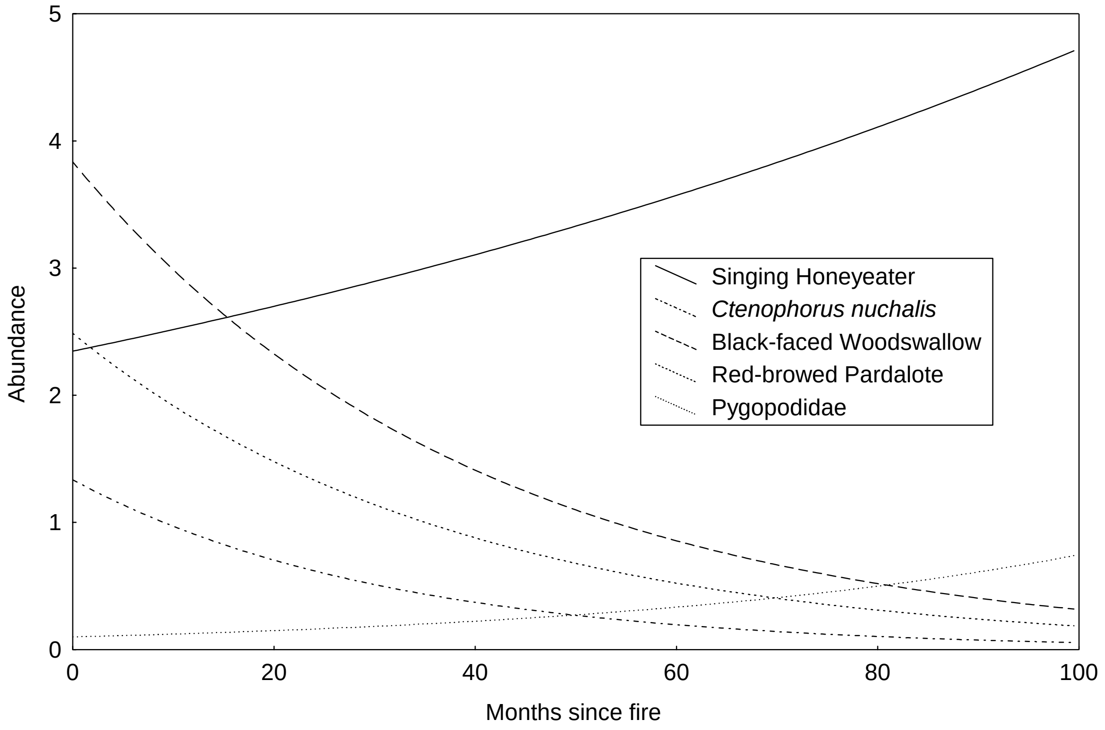


Figure 5.4 Modelled relationship between abundance of Rufous Whistler and Pallid Cuckoo with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.

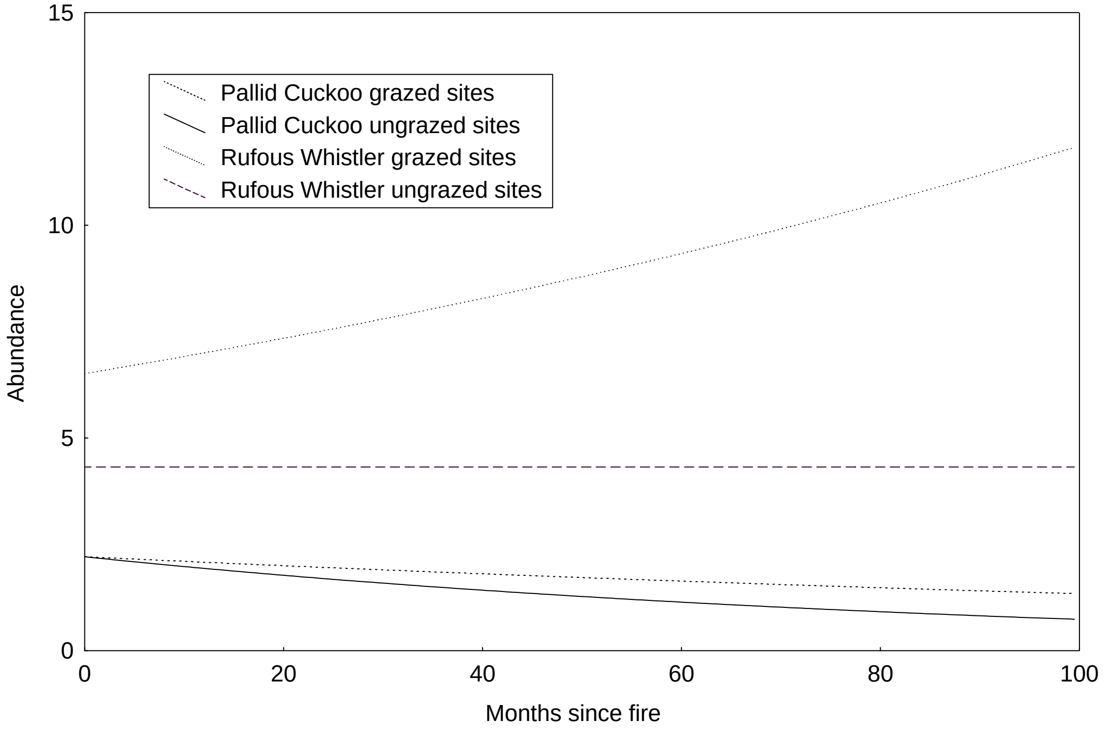


Figure 5.5 Modelled relationship between abundance of Jacky Winter and Rainbow Bee-eater with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.

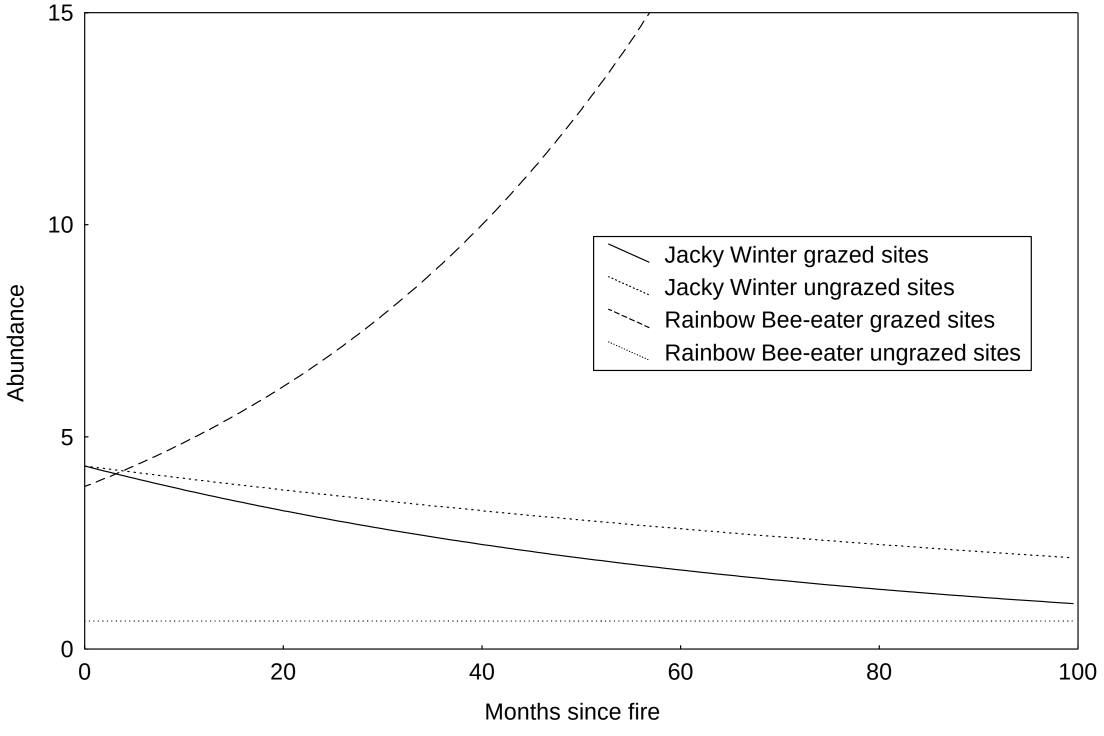
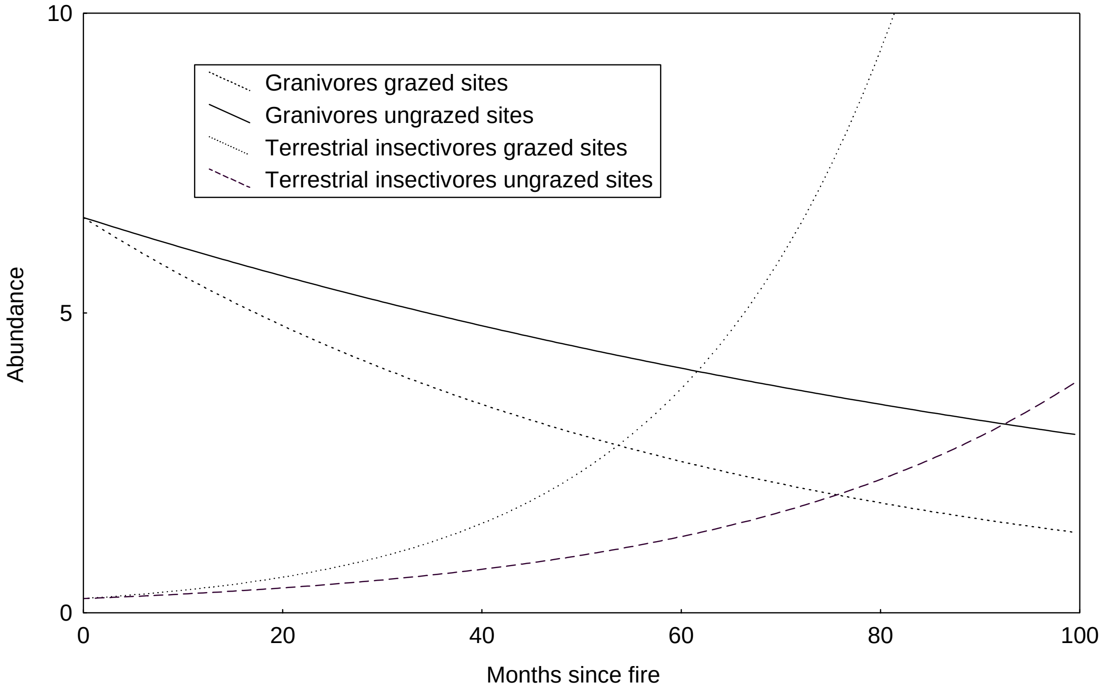


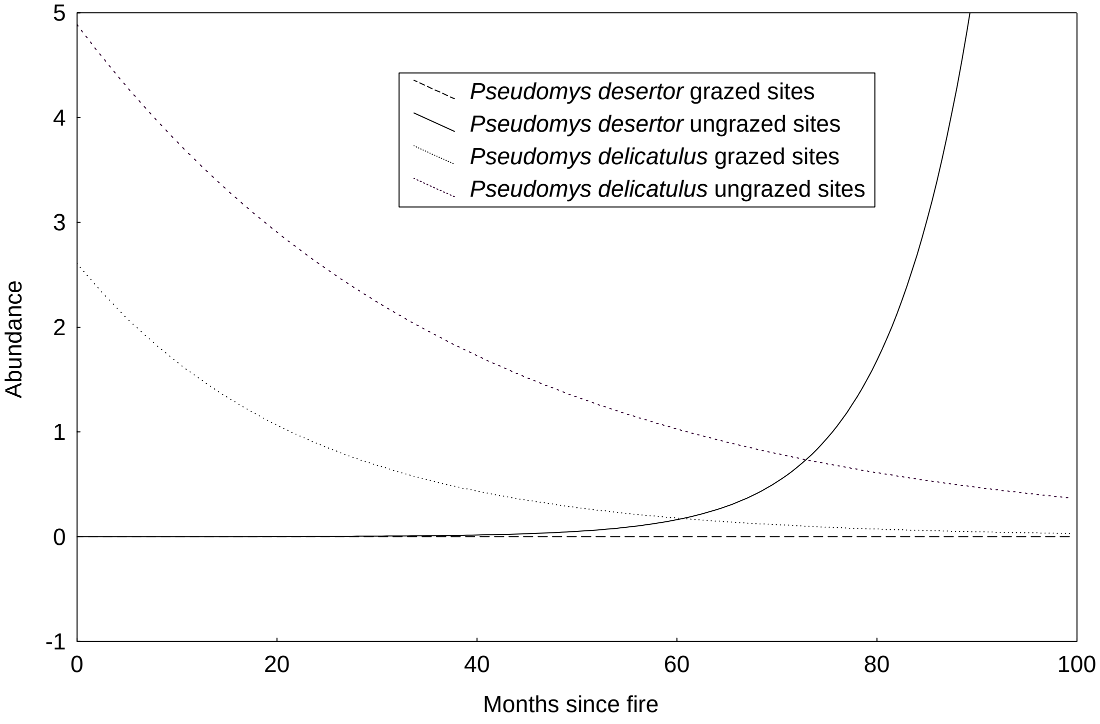
Figure 5.6 Modelled relationship between abundance of Granivores and Terrestrial Insectivores with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.



Mammal species and families

Mean mammal abundance varied significantly with the fire/grazing interaction term clearly increasing in abundance after fire in grazed sites, but remaining constant across fire ages in the absence of grazing. Mean mammal species richness was invariant across all treatment classes. Of the six mammal species used to model a response to the fire, grazing and site treatments, five species and three families recorded significant effects. Dasyuridae, *Sminthopsis macroura* and *Macropus giganteus* recorded a significant change in abundance across the two site groups only. *Macropus robustus* and Macropodidae abundance declined with increasing time after fire and decreased in grazing sites, though the response of Macropodidae in general was small. There was a fire/grazing interaction for both *Pseudomys delicatulus* and *P. desertor* (Figure 5.7). *Pseudomys delicatulus* was most abundant in quadrats recently burnt, with a steep decline as time since fire increases. A similar response is modelled with the addition of grazing, though the initial high abundance decreases more rapidly to close to zero when time since fire is beyond 80 months. Conversely *P. desertor* was almost entirely absent from quadrats recently burnt, and did not appear again until over three years post fire. In quadrats that were also grazed, re-establishment was strongly suppressed. Though the fitted curve suggests absence of *P. desertor* in sites grazed and burnt, some were recorded, though in the majority of sites they were absent.

Figure 5.7 Modelled relationship between abundance of *Pseudomys desertor* and *P. delicatulus* with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.



Reptile species and families

Agamidae, Scincidae, *Pogona barbata*, *Ctenotus rosarium* and *Menetia greyii* abundance all indicated a simple response to grazing, the first two families and species all decreasing in abundance and the latter skink increasing. *Ctenophorus nuchalis* demonstrated a simple fire increaser response, with Pygopodidae decreasing, not significantly influenced by grazing (Figure 5.3). *Ctenotus pantherinus* significantly decreased in abundance in response to both fire and grazing, without any interacting effect between the two, though abundance was markedly lower in quadrats that were grazed (Figure 5.8). Gekkonidae and *Ctenotus hebetior* abundance was significantly predicted by the interaction between grazing and fire (Figure 5.9). The abundance of Geckoes and *Ctenotus hebetior* remained constant with time since fire, but with the addition of grazing both decreased in abundance.

Figure 5.8 Modelled relationship between abundance of *Ctenotus pantherinus* with increasing time since fire, with and without grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.

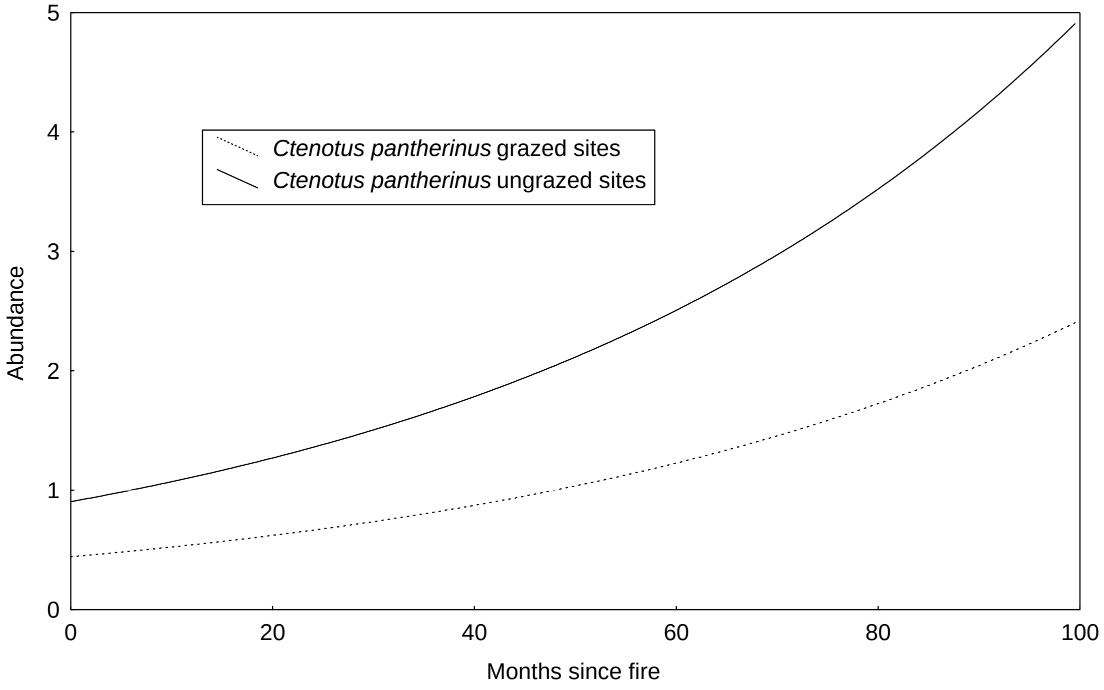
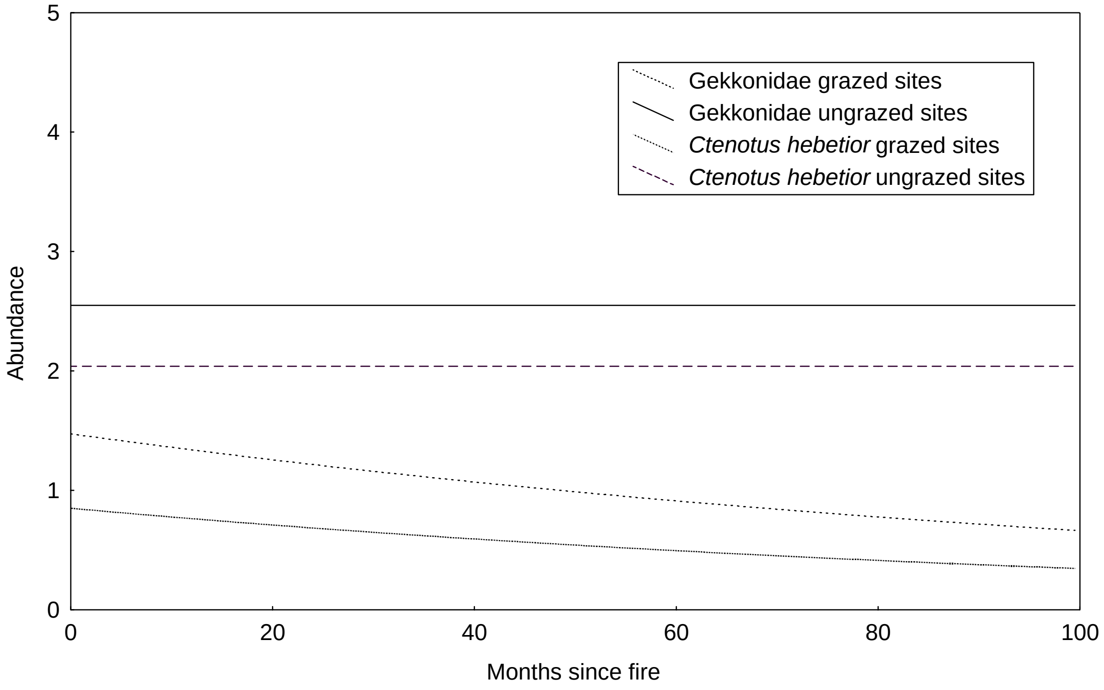


Figure 5.9 Modelled relationship between abundance of geckos (Gekkonidae) and *Ctenotus hebetior* with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.5.

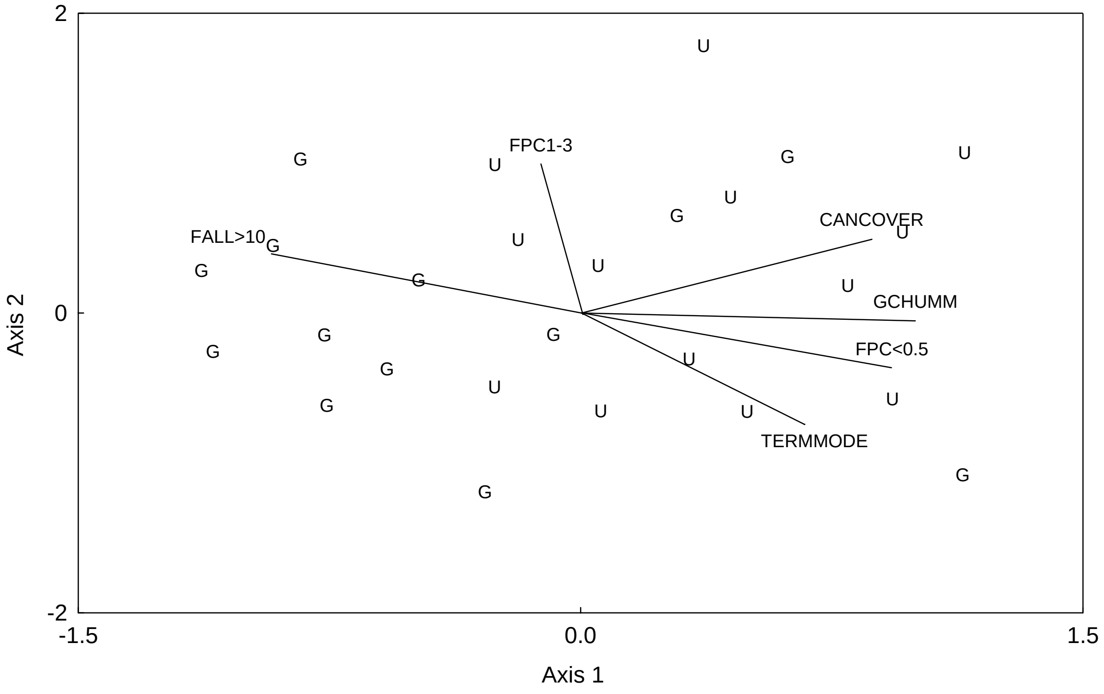


Ants

In contrast to vertebrate fauna, analysis of similarity indicated that the three treatments were moderately poor discriminators of ant species and functional group composition (Table 5.2). Ant species were weakly identified by site and grazing classes, while ant functional groups indicated no significant *a priori* response to any grouping. Variation among quadrats in species composition is indicated in a single ordination of all species abundances combined, again not robust (stress = 0.33), but also not substantially improved in three dimensions. Though site and grazing classes weakly characterise assemblage differences, quadrats labelled with these categories indicated a good segregation of quadrats, though only grazing types are shown in the ordination (Figure 5.10).

Six environmental variables significantly identify the gradients that separate the sites in the ordination (Figure 5.10). Quadrats that were ungrazed were characterised by high to intermediate canopy cover, hummock grass cover, foliage projective cover of species less than 0.5 m and termite mound size, while grazed sites were predominantly at the opposite end of this spectrum. A general gradient of high numbers of logs on the ground in grazed sites was also evident, and this variable was the most highly correlated with the ordination pattern (r=0.56). A vector perpendicular with the second ordination axis indicates a gradient of high to low foliage projective cover of plants from 1-3 m in height though this is independent of grazing category and is likely again reflecting site differences.

Figure 5.10 Two-dimensional ordination of quadrats by ant composition labelled with grazing class, including significant environmental vectors. Foliage projective cover 1-3m (FPC1-3) r=0.33*, Modal height of termite mounds (TERMMODE) r=0.37*, Foliage projective cover <0.5m (FPC<0.5) r=0.37*, Hummock grass cover (GCHUMM) r=0.42*, Canopy cover (CANCOVER) r=0.43*, Fallen trees diameter >10cm (FALL>10) r=0.56**. Probability levels are *p<0.5, **p<0.01, ***p<0.001.



Ant species and functional groups

A total of 39 ant species from six sub-families and six functional groups were collected during the study. The most abundant species (recorded in >50% of the quadrats) were *Myrmecia callima*, *Rhytidoponera* sp nr *hilli*, *Rhytidoponera* sp C (*mayri* gp), *Camponotus* sp nr *denticulatus* and *Melophorus* sp A (*aeneovirens* gp). Opportunists (8 species) and Subordinate Camponotus (18 species) were the most species rich and abundant groups.

Mean ant abundance was generally higher in unburnt and grazed sites, but was significantly explained by the grazing/fire interaction. Generally abundance increased in grazed sites, or in burnt sites, if they were also grazed. Of the 23 ant species used to model a response to the fire, grazing and site treatments, nine species and five functional groups recorded significant effects.

Myrmecia callima, *Rhytidoponera* sp A (*tyloxys* gp) and *Rhytidoponera* sp nr *rufithorax* abundances all responded simply to grazing alone, the first two being less abundant in quadrats that were grazed, and the latter more abundant in grazed sites (Figure 5.11). *Melophorus* sp A (*aeneovirens* gp) abundance decreased with time since fire, but with the overall pattern being muted in quadrats also grazed (Figure 5.12). As this species dominates the Hot Climate Specialist group it accounts for the same significant response and pattern to grazing and fire shown by this functional group.

Figure 5.11 Modelled relationship between abundance of *Rhytidoponera* sp nr (*rufithorax*) and *Myrmecia callima* with increasing time since fire, with and without grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.6.

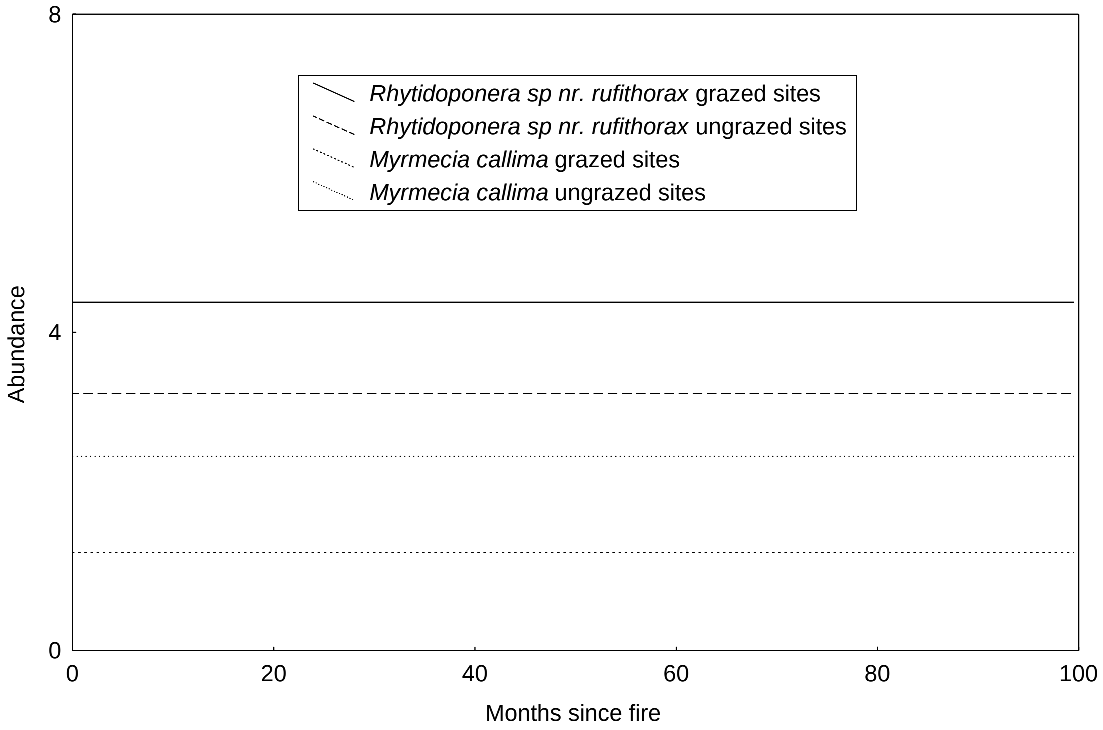
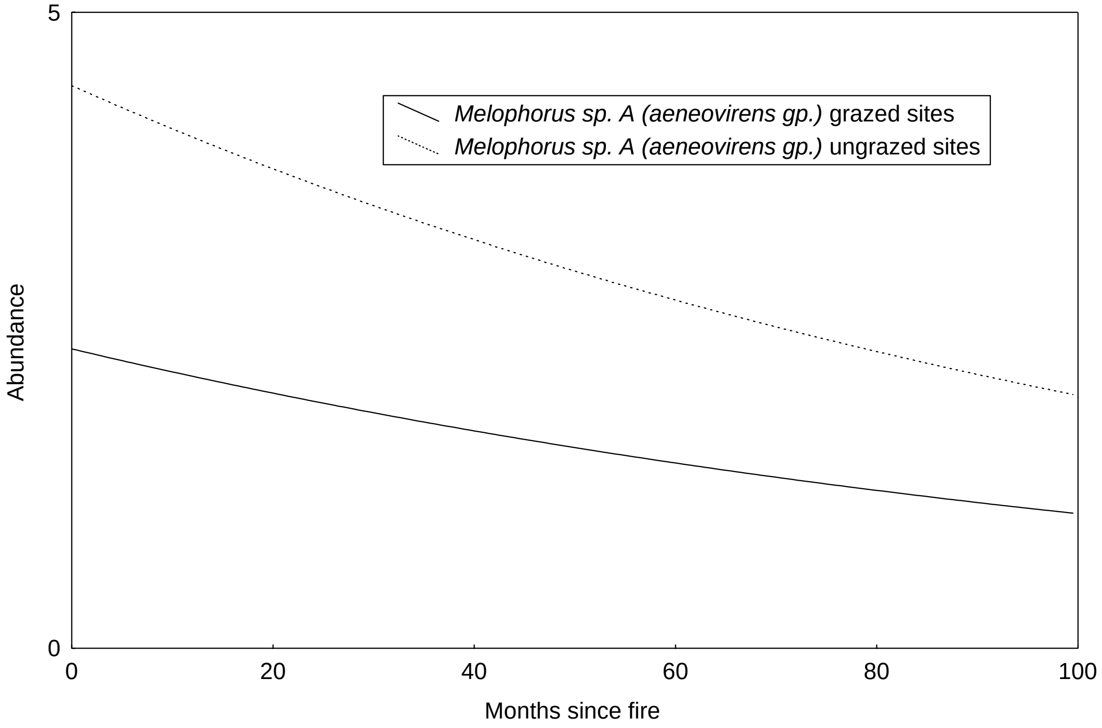


Figure 5.12 Modelled relationship between abundance of *Melophorus* sp A *(aeneovirens gp)* with increasing time since fire, with and without grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.6.



Abundances of six species and one functional group were best explained by grazing, site and grazing/fire interaction terms. Both *Iridomyrmex hartmeyeri* and *Tetramorium* ?*sjostedti* abundance illustrate the interacting relationship between grazing and fire (Figure 5.13). Both ant species were consistently abundant in quadrats over all fire ages if they were not grazed, but were recorded in low numbers in grazed sites where their abundance declined as time since last fire increased. *Rhytidoponera* sp C (*mayri* gp) and *Camponotus* sp nr *denticulatus* demonstrated an opposite interacting pattern to the previous example (Figure 5.14). Each species remained in consistent numbers over increasing time since fire, but in grazed sites both increased in abundance, *Rhytidoponera* sp C (*mayri* gp) initially at higher abundances in comparison to the ungrazed burnt sites, and *Camponotus* sp nr *denticulatus* at lower abundances. Specialist Predators, Opportunists and *Rhytidoponera* sp nr *hilli*, all similarly showed a positive and complex response in abundance due to the interaction between fire and grazing at each quadrat (Figure 5.15). They generally increased over time since fire, regardless if cattle were present or not.

Figure 5.13 Modelled relationship between abundance of *Iridomyrmex hartmeyeri* and *Tetramorium ?sjostedti* with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.6.

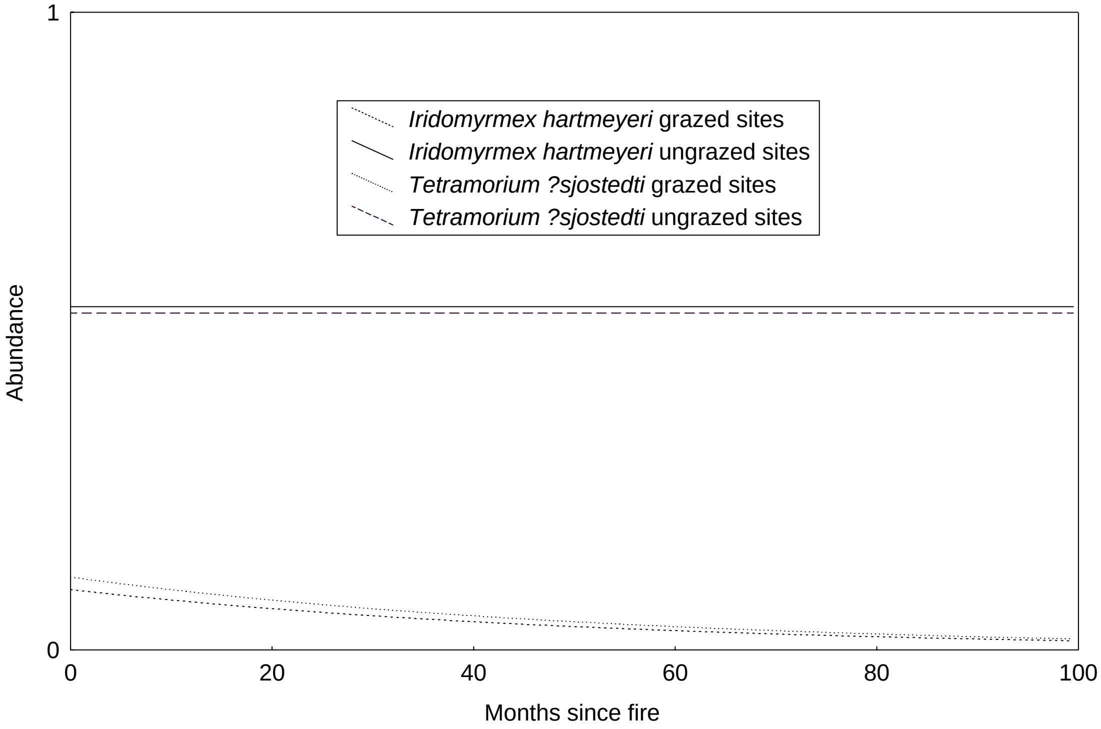


Figure 5.14 Modelled relationship between abundance of *Rhytidoponera* sp C (*mayri* gp) and *Camponotus* sp nr *denticulatus* with increasing time since fire, and including the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.6.

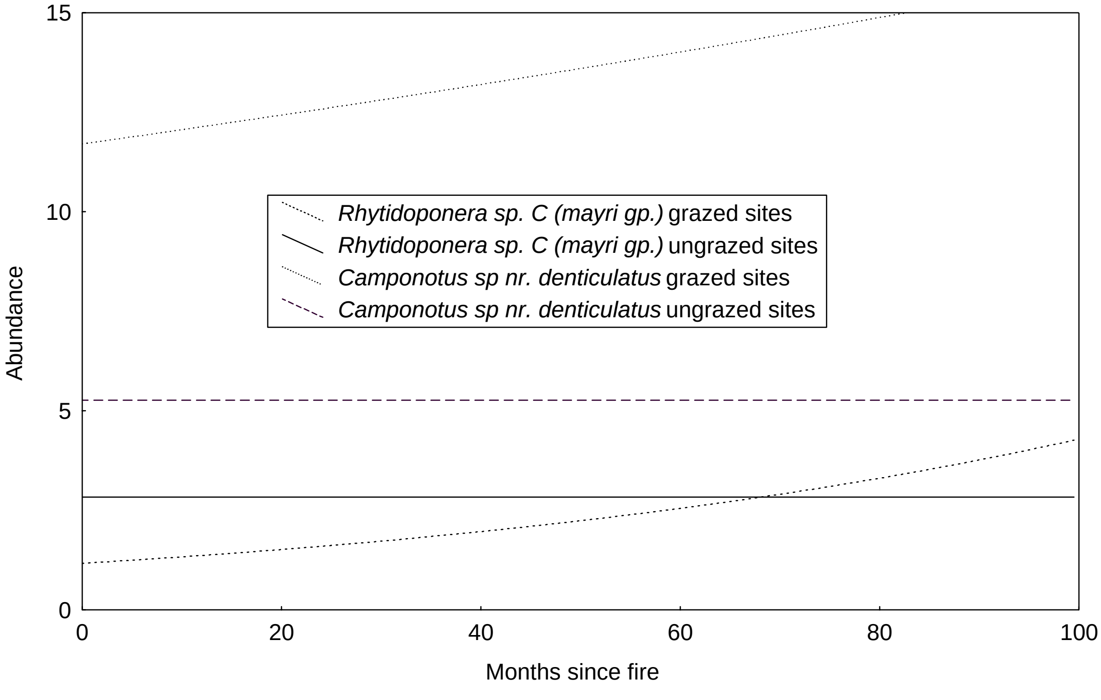
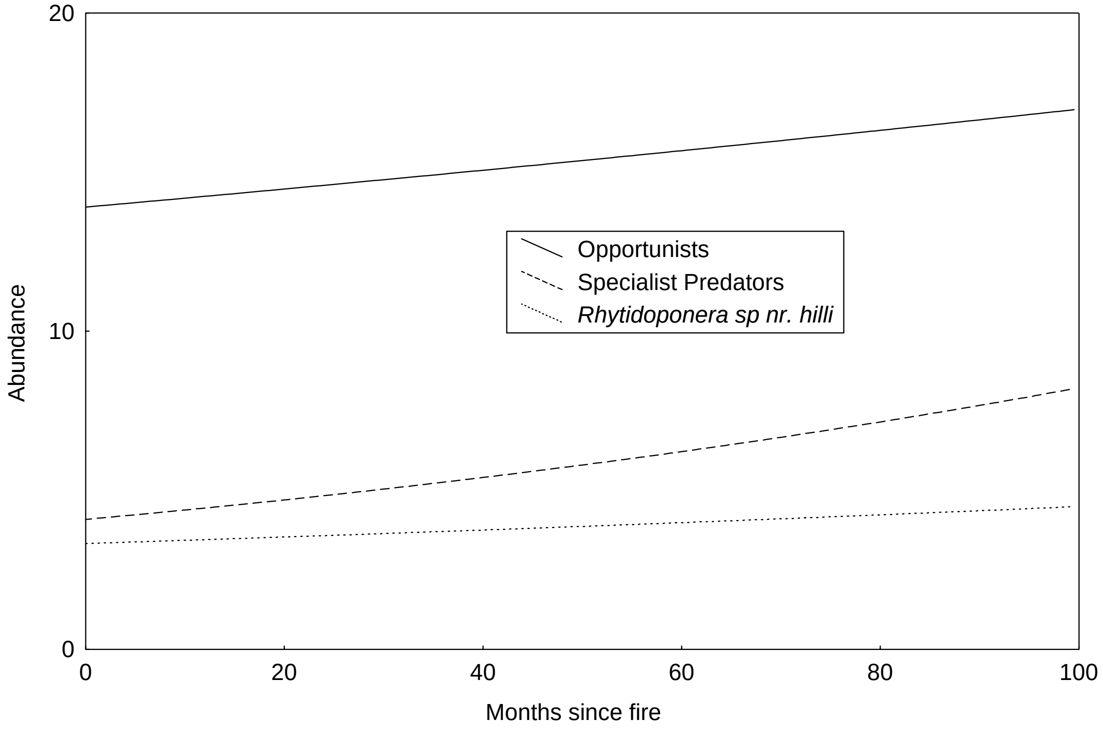


Figure 5.15 Modelled relationship between abundance of *Rhytidoponera* sp nr *hilli* Opportunists and Specialist Predators with increasing time since fire and the interaction with grazing. Model terms (variable, intercept, estimates and significance levels) are listed in Table 5.6.



Plant species composition

Analysis of similarity indicated that the responses of plant species composition to fire, grazing and site classification were the most complex (Table 5.2). The relationships between composition of all plant species and the three treatments were all significant, but mostly so for the grazing classes. Sub-groups indicated more precisely the varying responses of each stratum to the classifications. Canopy composition for all species was best discriminated by fire classes with no effect of site or grazing, while mid-storey composition was discriminated by all categories, but with a very strong site effect. Ground cover again was significantly discriminated by all, but with fire and grazing classes with equally highest R statistic.

A single ordination of all plant species composition in two dimensions (stress = 0.24) and labelled this time with both fire and grazing class indicated segregation according to fire along the second axis and grazing class on the first axis (Figure 5.16). Though the environmental variables measure generic vegetative features, they are instructive as to the broad structural change in the plant composition that controls the ordination pattern. This indicated high tussock cover, total ground cover, canopy height, ground cover height, foliage projective cover <0.5 m in unburnt quadrats, higher tussock cover, forb cover, ground cover richness and bare ground in grazed sites and high hummock grass cover characterising unburnt, ungrazed sites.

The correlation between plant and fauna dissimilarity matrices was examined in order to identify whether the patterns in structural composition had some relationship, and hence some ecological correspondence with fauna responses to fire and grazing effects (Table 5.3). Site composition for all plants and ground cover was significantly correlated with vertebrates, birds, mammals and reptiles, though examination of the different strata indicates which elements correlate best with the fauna groups: birds and mammals with canopy and ground cover; and reptiles with mid-storey and ground cover. Non-avian families were weakly correlated with total plant cover and ground cover and ants were correlated with total plant cover and mid-storey cover, whereas there were no significant correlations between the plant groups and ant and bird functional groups dissimilarity.

Table 5.3 Mantel tests estimating correlations between composition of vertebrates and plants and major taxa. Data indicates rank correlation coefficient using standardised Bray-Curtis dissimilarity matrices derived from abundance. Significance identified via permutation. Probability levels are *p<0.05, **p<0.01, ***p<0.001.

Taxon	Plants	Canopy	Mid-storey	Ground
Vertebrates	0.44***	0.199**	0.155**	0.421***
Birds	0.337***	0.171*	0.101	0.283**
Mammals	0.257***	0.202**	0.049	0.295***
Reptiles	0.377***	0.025	0.259***	0.373***
Non-avian families	0.183*	0.04	0.061	0.19**
Bird functional groups	0.107	0.065	0.046	0.108
Ants	0.172*	0.009	0.169**	0.105
Ant functional groups	0.095	0.044	-0.04	0.04

Plant species

Weighted mean ordination scores were calculated for all plant species recorded in more than five quadrats, and plotted on a separate ordination (Figure 5.17). Analysis of variance indicated that mean cover abundance of many of these species was significantly different within the four combinations of grazing and fire treatments (Table 5.4):

- ungrazed and unburnt quadrats were characterised by the hummock grass *Triodia pungens* (P<0.01) and the shrubs *Persoonia falcata* (P<0.05) and *Acacia stipuligera* (P<0.05);
- ungrazed and burnt quadrats by grasses *Aristida contorta* (P<0.01), *A. holathera*, the forb *Evolvulus alsinoides*, and the shrub *Dodonaea viscosa*;
- grazed and burnt sites by forbs such as *Tephrosia simplicifolia* (P<0.001), *Bonamia media* (P<0.001) and *Sida rohlenae*, the grass *Enneapogon polyphyllus* (P<0.001), and shrub *Acacia leptostachya*; and
- grazed and unburnt sites by grasses *Eriachne obtusa* (P<0.05), *Paraneurachne muelleri* (P<0.01), *Aristida calycina* (P<0.05), the forb *Sida fibulifera* (P<0.01) and the shrubs *Senna artemisioides* (P<0.01) and *Petalostigma pubescens* (P<0.01).

Figure 5.16 Two dimensional ordination of quadrats by plant composition labelled with fire and grazing class, including significant environmental vectors. Hummock grass cover (GCHUMM) r=0.83***, Bare ground cover (GCBARE) r=0.82***, Total ground cover (GSCOVER) r=0.81***, Foliage projective cover <0.5m (FPC<0.5) r=0.7994***, Tussock grass cover (GCTUSS) r=0.77***, Ground cover height (GSHEIGHT) r=0.76***, GCFORB, 0.72***, Ground cover richness (GSRICH) r=0.67***, Canopy height (CANHEIGH) r=0.56***. Probability levels are *p<0.05, **p<0.01, ***p<0.001.

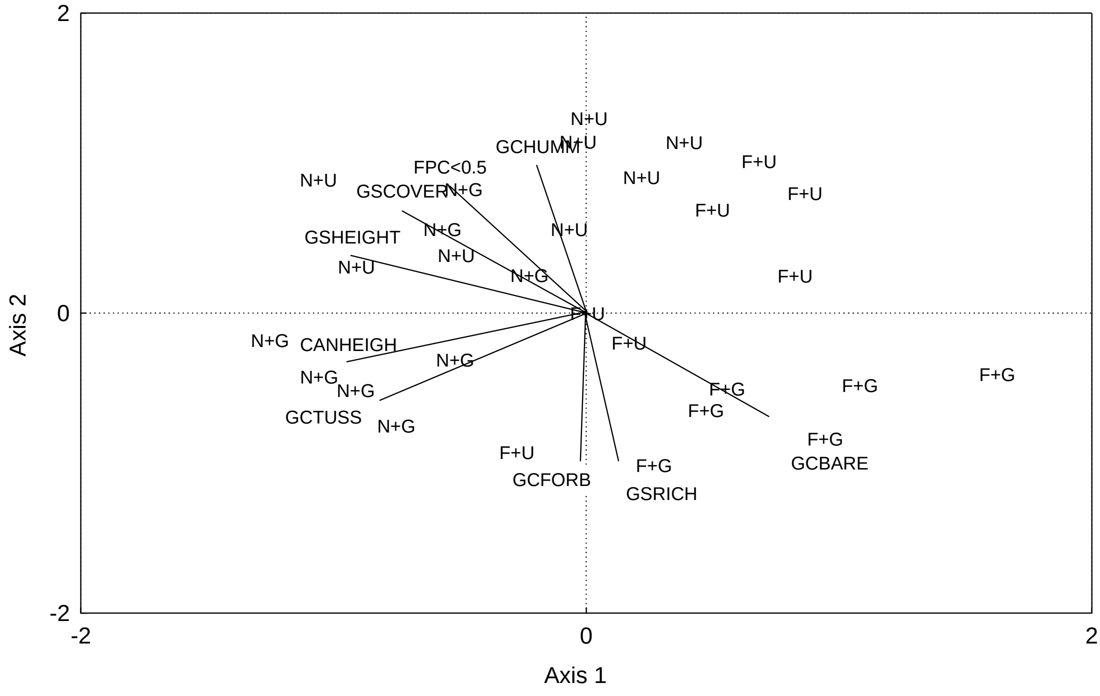


Figure 5.17 Weighted mean ordination score for plants recorded in more than five quadrats.
Canopy: BRPO *Brachychiton populneus*, COBR *Corymbia brachycarpa*, COSE *Corymbia setosa*, EUSI *Eucalyptus similis*.
Mid-storey: ACCO *Acacia coriacea*, ACLE *Acacia leptostachya*, ACME *Acacia melleodora*, ACST *Acacia stipuligera*, ACTE *Acacia tenuissima*, ALEX *Alphitonia excelsa*, CAAT *Canthium attenuatum*, CLFL *Clerodendrum floribundum*, DOVI *Dodonaea viscosa*, ERAU *Erythroxylum australe*, MACU *Maytenus cunninghamii*, PEFA *Persoonia falcata*, PEPU *Petalostigma pubescens*, SALA *Santalum lanceolatum*, SEAR *Senna artemisioides*, SECO *Senna costata*.
Ground cover: ARCA *Aristida calycina*, ARCO *Aristida contorta*, ARHO *Aristida holathera*, ARIN *Aristida ingrata*, BOME *Bonamia media*, CECI *Cenchrus ciliaris*, ENLI *Enneapogon lindleyanus*, ENPO *Enneapogon polyphyllus*, EROB *Eriachne obtusa*, EVAL *Evolvulus alsinoides*, PAEF *Panicum effusum*, PAMU *Paraneurachne muelleri*, PALA *Parsonsia lanceolata*, PHFU *Phyllanthus fuernrohrii*, PHVI *Phyllanthus virgatus*, SIFI *Sida fibulifera*, SIRO *Sida rohlenae*, TESI *Tephrosia simplicifolia*, TRPU *Triodia pungens*.

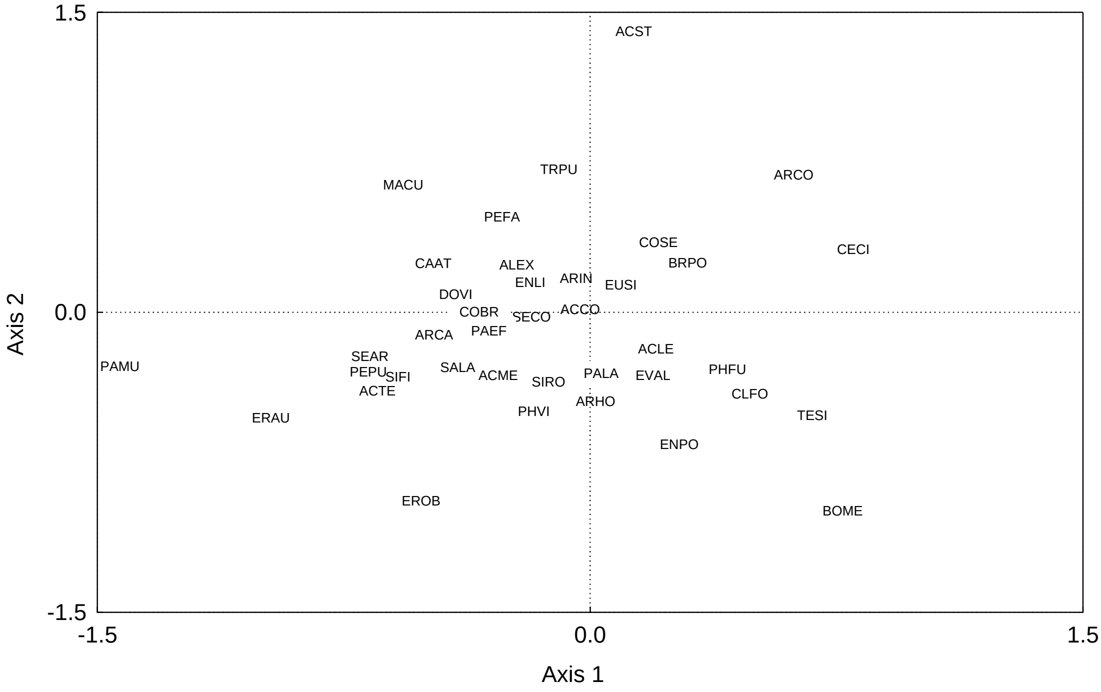


Table 5.4 Mean cover abundance score for all plant species recorded in five or more quadrats. Data provided includes both the means for simple fire and grazing treatments, and for the interaction of fire and grazing. N=no fire, F=fire, G=grazed, U=ungrazed. Kruskal-Wallis one way analysis of variance by ranks indicates which species were significantly different in the interacting treatments only. Probability levels are *p<0.05, **p<0.01, ***p<0.001, ns = not significant.

Family	Species	F	N	U	G	N+G	F+G	N+U	F+U	H	p
Asclepiadaceae	*Parsonsia lanceolata*	0.13	0.29	0.15	0.25	0.25	0.33	0.25	0		
Caesalpiniaceae	*Senna artemisioides*	0.13	0.43	0.08	0.44	**0.75**	0	0.13	0.14	12.8	**
	Senna costata	0.20	0.43	0.23	0.38	0.38	0.50	0.38	0		ns
Celastraceae	*Maytenus cunninghamii*	0.27	0.14	0	0.38	0.25	0	0.50	0		ns
Convolvulaceae	*Bonamia media*	0.13	0.64	0.85	0	0	**1.50**	0	0.29	21.8	***
	Evolvulus alsinoides	0.27	0.21	0.46	0.06	0.13	0.33	0	0.57		ns
Erythroxylaceae	*Erythroxylum australe*	0	0.21	0	0.19	**0.38**	0	0	0	8.7	*
Euphorbiaceae	*Petalostigma pubescens*	0.13	0.50	0.15	0.44	**0.88**	0	0	0.29	20.3	***
	Phyllanthus fuernrohrii	0.20	0.36	0.54	0.06	0.13	0.67	0	0.43		ns
	Phyllanthus virgatus	0.07	0.36	0.15	0.25	0.38	0.33	0.13	0		ns
Fabaceae	*Tephrosia simplicifolia*	0.20	0.36	0.62	0	0	**0.83**	0	0.43	16.2	***
Lamiaceae	*Clerodendrum floribundum*	0.13	0.29	0.38	0.06	0	**0.67**	0.13	0.14	10.3	*
Malvaceae	*Sida fibulifera*	0.13	0.29	0.15	0.25	**0.50**	0	0	0.29	8.1	*
	Sida rohlenae	0.20	0.79	0.54	0.44	0.75	**0.83**	0.13	0.29	10.4	**
Mimosaceae	*Acacia coriacea*	0.87	0.86	0.85	0.88	0.88	0.83	0.88	0.86		ns
	Acacia leptostachya	0.40	0.79	0.77	0.44	0.50	**1.17**	0.38	0.43	8.6	*
	Acacia melleodora	0.33	0.57	0.46	0.44	0.63	0.50	0.25	0.43		ns
	Acacia stipuligera	0.80	0.14	0.23	0.69	0.25	0	**1.13**	0.43	8.1	*
	Acacia tenuissima	0.07	0.43	0.08	0.38	**0.63**	0.17	0.13	0	9.4	*
Myrtaceae	*Corymbia brachycarpa*	0.53	0.50	0.38	0.63	0.75	0.17	0.50	0.57		ns
	Corymbia setosa	0.33	0.21	0.31	0.25	0.13	0.33	0.38	0.29		ns
	Eucalyptus similis	0.93	1.0	1.0	0.94	1.0	1.0	0.88	1.0		ns
Poaceae	*Aristida calycina*	0.27	0.43	0.23	0.44	**0.75**	0	0.13	0.43	8.1	*
	Aristida contorta	0.33	0	0.31	0.06	0	0	0.13	**0.57**	10.8	**
	Aristida holathera	0.40	0.29	0.54	0.19	0.25	0.33	0.13	0.71		ns
	Aristida ingrata	0.80	0.64	0.69	0.75	0.88	0.33	0.63	1.0		ns
	Cenchrus ciliaris	0.27	0.21	0.38	0.13	0	0.50	0.25	0.29		ns
	Enneapogon lindleyanus	0.40	0.71	0.31	0.75	1.0	0.33	0.50	0.29		ns
	Enneapogon polyphyllus	0	0.50	0.38	0.13	0.25	**0.83**	0	0	16.2	***
	Eriachne obtusa	0	0.57	0.23	0.31	**0.63**	0.50	0	0	8.4	*
	Panicum effusum	0.27	0.36	0.15	0.44	0.63	0	0.25	0.29		ns
	Paraneurachne muelleri	0	0.86	0	0.75	**1.50**	0	0	0	10.8	**
	Triodia pungens	3.67	2.50	2.46	3.63	3.0	1.83	**4.25**	3.0	13.6	**
Proteaceae	*Persoonia falcata*	0.40	0	0.15	0.25	0	0	**0.50**	0.29	8.1	*
Rhamnaceae	*Alphitonia excelsa*	1.0	0.71	0.62	1.06	1.13	0.17	1.0	1.0		ns
Rubiaceae	*Canthium attenuatum*	0.53	0.50	0.15	0.81	0.88	0	0.75	0.29		ns
Santalaceae	*Santalum lanceolatum*	0.20	0.21	0.15	0.25	0.25	0.17	0.25	0.14		ns
Sapindaceae	*Dodonaea viscosa*	0.47	0.21	0.31	0.38	0.38	0	0.38	0.57		ns
Sterculiaceae	*Brachychiton populneus*	0.20	0.21	0.23	0.19	0.13	0.33	0.25	0.14		ns

Discussion

Patterns of composition and abundance of vertebrates, ants and plants in the *Eucalyptus similis* vegetation type indicate some clear responses to grazing and fire impacts, though in varying ways for different taxa, group and species. A number of species and groups responded to the interacting effects of fire and grazing, either amplifying or attenuating changes in abundances. It is recognised that the sample size is modest, from a single season and restricted to a small geographic area. Additionally past reviews have indicated that local factors such as climate and longer-term fire and grazing history can markedly influence the nature of biotic response (Gill *et al.* 1999). However there are some distinct patterns that correspond to previously reported changes in species composition and abundance (Woinarski and Recher 1997; James *et al.* 1999). The intent of the survey was to choose a local area where all conditions other than grazing pressure and fire history (i.e. vegetation type, climate, distance from water and stocking rates and history of grazing and fire) were constant. The prevalence of a site effect in many of the models for species and functional groups suggests that this was not entirely successful, however it will be presumed that measured effects of the grazing and fire treatments are generally reflective of a genuine response.

The general pattern of vertebrate response recorded in this study indicates that fire class was the best discriminator of composition, while for ants, grazing class was superior. The most significant effect of fire was the re-configuration of the local environment to favour a particular suite of species, and an associated release of a range of new resources such as food, shelter and breeding sites (Williams and Gill 1985). In the case of plants, it may trigger flowering, seed germination and regeneration (Williams and Gill 1985). The effect on animal population is variable. Changes include shifts caused by mortality or emigration, altered food resources, cover and nesting resources, increased predation, increased competition, or reduced individual fitness (Sutherland and Dickman 1999), though many of these outcomes have been inferred from habitat and species changes rather than being directly measured. Grazing similarly creates changes in composition, though rather than being cyclical, the pattern is one that creates stable gradients along which species either decline or increase in abundance in response to grazing pressure determined by stocking rate or piosphere density (Landsberg *et al.* 1997; Fisher 2001a).

Plants

Vegetation composition and structure, and changes caused by fire and grazing, can be a primary influence on fauna assemblages (Williams and Gill 1995; Fisher 2001a). As such, vegetation patterning has been consistently used as a measure of resource availability, microclimate and microhabitat variation (e.g. Masters 1993, 1996). In this study, fire in ungrazed sites caused a shift from a community with a tall, dense ground cover dominated by *Triodia pungens* and more mid-storey species (e.g. *Persoonia falcata*, *Maytenus cunninghami, Alphitonia excelsa*), to one with a patchy but diverse ground cover, comprising a mixture of forbs, tussock and hummock grasses (e.g. *Phyllanthus* spp, *Tephrosia simplicifolia*, *Evolvulus alsinoides*, *Aristida* spp). Canopy cover also declined. Grazing in the absence of fire also creates a structural and floristic shift. Most notably this resulted in reduced ground cover (especially of *Triodia*, albeit with some increase in tussock grasses and forbs). Composition also altered with an increase in some tussock grass species (*Aristida* spp *Enneapogon* spp, *Eriachne obtusa*, *Paraneurachne muelleri*, *Panicum effusum*), forbs (*Phyllanthus* spp *Sida* spp) and shrubs (*Senna* spp, *Acacia* spp) compared to the burnt sites. Regardless of the agent of change, ground cover declines, though species richness increases.

The impacts of grazing on rangeland vegetation have been examined and reviewed by Harrington *et al.* (1984), Wilson (1990), James *et al.* (1995), James *et al.* (1999), Landsberg *et al.* (1999) and Woinarski *et al.* (2001a). The general pattern is one where palatable perennial grasses are reduced and there is a corresponding increase in annual, ephemeral and unpalatable species (James *et al.* 1999). Some examples include:

- a shift from palatable perennials *Thyridolepis mitchelliana* and *Themeda australis* to unpalatable *Aristida* spp (Hodgkinson and Griffin 1992);
- changes in dominance from *Themeda australis* to *Heteropogon contortus* (Crowley and Garnett 1998);
- increases in unpalatable shrubs such as *Senna*, *Acacia* spp (Friedel *et al.* 1990); and

- disappearance locally of the grass species *Capillipedium parviflorum* and *Sehima nervosa* (Fensham and Skull 1999).

At intermediate grazing levels within-habitat species diversity increases (Landsberg *et al.* 1997), or at least fails to decline (Fensham and Skull 1999), with bell-shaped response most typically reported (Landsberg *et al.* 1997). However heavy grazing clearly causes total decrease in richness and may result in local losses of at least some species (Hodgkinson 1992; McIvor 1998). The results of this study suggest a concurrence with these reported patterns.

The responses of vegetation to fire in tropical savannas have been thoroughly examined in the Northern Territory (see Introduction), but less so in Queensland partly because grazing studies have been driven by predominantly pastoral concerns (e.g. Ash *et al.* 1994). The question of fire regimes and impacts is a concern largely of conservation management (e.g. Lonsdale and Braithwaite 1991), despite being a significant component of pastoral land management in some regions (Crowley and Garnett 2000). As with grazing, fire creates floristic and structural change to vegetation communities. In *Triodia* grasslands, burning decreases cover and increases the richness of ephemeral species that subsequently decline in abundance (Griffin and Friedel 1984; Bowman *et al.* 1990). Large scale, frequent fires have allowed *Triodia* to invade Mulga *Acacia aneura* woodlands, thereby decreasing between-habitat heterogeneity (Bowman *et al.* 1994). Conversely the exclusion of fire has been implicated in the increase of woody shrub density (Noble 1977), invasion of rainforest species in adjoining woodland (Hill *et al.* 2002) and again in the loss of ground cover heterogeneity (Franklin 1999; Woinarski 1999b). Frequent or intense fires can also affect fire-sensitive communities such as monsoon forest and sandstone heaths (Russell-Smith and Bowman 1992; Russell-Smith *et al.* 1998, 2001), or cause the loss of species that require long periods between burns to set seed for regeneration (Bowman and Panton 1993). The inter-fire interval is critical to obligate seeding species (Rice and Westoby 1999). Implicit in these examples is the notion that fire frequency and timing variously affect floristic and structural diversity, with little clear geographic formula. However the results of this study identifies a simple scenario that matches existing patterns - that fire reduces the cover of *Triodia* and canopy species, and increases the richness of the ephemeral and perennial species, creating a patchier environment.

The interaction between impacts of fire and grazing are little studied. Hill *et al.* (2002) identified an increase in the rate of rainforest invasion into open forest, where continued Aboriginal fire management occurred in concert with cattle and horse grazing, though they provided little detail on the floristic dynamics. Crowley and Garnett (2000) identify the use of fire as a management tool in Cape York pastoral holdings, both for stock management and as a means of enhancing native pasture productivity, though effects on vegetation are anecdotal (e.g. fire helps control woody weeds or prevents native species thickening). The results of this study suggest that there is a compounding effect of burning and grazing on floristics and structure. Fire increased the extent of bare ground and decreased hummock grass cover, tussock grass cover and canopy cover, although species richness remained high. Species such as *Bonamia media*, *Tephrosia simplicifolia*, *Clerodendrum floribundum*, *Sida rohlenae* and *Enneapogon polyphyllus* were all most abundant in burnt grazed sites. Tongway and Ludwig (1997) emphasise that such open rangelands with low ground cover leads to dysfunction and degradation, and the influence on fauna assemblages and species reliant on either more variable habitats or at least more extensive ground cover, could be predicted.

Birds

Birds have been the most frequently studied vertebrate in regards to fire response (Woinarski 1999a), not the least for their abundance, ease of survey, conspicuousness and rapid post-fire response. Despite a lack of detailed long-term examinations there are clear progressive post-fire patterns within Australia, though these vary regionally due to climate, vegetation and fire differences (Woinarski and Recher 1997). In this study bird composition at sites was best defined by fire and was directly correlated with ground and canopy cover composition. The relationships of bird communities to structural complexity and shifts driven by fire effects are well established (Woinarski and Recher 1997; Woinarski 1999a). In this study, bird abundance decreased significantly with increasing time since fire, a similar pattern to burnt tropical woodlands in the Northern Territory (Woinarski 1990). Although this may be in part a function of more open ground and greater census visibility of some terrestrial guilds (terrestrial omnivores, pouncing insectivores, granivores), compared to wetter temperate forests, few species are considered disadvantaged in tropical savannas where vegetation regrowth is rapid (Woinarski and Recher 1997). At least some available food resources increase soon after fire in these environments (Braithwaite and Estbergs 1985).

Given the large number of birds recorded in comparison to other faunal groups, proportionally very few species and guilds varied significantly with treatment effects, and for those that did, the response was sometimes ambiguous. Short-term temporal and spatial variability of bird communities, lack of patterning and ability to rapidly respond to changes in resources may mute seral response more typical of temperate systems (Woinarski 1990; Woinarski and Tidemann 1991; Woinarski and Recher 1997). In addition the generally high fire frequency in monsoonal Australia may curtail any long-term plant succession that may influence bird community responses (Woinarski 1990; Woinarski and Recher 1997). Black-faced Woodswallows (and the hawker guild to which it belongs) increased in abundance post-fire, taking advantage of the open habitat and even feeding on the ground (Woinarski 1990). Conversely there was a decline in Singing Honeyeaters, a species dependent on dense low and mid-strata flowering plant species that are at least temporarily removed after fire. Red-browed Pardalotes, which are foliage gleaners, may have been expected to decrease with fire with the loss of mid-storey and a more open canopy, however, it was at highest abundances in the burnt sites. As a nomadic and patchily distributed northern savanna species, it may have been responding to a local invertebrate resource flush, or lack of competition from other gleaners such as Weebills and Yellow-rumped Thornbill, recorded in lower numbers. Woodland canopy can be unaffected in cool fires, thus not impacting on upper foliage gleaning species (Woinarski 1990), though on average the canopy cover did decline in burnt sites. Salliers and trunk gleaners also increased, again due to a possible resource response (Woinarski 1990), though Jacky Winters decreased in sites if they were grazed and burnt, whereas Pallid Cuckoos also decreased, but remained at higher abundances in grazed quadrats. This begins to hint at how interference to the recovery of vegetation after fire by the addition of grazing, which may affect the restoration and abundance of some fauna species.

The influence of grazing on both vegetation structure and bird communities has been adequately demonstrated. Landsberg *et al.* (1997) and Fisher (2001a) identified clear suites of increaser (e.g. Australian Magpie, Galah, Crested Pigeon, Yellow-throated Miner) and decreaser species (Little Button-quail, Red-chested Button-quail, Singing

Honeyeater, Australian Bustard, Zebra Finch), responding to the changes in ground cover and plant composition. Both of these studies examined semi-arid, open environments, however similar patterns have been noted in wetter tropical woodlands (Woinarski and Ash 2002) with some species more prevalent in grazed areas (Willie Wagtail, Torresian Crow, Yellow-throated Miner, Laughing Kookaburra, Magpie-lark) and other in ungrazed sites (Pheasant Coucal, Noisy Miner, Blue-winged Kookaburra, nectarivore species). The most dramatic reported impact of widespread pastoralism is the decline of many savanna granivores. These species are dependent on continuous seed supply and availability across the entire annual cycle, shifting from food plants across this period (Woinarski 1993; Garnett and Crowley 1994). Grazing coupled with inappropriate fire season and frequency has caused a shift in floristic dominance and coincident dramatic decline of many key bird species (Franklin 1999).

In this study grazing responses were in some respects unclear. Grey-crowned Babblers, which are terrestrial omnivores, and foliage gleaners significantly increased in abundance in grazed sites, perhaps the former in response to the variability and diversity in ground cover and increase in mid-storey cover, and the latter to mid-storey shrub complexity only. Cockatiel numbers decreased, in direct contrast to their positive response to fire (Woinarski 1990). Whereas fire may encourage a bloom of ephemeral plants, seed release and create open ground for foraging (Woinarski 1990), grazing typically causes no such change in either vegetation architecture, or resource flush.

Rufous Whistlers (foliage gleaner) and Rainbow Bee-eaters (sallier) both were grazing increasers, a pattern accentuated by fire in these sites, but stifled if the fire was in an ungrazed environment. This is in contrast to the earlier situation for Jacky Winter (sallier) and the Pallid Cuckoo (foliage gleaner), with a negative effect with the addition of fire in grazed sites. The cause is difficult to ascertain, but the combined effects must create a situation where some sort of resource effect or threshold is breached that causes a positive or negative abundance response. One could speculate such a scenario regarding foraging or behaviour: the Pallid Cuckoo and Jacky Winter being more secretive preferring an intermediate vegetation community structure, compared to the gregarious Rainbow-Bee-eater and more aggressive Rufous Whistler, suited to open disturbed environments.

The complex and interacting manner in which granivores and terrestrial insectivores responded to fire and grazing further emphasises the fluidity of responses of bird assemblages to short term environmental change (fire) coupled with a more persistent structural impact of grazing. Granivore abundance increased post-fire, while terrestrial insectivores decreased, though the granivore guilds declined with grazing pressure overall. The increase in abundance of Grey-crowned Babblers and Magpie-larks in grazed sites dominated the terrestrial insectivore response, both preferring open ground to forage, and masking the decline of Variegated Fairy-wrens in burnt and grazed environments. Woinarski (1990) reported a similar post -fire pattern (e.g finches *Poephila* spp, Galah, Cockatiel, increasing, Red-backed Fairy-wren decreasing), and the intolerance of granivores and terrestrial insectivores to consistent pastoral pressure is also evident in other studies (Reid and Fleming 1992; Franklin 1999).

Mammals

The pyrrhic succession of mammal populations, particularly small terrestrial species, has been a fruitful area of study, and has been extensively reviewed (Christensen and Kimber 1975; Catling and Newsome 1981; Friend 1993; Whelan 1995; Williams and Gill 1995; Wilson 1996; Sutherland and Dickman 1999). There is a clear research bias to south-eastern Australian forests, and many of the studies investigate the response of the community rather than the associations with particular environmental changes (Sutherland and Dickman 1999).

There have been few studies in tropical and arid Australia. Reid *et al.* (1993), Masters (1993) and Southgate and Masters (1996) examined patterns of small mammals in hummock grasslands of central Australia. Though complicated by climatic variation, these authors documented patterns of assemblage shift (*Notomys alexis*, *Sminthopsis hirtipes* as fire increasers, *Pseudomys desertor*, *Mus musculus*, *Sminthopsis youngsoni* as decreasers and *P. hermannsburgensis* and *Dasycercus cristicauda* indeterminate). This shift was generally correlated with changes in vegetation cover and rainfall increase. Rainfall can independently cause irruption of rodents in arid environments irrespective of fire age (Dickman *et al.* 1999), though as all vegetation has an inherent fire age, extricating clear effects of rainfall, vegetation age, fire history or other community or environmental events is difficult (Southgate and Masters 1996).

More generally, wholesale changes in traditional Aboriginal burning practices have been implicated in mammal species decline (Burbidge and McKenzie 1989; Morton 1990; Woinarski *et al.* 2001b). The shift to higher frequency, more extensive destructive burns, has caused a change in floristic resources (loss of mid-storey shrubs, decrease in grass diversity). This seems to relate to decline in some species (Bolton and Latz 1978; Friend 1993; Kerle 1998) and potentially to the advantage of some generalists such as rodents (Braithwaite and Brady 1993; Braithwaite and Muller 1997).

There have been surprisingly very few direct examinations of grazing impacts on mammal fauna in Australia, despite a very strong inference that grazing has substantial effects on mammal communities (Morton 1990), even historically (Krefft 1886; Lunney 2001). The consistent loss of cover caused by grazing has been suggested as a prime reason for increase and possibly enormous impact of feral predators on native mammalian prey (Burbidge and McKenzie 1989; Short and Smith 1994; Smith and Quin 1997). Studies in the United States have indicated changes in mammal density and diversity directly due to grazing pressure (Fleischner 1994). In the Queensland dry tropics, Woinarski *et al.* (2002) compared vertebrate abundance in long ungrazed and grazed habitats and identified higher abundances of *Mus musculus*, *Pseudomys gracilicaudatus*, *Macropus giganteus* and *Isoodon macrourus* in ungrazed sites.

Despite the simplicity of the community structure, the pattern of the rodent species recorded in relation to fire provided the most concise illustration of the interacting fire and grazing effects. In the absence of grazing, *Pseudomys delicatulus* is abundant in burnt sites, declining markedly in unburnt sites. Conversely *P. desertor* is exceptionally uncommon in burnt sites, increasing in abundance by ten-fold in sites unburnt for up to 8 years. However in the absence of fire, grazing reproduces the fire response, with *P. delicatulus* remaining abundant in an environment with decreased ground cover and *P. desertor* declining by half. In sites that were both grazed and burnt, *P. desertor* was absent and there was a small increase in *P. delicatulus* from sites burnt and ungrazed. What is important here is that both grazing and fire cause significant decline of *P. desertor*, and there is a possible scenario where under consistent or high grazing pressure compounded by frequent burning, the ground cover may decline to a point beyond the capacity for localised persistence. The extinction of *P. desertor* in western

New South Wales has been clearly linked to overgrazing (Krefft 1886; Dickman 1993), and the high abundance of this species in the *E. similis* woodlands may be due to low or absent historical grazing pressure.

These results are also consistent with the other evidence that *P. desertor* is fire sensitive (fire decreaser), re-colonising burnt sites over time as vegetation cover increases (Masters 1993; Sutherland and Dickman 1999). In the Northern Territory, *Pseudomys delicatulus* is irruptive and extremely well adapted to sparsely vegetated post-fire environments (Braithwaite and Brady 1993). Populations of *P. desertor* in central Australia are recorded as taking between 11 to 15 years to fully re-establish post-fire (Masters 1993), and this lag time may relate in part to slower re-establishment of vegetation cover there. In the Desert Uplands, *P. desertor* re-colonisation time is quicker with populations abundant within eight years. This shorter repopulation time may relate to a more rapid increase in vegetation time after fire due to a higher rainfall and more productive environment than arid hummock grass areas. Property and paddock sizes are comparatively small, and fires are more generally controlled and restricted in size. Small-scale fires that leave adjacent pockets of refugia and more rapid post-fire regrowth due to climate may allow faster population irruption. Post-fire rate of recovery of small mammals can be related to vegetation density recovery rather than fire-age itself (Monamy and Fox 2000). The patterns of distribution, abundance and habitat for *P. desertor* in Queensland have been examined in more detail in Kutt *et al.* (in press, 2003) (Appendix 6).

Reptiles

High reptile species richness and co-existence in Australia has been clearly linked to fine-scale spatial habitat diversity and niche partitioning (Pianka 1966; James 1991; Read 1995). As such reptiles may be considered to respond measurably to habitat changes wrought by fire and cattle (Read 2002). Previous studies of fire impacts have identified fire characteristics, differential survivorship, micro-habitat, cover and associated changes in insolation, diet changes and reptile life-history characteristics as influencing changes in reptile communities (Williams and Gill 1995), though again these are generally inferred rather than measured (e.g. Masters 1996). The relationship between herpetofauna and grazing has been less commonly examined (James *et al.*

1999), though there is an expectation that, similar to fire impacts, loss of ground cover and microhabitat changes will also alter the composition and abundance of reptiles (Read 2002). Land clearance and over-grazing have been linked with the contraction in range and abundance of many reptile species (Cogger *et al.* 1993; Covacevich *et al.* 1998).

Unlike birds and mammals, there is seemingly greater scope for variable patterning of reptile response. Landsberg *et al.* (1997) examined responses of fauna along grazing gradients and found little consistency of effect for reptiles, suggesting that they may have been insensitive to piosphere effects. However on individual gradients within a particular region, clear increaser and decreaser species were evident. Fisher (2001a) similarly found a suite of increaser (e.g. *Tympanocryptis lineata*, *Diplodactylus tessellaris*) and decreaser species (e.g. *Delma tincta*, *Ctenotus rimacola*) on grazing gradients in Mitchell Grass Downs, though one species *Ctenotus joanae* was identified in both categories. Fisher (2001a) further identified *Heteronotia binoei* as a decreaser, as did Thurgate (1997), yet in other studies this species has been recorded to increase in abundance in grazed sites (Woinarski and Ash 2002). Regional variation due to climatic, historical and environmental conditions would certainly occur, and it has been suggested that underlying stronger relationships with environmental gradients (soil, moisture, substrate) exert a deeper influence on reptile composition than cover change due to fire (Gambold and Woinarski 1992; Trainor and Woinarski 1994). A similar result is implied for grazing (Landsberg *et al.* 1997)

There are some broad, ubiquitous patterns regarding the change in ground cover and microhabitat caused by both fire and grazing, and the influence on herpetofauna. After burning, there are increases in species with strategies designed to cope with the cover change. This includes reptiles that burrow to escape fire, reptiles that prefer open ground for foraging or reptiles that have higher thermal tolerance in open ground (Caughley 1985; *Rhynchoedura ornata*, *Diplodactylus* spp, *Ctenophorus nuchalis*, and some *Ctenotus* spp, Fyfe 1980; Reid *et al.* 1993; Masters 1996). Subsequent to this there is a shift in long unburnt sites to species assemblages associated with regrowing or dense vegetation (Caughley 1985; *Ctenotus* spp, *Varanus eremius*, *Delma* spp, *Menetia greyii*, Fyfe 1980; Reid *et al.* 1993; Masters 1996). In tropical savannas, where fire frequency is greater than arid *Triodia* or Mallee communities, the timing of burn has been considered an influential factor for fauna (Woinarski 1999a). In Kakadu, Braithwaite (1987) concluded that *Diporiphora australis (=D. bilineata)*, *Carlia triacantha* and *Carlia foliorum* (= *C. munda*) prefer high intensity dry season fires that create open ground, *Heteronotia binoei*, *C. amax* and *C. gracilis* prefer unburnt sites and *Ctenotus* spp and *Sphenomorphus* (*Glaphyromorphus*) spp patchy, cooler burns. A mosaic of fire frequencies and timing promote maximum diversity (Braithwaite 1987) a result also found in the Victoria River District (Woinarski *et al*. 1999a). Gambold and Woinarski (1992) and Trainor and Woinarski (1994) concluded that perhaps because of the consistency of fire in savanna woodlands, habitat characteristics are the overriding control on reptile assemblage structure.

Similarly shifts in reptile community structure have been noted in other grazing studies in northern Australia. Thurgate (1997) surveyed ungrazed pockets within the Great Basalt Wall and concluded that reptile abundance and diversity were significantly lower in grazed sites, with species such as *Gehyra catenata*, *Morethia taeniopleura*, *Ctenotus robustus*, *Carlia jarnoldae* and *Heteronotia binoei* decreasing in association with decline in ground cover and live trees. Nine other species showed no marked response, with only *Carlia munda* and *C. pectoralis* potentially positively associated with grazed sites. Woinarski *et al.* (2002) identified greater abundance and richness in ungrazed sites, with geckos increasing (*Gehyra dubia*, *Heteronotia binoei*) and skinks (*Menetia greyii*, *Ctenotus eutaenius*, *Carlia munda*) decreasing under increased grazing pressure.

This study provides further evidence for variation in response of reptiles to both grazing and fire. Of all vertebrate taxa examined, reptiles were the only group to indicate a more pronounced response to grazing than to fire, though fire was still influential. This is likely due to a strong association and response to coarse structural change in the ground cover that affects insolation and microhabitat. The strong correlation of reptile composition with ground strata and mid-storey composition tends to suggest these structural layers are more influential on reptile communities, and as described earlier, there is a shift in the proportion of bare ground and vegetation cover in sites affected by fire, grazing or a combination of both. Reptile abundance significantly increased in grazed sites, though richness remained constant in both grazing and fire treatments, as did abundance in response to fire. Other studies indicate that richness of communities remains moderately stable despite impacts of fire and grazing, though abundance and composition varies (Thurgate 1997; Schlesinger 1999; Fisher 2001a; Woinarski and Ash 2002).

Patterns for species significantly explained by the fire and grazing treatments, also parallel previous results. *Ctenophorus nuchalis* abundance increased as a simple response to fire, and this species has been recorded previously to increase in abundance post-fire (Woinarski *et al.* 1999a) and in grazed sites (Schlesinger *et al.* 1997; Schlesinger 1999; Read 2002). This has been linked to known heat tolerance and burrowing behaviour (Bradshaw and Main 1968; Read 2002), and hence an ability to survive in conditions of less ground cover. Burrowing life-traits have been associated with increased post-fire survivorship (Fyfe 1980). Other small, fast-moving, cryptic agamids have been recorded as increasing post-fire (*Diporiphora australis*, Braithwaite 1987) or as grazing increasers (*Tympanocryptis lineata*, Fisher 2001a) for similar reasons. This is not a universal feature of agamids, however, as non-burrowing (*Triodia* sheltering) species decline post fire (*C. isolepis*, Masters 1996) or with grazing (*C. fordi*, Read 2002) due to the loss of ground cover. In this study the large-bodied terrestrial and scansorial dragon *Pogona barbata*, significantly declined in response to grazing.

Pygopodids and *Ctenotus pantherinus*, both large-bodied and robust reptiles, also declined in response to fire and the reduction in ground cover. Reid *et al.* (1993) and Masters (1996) recorded significantly lower abundance of *Delma* spp and *Ctenotus pantherinus* in regenerating *Triodia* after burning, relating this to possible prey availability, shelter, activity period and thermal preferences. *Delma tincta* is reported as declining due to loss in ground cover in grazing piospheres (Fisher 2001a), also speculated to be in response to high temperature and low heat intolerance. On a number of occasions Pygopodids have been observed to bask at the clearings made by the installation of the drift fence (pers. obs.). In four instances animals (*Delma*, *Lialis* and *Pygopus*) have been found dead at the fence-line (unpubl. data), all in the late afternoon on very hot days. Anecdotally this suggests a general tendency to overheat and expire when trapped behind a barrier such as a pitfall line, a notion supported by Heatwole and Taylor (1987) who indicate that despite Pygopodids having reasonable thermal tolerance, they have very low survival times at high temperatures. Large skinks such as

C. pantherinus (snout-vent 100 mm) are similarly vulnerable to rapid over-heating without adequate shelter (Heatwole and Taylor 1987).

Ctenotus pantherinus, *C. rosarium* sp nov (snout-vent 40 mm) and *C. hebetior* (snout-vent 60 mm), all decreased in abundance with grazing, and it would be expected that fast moving diurnal shuttling heliotherms (Heatwole and Taylor 1987), would respond in abundance with changes in ground cover. Thurgate (1997) noted significant decline of a large species, *Ctenotus robustus*, in grazed savanna woodlands. Fisher (2001a) reported decline for three moderate to large sized *Ctenotus* also associated with reduced cover. Similar differential responses for cover changes wrought by fire are recorded in species-rich *Ctenotus* communities (Reid *et al.* 1993; Masters 1996), and body sizes, thermal tolerances, activity periods, sheltering characteristics and diet (Heatwole and Taylor 1987) would suggest variation in pattern as typical. The changes in abundance of *Ctenotus hebetior* illustrate the confounding interaction between fire and grazing, decreasing in abundance with time since fire, but remaining at stable in sites both grazed and unburnt. This provides a clue that species that are less suited to dense ground cover gain some advantage from grazing that moderates the increase in ground cover post-fire. Compare this to *C. pantherinus* that decreases in this scenario. Typical post-fire patterns of increase or decrease can shift with the introduction of grazing.

Curiously *Menetia greyii* increased in abundance with grazing, and this small fossorial species has been generally thought to decline with loss of litter cover and increase of bare ground (Caughley 1985; Thurgate 1997; Fisher 2001a; Woinarski *et al.* 2002). Intuitively, one may expect such a small species (snout-vent <20 mm) would be resilient to loss of cover, being able to shelter adequately in small pockets of microhabitat. However assessment techniques may unduly influence a result for a reptile of very small size. For example Thurgate (1997) used visual census and recorded low abundance, but a nominal increase in grazed sites, though bias in the technique (small reptiles possibly more visible in open sites and less so in dense ground cover) may have been one cause of the result.

Ants

Invertebrates contribute the majority of species diversity in tropical savannas (Hoffman 2000) and their importance to ecosystem structure and function is widely acknowledged, but they receive less research attention than do vertebrates (Andersen and Lonsdale 1990). Ants are a particularly diverse and abundant group in northern Australia (Andersen 1995, 2000). Recent work has highlighted their significant role in soil nutrient recycling (Lobry de Bruyn and Conacher 1990), soil structuring (Lobry de Bruyn and Conacher 1994), seed harvesting and vegetation dynamics (Andersen and Morrison 1998; Andersen *et al.* 2000) and as valuable prey for vertebrates (Abensperg-Traun and Steven 1998).

Ants have also received particular attention for their potential as bio-indicators of environmental disturbance (Andersen 1990) and their responses acting in concert with other biota (Landsberg *et al.* 1997). The hope is that ants may be sensitive early indicators of environmental change, acting as a sentinel for change against which other higher trophic species may lag in response (Andersen 1995). One major complicating factor in measuring ant responses to disturbance is a developing but still uncertain taxonomic knowledge (Andersen 2000), and despite the use of functional group classifications to overcome this limitation (Andersen 1995; Andersen *et al.* 2002), mixed responses have been recorded (Landsberg *et al.* 1997; Hoffman 2000).

Changes in composition of ant fauna in response to grazing impacts in northern Australia have been examined a number of times. Landsberg *et al.* (1997) identified a small suite of consistent increasers (e.g. *Camponotus*, *Iridomyrmex*, *Rhytidoponera* and *Tapinoma*) and decreasers (e.g. *Calomyrmex*, *Cerapachys* and *Leptogenys*). Woinarski *et al.* (2002) also identified a general increase in richness and abundance in sites undisturbed by grazing impacts, with the group Subordinate Camponotini and species *Leptogenys adlerzi*, *Iridomyrmex* spp, *Camponotus* spp and *Opisthopsis haddoni* at higher abundances in the grazed sites. Structural changes in grazed sites included increased areas of bare ground and dead trees and a clear shift from native to exotic ground cover grass and forb species. Conversely Read and Andersen (2000) identified little significant change in abundance or richness of common species or functional groups in response to a small scale grazing experiment, though there was a trend for *Rhytidoponera metallica* to decrease and *Iridomyrmex* spp, Generalised Myrmicinae and Hot Climate Specialists to increase after grazing.

Hoffman (2000) examined grazing gradients in the Victoria River District and identified a change in composition due to grazing intensity, though species richness had a lesser or no response. All ant species persisted with regular grazing, but as most of the area has been chronically grazed, it was suggested that the most sensitive species might already have disappeared. However some functional groups also generated little clear pattern, suggesting this scheme may be less sensitive to change, compared to fire studies (Andersen 1991). Regardless, there was some indication that Dominant Dolichoderinae, Cryptic, Subordinate Camponotini were all grazing decreasers, and Hot Climate specialists increasers (Hoffman 2000).

In comparison to grazing, the response of ant communities to fire has been infrequently studied in Australia. In the northern tropical savannas Andersen (1991a) examined an experimental fire regime and identified two clear responses: in annually burnt sites there was an increase in *Iridomyrmex* species, Hot Climate Specialists and Opportunists *Rhytidoponera aurata*; and in fire excluded sites high proportions of Generalised Myrmicinae and Cryptic species were recorded. It was predicted that as ants escape the fire front in burrows, the resultant change was associated with alteration of vegetation structure and competition between remaining species (Andersen 1991). The richness and abundance of Dominant Dolichoderinae and Hot Climate specialists have been positively related to an open ground layer (Andersen 1995).

In this study ant composition identified perhaps the weakest relationship to the grazing and fire impacts of all the fauna groups examined. There was some characterisation of the ant composition by grazing treatments, and no significant relationship with functional groups, as well as low correlation with plant composition. The ordination identified a pattern between grazed and ungrazed sites spread along an axis of high canopy and hummock cover at ungrazed sites, and high level of fallen timber in the grazed sites. Andersen *et al.* (2002) concluded a simplified assessment of ant fauna and functional groups using a subset (ants >4 mm) adequately matched the patterns of a more comprehensive analysis of disturbance response for species. However Hoffman

(2000) suggested that despite the method being able to detect large habitat impacts, functional groups were less sensitive to environmental changes created by grazing gradients. In this study, functional groups were also less sensitive to fire and grazing impacts, though it is also recognised that the nature and scale of the grazing and fire change within the sites in this study are not dramatic.

Ant richness was generally insensitive to fire and grazing treatments, a result similar to others (Hoffman 2000, Read and Andersen 2000; Fisher 2001a), though as with most vertebrates, abundance and composition varied, when overall richness did not. Because of the general failure of the grazing and fire treatments to clearly characterise the ant composition, the patterns of abundance for species and functional groups were complex. The key patterns are summarised under functional group headings.

Hot Climate Specialists: This group was dominated by a single species *Melophorus* sp A (*aeneovirens gp*)which significantly decreased with increasing time since fire, a pattern accentuated by grazing. This is contrary to expectations that this functional group is associated with an open ground layer (Andersen 1995). Hoffman (2000) and Read and Andersen (2000) also recorded general grazing increaser responses, though Fisher (2001a) identified Hot Climate species as both increasing and decreasing.

Specialist Predator: Within this group the species *Myrmecia callima* and *Bothroponera* sp A (*sublaevis* gp) were all identified as simple grazing decreasers. Fisher (2001a) recorded Specialist Predators as consistently increasing with distance from water (grazing decreasers), as did Landsberg *et al.* (1997) for some Specialist Predators species. Conversely Woinarski *et al.* (2002) identified some species (*Leptogenys)* as increasers.

Opportunist: Within this group the species were the most inconsistent in response to the treatment effects. *Tetramorium* ?*sjostedti* and *Rhytidoponera* sp A (*tyloxys* gp) decreased in abundance in grazed sites, though the former at high number in sites ungrazed, but clearly at lower abundances and decreasing in time since fire in grazed quadrats. *Rhytidoponera* sp nr *hilli* was generally a grazing decreaser, but in ungrazed sites increased after fire. *Rhytidoponera* sp nr *rufithorax* were consistently more common in grazed sites, though with *Rhytidoponera* sp C (*mayri* gp), grazing altered a consistent low abundance over all fire ages, to one that was low and increased with time since fire. Equal increaser and decreaser responses to grazing were identified for this group in the Mitchell Grass Downs (Fisher 2001a). Opportunists are considered characteristic of high stress environments, but also unspecialised and poor competitors, which may account for the lack of any clear pattern within the group (Andersen 1995).

<u>Subordinate</u> <u>Camponotus</u>: This group was dominated by a single species, *Camponotus* sp nr *denticulatus,* which increased dramatically with grazing and time since fire, compared to a recorded steady abundance in ungrazed sites across all fire ages. Hoffman (2000) and Woinarski *et al.* (2002) both identified species in this group as increasers with grazing.

<u>Dominant</u> <u>Dolichoderinae</u>: This group consisted of predominately one species, *Iridomyrmex hartmeyeri*, which remained at balanced numbers across fire ages if the sites were ungrazed, but was recorded in low and declining abundance with increasing time since fire in grazed sites. Andersen (1995) identified this group as increasing with increasing open ground with fire, and Hoffman (2000) and Fisher (2001a) found a negative effect with grazing increase, though some species of *Iridomyrmex* recorded by Fisher (2001a) both increased and decreased.

Though it is recognised that the sample size is small, compared to the vertebrate fauna there are a reasonable number of ants and functional groups that respond significantly to the grazing and fire effects. Conversely, ant composition on the whole was invariant against the treatment categories and poorly correlated to plant composition, counter to expectations that ant and plant communities are allied in life form and local scale environmental response (Andersen 1995; Fisher 2001a). This suggests that ants are a useful indicator of disturbance, but less sensitive where the impacts are subtle and therefore no more useful as environmental indicators than the vertebrate fauna. Most ants consistently responded to both grazing and the interaction with fire, hinting that perhaps fire effects alone results in little change to the ant communities in structurally and floristically simple woodlands (open woodland with dominant *Triodia* ground cover). However with the interference of grazing and the associated floristic and structural changes, ant assemblages tend to respond. It has been predicted that post-fire survivorship of ants is high, any resultant change being associated with both alteration of vegetation structure and competition between remaining species (Andersen 1991). Grazing effects coupled with fire response may have altered competitive interactions to significant and measurable levels. This is alluded to where species or groups alter their response from increaser to decreaser where grazing amplifies vegetation structural change.

One other feature of the ant response is a somewhat inconsistent pattern with some species and groups in comparison to other literature. The high species turnover between sites and predicted response to a more subtle variation in microhabitat and landscape position has been suggested as a cause of variation in patterns across studies (Hoffman 2000; Fisher 2001a). Though the functional group system and the use of a subset of species are known to parallel patterns of impact response for entire ant assemblages (Andersen 1990, 1995, 2002), there is also evidence that functional groups themselves are insensitive to grazing changes (Hoffman *et al.* 2000; Hoffman 2001). Ants and other invertebrates have been considered a valuable surrogate for capturing diversity of other vertebrate and plant species because of their high species richness and smaller scale patterning (Ferrier *et al.* 1999; Moritz *et al.* 2001). They are also considered useful bio-indicators for less sensitive vertebrate fauna groups for similar reasons (Andersen 1990). The paradox is that their very diversity may complicate their value in identifying consistent pattern of response to impacts. Unless sampling adequately covers the range and small-scale variation in ant assemblages at a site, comparisons across treatments examining patterns of change may not be valid. Use of functional groups seems a useful counter to this, but if there are multiple species interactions within a group, they may neutralise a response of a few key species. Perhaps intensive survey of few functional groups, and associated species is a better approach, and Hoffman (2001) has suggested that Hot Climate Specialists may be an ecologically significant group for understanding ant community organisation in northern tropical savannas.

Conclusions

In this chapter I demonstrated that fire and grazing have a significant, and often interacting influence on the distribution and abundance of a number of fauna and flora species and guilds in the *Eucalyptus similis* vegetation community. Though the sample size was small, the results are an insight into perhaps a fluid and complicated interaction that can differentially advantage or disadvantage biota. The general pattern of vertebrate response recorded in this study indicated that fire class is the best discriminator of composition, while for ants, grazing class was superior. However within the vertebrate taxa, terrestrial species such as reptiles and small mammals, the grazing effects were quite marked. For a number of species the patterns were in fact dramatic some acting a fire increasers (Singing Honeyeater, Pygopodidae) and decreasers (Black-faced Woodswallow, *Ctenophorus nuchalis*), while other were grazing increasers (Pallid Cuckoo, Rainbow Bee-eater) and decreasers (Granivores, *Ctenotus hebetior*). The interaction of fire and grazing was clearly evident for some ground dwelling species, most notably *Pseudomys desertor* (decreaser) and *P. delicatulus* (increaser). Though plants were not a central focus of this chapter, there were also changes in community structure, the addition of grazing causing a shift from a more typical fire response pattern (ground cover comprising of forbs, tussock and hummock grasses evolving to one dominated by dense hummock grass cover), to composition with more consistent bare ground, tussock grass, forb and shrub cover.

These results have a number of management and research implications. In general studies of fauna response in tropical savanna systems often examine a single process, (e.g. fire) in active pastoral systems. Failing to quantify grazing and piosphere effects (or vice versa) may provide misleading patterns in regards to measured species responses. The complexity of the some patterns, and a tendency for grazed systems to have moderate to high species richness, could perhaps mask underlying deleterious population impacts on a few species (e.g. some species of Granivore, *P. desertor, Ctenotus pantherinus*). For example the contention that intermediate grazing pressure creates higher species richness suggests that this situation is ideal. However on a landscape scale similar species richness is achieved from a mosaic of habitats with a range of fire ages or grazing states. As some species may be both fire increasers and grazing decreasers (e.g. *P. desertor*), habitats kept at an intermediate condition may cause a slow bleed of species that typically need patches of long undisturbed habitat refugia.

Though many patterns were clear, there are a few *caveats* to temper the results. As indicated in the methods attempts were made to unify the choice of sample sites. However there may have been pre-existing differences between the sites unrelated to treatment. For example, the grazed paddocks may have always had fewer *Gastrolobium* and hence probably some other floristic differences which may relate to subtle edaphic factors. Also the mechanical removal of *Gastrolobium* from paddocks that are grazed may have had some influence. These differences that preceded the imposition of treatment may have influenced the faunal composition in some manner. Naturally the interacting pattern of effect of fire regimes and cattle grazing need further examination.

Table 5.5 Minimum adequate models derived for fauna species and groups (bird guilds, non-avian families) utilising GLIM and Poisson (log-link) distribution error and four model terms (grazing, fire, grazing and fire interaction and site). Table indicates parameter estimate and significance (Wald statistic *p<0.05, **p<0.01, ***p<0.001), number of quadrats species recorded from (n) and total deviance explained (%). Mean abundance given for simple grazing and fire treatments, and interacting terms (N=no fire, F=fire, G=grazed, U=ungrazed). For species with significant model terms, mean abundance for significant term category is highlighted in bold. Species recorded in less than two quadrats, but included in the bird guild and family groups are listed below the table.

Species	n	%	Intercept	Grazing	Fire	FxG	Site	No fire	Fire	Ungrazed	Grazed	N+G	F+G	N+U	F+U
Bird abundance	29	11	3.955		-0.002***			**42.6**	**50.2**	48.6	43.5	43.5	55.5	41.63	45.71
Mammal abundance	29	14	2.807			0.003***	-0.184***	15.7	20.4	15.7	19.7	**11.5**	**21.5**	**19.8**	**19.5**
Reptile abundance	29	36	2.765	-0.178***				16.3	16.2	**13.2**	**19.0**	14	12.33	18.5	19.57
Bird richness	29							15.4	17.3	15.5	17.1	15.88	18.67	15.0	16.14
Mammal richness	29							3.1	2.9	2.9	3.1	3.0	2.67	3.13	3.14
Reptile richness	29							7.5	7.5	6.8	8.2	7.38	6.0	7.63	8.86
FRUGIVORES	5							0.25	0.08	0.13	0.21	0.25	0.17	0.25	0.0
Mistletoebird	5							0.25	0.08	0.13	0.21	0.25	0.17	0.25	0.0
FOLIAGE GLEANER	28	6	2.391	0.135*				10.81	11.15	**9.53**	**12.50**	11.75	13.50	9.88	9.14
Black-faced Cuckoo-shrike	11							0.56	1.08	0.73	0.86	0.63	1.17	0.50	1.0
Chestnut-rumped Thornbill	2							0.31	0.31	0.0	0.64	0.63	0.67	0.0	0.0
Horsfield's Bronze-Cuckoo	12							0.69	0.54	0.60	0.64	0.50	0.83	0.88	0.29
Pallid Cuckoo	17	25	0.792		-0.011*	0.006*		**1.0**	**1.92**	1.53	1.29	**0.5**	**2.3**	**1.5**	**1.6**
Red-browed Pardalote	9	31	0.911		-0.026***			**0.13**	**1.77**	0.67	1.07	0.13	2.33	0.13	1.29
Rufous Whistler	27	18	1.463	0.411**		0.006*		4.44	4.54	**4.13**	**4.86**	**3.87**	**6.17**	**5.0**	**3.14**
Striated Pardalote	3							0.81	0.0	0.0	0.93	1.63	0.0	0.0	0.0
Weebill	3							0.75	0.0	0.20	0.64	1.13	0.0	0.38	0.0
Western Gerygone	4							0.19	0.23	0.33	0.07	0.13	0.0	0.25	0.43
Yellow-Rumped Thornbill	7							1.38	0.62	1.07	1.0	1.75	0.0	1.0	1.14
FOLIAGE GLEANER/SALLIER	16							0.81	0.92	0.87	0.86	0.88	0.83	0.75	1.0
Grey Shrike-Thrush	14							0.69	0.92	0.80	0.79	0.75	0.83	0.63	1.0
White-winged Triller	7							0.31	2.0	0.87	1.29	0.0	3.0	0.63	1.14
GRANIVORES	27	22	1.886	0.309*	-0.008***	-0.008***		**3.50**	**6.15**	**4.87**	**4.50**	**1.86**	**8.0**	**5.13**	**4.57**
Australian Ringneck	3							0.75	0.77	1.47	0.0	0.0	0.0	1.50	1.43
Cockatiel	5	18	-0.699	-0.913***			-0.578*	0.75	1.0	**1.40**	**0.29**	0.0	0.67	1.50	1.29
Common Bronzewing	10							0.63	0.54	0.73	0.43	0.50	0.33	0.75	0.71
Crested Pigeon	6							0.0	2.15	0.13	1.86	0.0	4.33	0.0	0.29
Diamond Dove	2							0.0	0.46	0.0	0.43	0.0	1.0	0.0	0.0
Little Button-Quail	4							0.19	0.23	0.40	0.0	0.0	0.0	0.38	0.43
Pale-headed Rosella	2							0.25	0.0	0.0	0.29	0.50	0.0	0.0	0.0
Peaceful Dove	3							0.0	0.77	0.0	0.71	0.0	1.67	0.0	0.0
Red-winged Parrot	3							0.44	0.0	0.33	0.14	0.25	0.0	0.63	0.0
HAWKERS	21	17	1.678		-0.012***			**0.63**	**1.15**	0.67	1.07	0.88	4.83	2.25	4.29
Black-faced Woodswallow	11	31	1.344		-0.025***			**0.31**	**2.69**	1.20	1.57	0.13	3.50	0.50	2.0
Dollarbird	4							0.19	0.23	0.33	0.07	0.13	0.0	0.25	0.43

Species	n	%	Intercept	Grazing	Fire	FxG	Site	No fire	Fire	Ungrazed	Grazed	N+G	F+G	N+U	F+U
Little Woodswallow	11							0.81	1.46	1.40	0.79	0.63	1.0	1.0	1.86
Masked Woodswallow	2							0.25	0.15	0.27	0.14	0.0	0.33	0.50	0.0
NECTARIVORES	21	8	-0.232			-0.006*		0.63	1.15	0.67	1.07	**1.25**	**0.83**	**0.0**	**1.43**
Little Friarbird	5							0.13	0.69	0.27	0.50	0.25	0.83	0.0	0.57
Noisy Friarbird	2							0.50	0.0	0.0	0.57	1.0	0.0	0.0	0.0
NECTARIVORE/ GLEANER	27	16	1.054		0.007**			**5.75**	**3.23**	3.93	5.36	0.0	3.0	0.63	1.14
Singing Honeyeater	25	17	0.853		0.007**			**4.75**	**2.69**	3.47	4.21	5.13	3.0	4.38	2.43
Spiny-cheeked Honeyeater	2							0.44	0.0	0.0	0.50	0.88	0.0	0.0	0.0
Striped Honeyeater	6	21	-0.827				0.907**	0.56	0.54	0.47	0.64	0.75	0.50	0.38	0.57
POUNCING INSECTIVORE	5							0.0	1.46	1.0	0.29	0.0	0.67	0.0	2.14
Hooded Robin	5							0.0	1.31	0.87	0.29	0.0	0.67	0.0	1.86
Tawny Frogmouth	2							0.0	0.15	0.13	0.0	0.0	0.0	0.0	0.29
SALLIERS	29	25	2.034		-0.004*	-0.002*		**5.25**	**6.85**	5.13	6.86	**6.34**	**7.5**	**4.13**	**6.29**
Australian Owlet-nightjar	26							1.38	1.23	1.33	1.29	1.50	1.0	1.25	1.43
Jacky Winter	20	34	1.462		-0.007***	-0.007**		**2.0**	**2.69**	1.80	2.86	**3.25**	**2.33**	**0.75**	**3.0**
Rainbow Bee-eater	10	47	-0.419	1.762***		0.024**		0.56	1.62	**0.60**	**1.50**	**0.25**	**3.2**	**0.88**	**0.29**
Spotted Nightjar	6							0.38	0.15	0.13	0.43	0.63	0.17	0.13	0.14
Willie Wagtail	15							0.88	1.15	1.20	0.79	0.75	0.83	1.0	1.43
TRUNK GLEANER	2		0.723		-0.031*	0.017*		**0.38**	**1.38**	0.80	0.86	**0.0**	**2.0**	**0.75**	**0.86**
Varied Sittella	4							0.38	1.15	0.80	0.64	0.0	1.50	0.75	0.86
TERRESTRIAL INSECTIVORES	15	36	-1.441	1.549**	0.028**	0.018**		**3.19**	**0.62**	**2.07**	**2.0**	**2.63**	**1.17**	**3.75**	**0.14**
Grey-crowned Babbler	4	8	-0.737	0.583*				0.75	0.31	**0.27**	**0.86**	1.0	0.67	0.50	0.0
Magpie-Lark	5							0.13	0.31	0.07	0.36	0.25	0.50	0.0	0.14
Variegated Fairy-wren	6							2.0	0.0	1.73	0.43	0.75	0.0	3.25	0.0
TERRESTRIAL OMNIVORES	29							9.69	10.23	9.87	10.0	10.50	9.33	8.88	11.0
Australian Magpie	14							0.88	0.92	0.73	1.07	0.75	1.50	1.0	0.43
Australian Raven	6							0.31	0.38	0.13	0.57	0.38	0.83	0.25	0.0
Barn Owl	7							0.38	0.08	0.27	0.21	0.25	0.17	0.50	0.0
Brown Falcon	9							0.25	0.77	0.33	0.64	0.38	1.0	0.13	0.57
Crested Bellbird	28							3.06	2.69	3.13	2.64	2.88	2.33	3.25	3.0
Grey Butcherbird	9							0.94	0.38	0.60	0.79	1.25	0.17	0.63	0.57
Pheasant Coucal	2							0.13	0.0	0.13	0.0	0.0	0.0	0.25	0.0
Pied Butcherbird	20	14	0.479				0.368*	1.69	1.54	1.73	1.50	1.88	1.0	1.50	2.0
Red-backed Kingfisher	6							0.06	0.62	0.13	0.50	0.0	1.17	0.13	0.14
Sacred Kingfisher	3							0.19	0.15	0.07	0.29	0.25	0.33	0.13	0.0
Southern Boobook	7							0.25	0.31	0.27	0.29	0.25	0.33	0.25	0.29
Yellow-throated Miner	12							1.50	2.23	2.40	1.21	1.63	0.67	1.38	3.57
DASYURIDAE	8	26	-1.271				-1.211*	0.5	0.69	0.6	0.5	0.38	0.67	0.63	0.71
Sminthopsis macroura	8	24	-1.339				-1.145*	0.50	0.54	0.67	0.36	0.38	0.33	0.63	0.71
MACROPODIDAE	21	32	2.551	-0.262***	-0.009***		-0.591***	**5.6**	**15.9**	**10.7**	**9.7**	3.50	18.17	7.88	14.0
Macropus giganteus	17	15	1.311				-0.583***	3.25	6.31	3.87	5.43	3.0	8.67	3.50	4.29
Macropus robustus	16	38	2.167	-0.529***	-0.019***		-0.671***	**1.94**	**9.62**	**6.33**	**4.36**	0.50	9.50	3.38	9.71

Species	n	%	Intercept	Grazing	Fire	FxG	Site	No fire	Fire	Ungrazed	Grazed	N+G	F+G	N+U	F+U
MURIDAE	28	53	0.973	-0.224**	0.134***			**9.4**	**3.5**	8.2	5.2	**7.25**	**2.5**	**11.62**	**4.42**
Pseudomys delicatulus	16	45	1.587	-0.628**	-0.0258***	-0.019**		**0.81**	**2.92**	1.67	1.86	**1.38**	**2.5**	**0.25**	**3.29**
Pseudomys desertor	16	76	-8.84	-7.801**	0.117***	-0.794*		**8.63**	**0.54**	**6.53**	**3.36**	**5.88**	**0.0**	**11.38**	**1.0**
TACHYGLOSSIDAE	12							0.56	0.38	0.67	0.29	0.38	0.17	0.75	0.57
Tachyglossus aculeatus	13							0.56	0.38	0.67	0.29	0.38	0.17	0.75	0.57
AGAMIDAE	22	13	0.458	-0.389*				1.5	2.0	**2.3**	**1.1**	1.00	1.17	2.00	2.71
Amphibolurus nobbi	14							1.06	0.77	1.13	0.71	0.88	0.50	1.25	1.0
Ctenophorus nuchalis	6	45	0.289		-0.032**			**0.06**	**0.85**	0.53	0.29	0.0	0.67	0.13	1.0
Pogona barbata	8	26	-1.522**	-1.116*				0.38	0.38	**0.67**	**0.07**	0.13	0.0	0.63	0.71
ELAPIDAE	4							0.13	0.15	0.2	0.07	0.13	0.00	0.13	0.29
Simoselaps australis	2							0.06	0.08	0.07	0.07	0.13	0.0	0.0	0.14
GEKKONIDAE	26	14	0.936	-0.548*		-0.008**		2.5	2.8	**2.7**	**2.6**	**3.25**	**1.6**	**1.75**	**3.85**
Diplodactylus conspicillatus	7	37	-1.339				1.493**	0.44	0.62	0.87	0.14	0.13	0.17	0.75	1.0
Diplodactylus steindachneri	13							0.88	1.15	1.0	1.0	1.38	0.50	0.38	1.71
Diplodactylus williamsi	4							0.19	0.15	0.20	0.14	0.13	0.17	0.25	0.14
Heteronotia binoei	5							0.25	0.23	0.13	0.36	0.50	0.17	0.0	0.29
Rhynchoedura ornata	14							0.63	0.69	0.53	0.79	0.88	0.67	0.38	0.71
PYGOPODIDAE	9	19	-2.303		0.0201*			**0.68**	**0.15**	0.4	0.5	0.75	0.17	0.63	0.14
Lialis burtonis	7							0.44	0.15	0.27	0.36	0.50	0.17	0.38	0.14
Pygopus nigriceps	4							0.25	0.0	0.13	0.14	0.25	0.0	0.25	0.0
SCINCIDAE	29	25	2.172	-0.237***				9.87	8.15	**11.1**	**6.9**	7.88	5.67	11.88	10.29
Carlia munda								0.06	0.08	0.0	0.14	0.13	0.17	0.0	0.0
Cryptoblepharus carnabyi								0.06	0.08	0.07	0.07	0.0	0.17	0.13	0.0
Ctenotus capricorni	20							1.19	1.85	1.60	1.36	1.0	1.83	1.38	1.86
Ctenotus hebetior	19	32	0.713	-0.874***		-0.009**	0.667***	2.44	3.23	**3.40**	**2.14**	**2.25**	**2.0**	**2.63**	**4.29**
Ctenotus pantherinus	17	47	-0.815	-0.714***	0.017***			**2.81**	**0.77**	**3.0**	**0.71**	1.25	0.0	4.38	1.43
Ctenotus rosarium	14	55	-0.332	-0.654**			0.803***	1.31	1.0	**1.93**	**0.36**	0.63	0.0	2.0	1.86
Ctenotus strauchii	9							0.63	0.31	0.40	0.57	0.75	0.33	0.50	0.29
Lerista muelleri	2							0.19	0.0	0.0	0.21	0.38	0.0	0.0	0.0
Menetia greyii	8	43	-0.941	-1.074***				0.63	0.62	**0.13**	**1.14**	1.25	1.0	0.0	0.29
Morethia taeniopleura	5							0.25	0.08	0.20	0.14	0.25	0.0	0.25	0.14
Tiliqua scincoides	2							0.06	0.08	0.13	0.0	0.0	0.0	0.13	0.14
VARANIDAE	12							0.68	0.38	0.67	0.42	0.50	0.33	0.88	0.43
Varanus gouldii	3							0.13	0.08	0.0	0.21	0.25	0.17	0.0	0.0
Varanus tristis	9							0.56	0.31	0.67	0.21	0.25	0.17	0.88	0.43

Foliage gleaner/sallier Spotted Bowerbird, Olive-backed Oriole, *Foliage gleaners*, White-throated Gerygone, Inland Thornbill, Black-eared Cuckoo, *Granivores* Zebra Finch, Sulphur-crested Cockatoo, Red-tailed Black Cockatoo, Galah, Black-throated Finch, *Nectarivore/foliage gleaner* Black-chinned Honeyeater, *Nectarivores* Rainbow Lorikeet, *Raptors* Collared Sparrowhawk, Brown Goshawk, *Salliers* Restless Flycatcher, *Terrestrial insectivores* Red-backed Fairy-wren, *Terrestrial omnivores* Wedge-tailed Eagle, Torresian Crow, Little Eagle, *Trunk gleaner* Brown Treecreeper, Macropodidae, *Macropus rufus*,, Elapidae, *Demansia psammophis, Simoselaps warro, Suta suta,* Gekkonidae, *Oedura marmorata,* Scincidae, *Lerista* sp nov, *Lerista punctatovittata, Proablepharus tenuis,* Typhlopidae, *Ramphotyphlops unguirostris.*

Table 5.6 Minimum adequate models derived for ant species and functional groups utilising GLIM and Poisson (log-link) distribution error and four model terms (grazing, fire, grazing and fire interaction and site). Table indicates parameter estimate and significance (Wald statistic *p<0.05, **p<0.01, ***p<0.001), number of quadrats species recorded from (n) and total deviance explained (%). Mean abundance given for simple grazing and fire treatments, and interacting terms (N=no fire, F=fire, G=grazed, U=ungrazed). For species with significant model terms, mean abundance for significant term category is highlighted in bold. Species recorded in less than two quadrats, but included in the bird guild and family groups are listed below the table.

SPECIES	N	%	Intercept	Grazing	Fire	G x F	Site	No fire	Fire	Ungrazed	Grazed	N+G	F+G	N+U	F+U
Ant abundance	26	5	3.481			0.002**		34.8	31.2	30.6	35.1	**26.85**	**35.0**	**35.57**	**34.67**
Ant species	26							7.8	7.0	7.2	7.8	7.0	7.33	7.29	8.33
CRYPTIC															
Brachyponera lutea	4							0.08	0.21	0.15	0.15	0.29	0.0	0.14	0.17
SPECIALIST PREDATORS	23	26	1.407			0.007***		4.33	5.21	7.07	2.53	**2.0**	**3.17**	**8.43**	**5.5**
Bothroponera sp A (*sublaevis* gp)	9	36	-0.334	0.601**		0.021***		1.0	1.36	**1.77**	**0.62**	**0.0**	**1.33**	**2.71**	**0.67**
Leptogenys adlerzi	4							0.42	0.14	0.23	0.31	0.0	0.67	0.29	0.17
Leptogenys sp (*adlerzi* gp)	3							0.0	0.21	0.08	0.15	0.29	0.0	0.14	0.0
Myrmecia callima	19	30	0.892	-0.685***				2.92	3.14	**4.85**	**1.23**	1.29	1.17	5.0	4.67
OPPORTUNISTS	26	9	2.632			0.002**		12.67	15.57	16.08	12.38	**12.43**	**12.33**	**18.71**	**13.0**
Odontomachus sp (*ruficeps* gp)	5							0.25	0.29	0.54	0.0	0.0	0.0	0.57	0.50
Rhytidoponera sp nr *hilli*	15	34	1.201			0.003**	0.736***	4.17	4.36	6.08	2.46	**3.0**	**1.83**	**5.71**	**6.5**
Rhytidoponera metallica	5							0.25	1.64	1.38	0.62	0.71	0.50	2.57	0.0
Rhytidoponera sp nr *rufithorax*	16	6	1.173	0.304**				2.50	4.14	**2.38**	**4.38**	4.86	3.83	3.43	1.17
Rhytidoponera sp A (*tyloxys* gp)	4							0.25	0.64	0.77	0.15	0.29	0.0	1.0	0.50
Rhytidoponera sp B (*tyloxys* gp)	8	9	-0.441	-0.514*				0.42	1.0	**1.08**	**0.38**	0.71	0.0	1.29	0.83
Rhytidoponera sp C (*mayri* gp)	17	30	1.041	0.885*		0.013**		3.75	3.14	**2.92**	**3.92**	**2.14**	**6.0**	**4.14**	**1.5**
Tetramorium ?*sjostedti*	5	55	-0.638	-1.532***		-0.019***		1.08	0.36	**0.92**	**0.46**	**0.71**	**0.17**	**0.0**	**2.0**
SUBORDINATE CAMPONOTUS	25	22	1.988	0.928***		0.006**	0.244**	9.50	7.50	**4.77**	**12.08**	**10.14**	**14.3**	**4.86**	**4.67**
Camponotus sp nr *denticulatus*	20	21	1.661	0.799***		0.003*		7.0	6.0	**2.85**	**10.08**	**9.0**	**11.3**	**3.0**	**2.67**
Camponotus dromas	4							0.33	0.14	0.0	0.46	0.29	0.67	0.0	0.0
Camponotus fieldae	3							0.42	0.07	0.23	0.23	0.0	0.50	0.14	0.33
Opisthopsis rufoniger	5							0.42	0.14	0.08	0.46	0.29	0.67	0.0	0.17
Polyrhachis sp A (*schwiedlandi gp*)	5							0.17	0.50	0.54	0.15	0.14	0.17	0.86	0.17
Polyrhachis sp B (*schwiedlandi gp*)	6							0.25	0.36	0.31	0.31	0.0	0.0	0.0	0.33
Polyrhachis sp D (*inconspicua gp*)	2							0.0	0.21	0.23	0.0	0.43	0.17	0.29	0.33
DOMINANT DOLICHODERINAE	6	39	0.603	-1.421***	-0.028**	-0.021*	-1.539***	**2.17**	**0.29**	**1.15**	**1.15**	**0.57**	**1.83**	**0.0**	**2.5**
Iridomyrmex hartmeyeri	5	53	-0.619	-1.738***		-0.019***		1.33	0.29	**1.15**	**0.38**	**0.57**	**0.17**	**0.0**	**2.5**
HOT CLIMATE SPECIALISTS	19	30	1.739	-0.657***	-0.011***		-0.305**	**6.08**	**2.43**	**5.92**	**2.31**	1.42	3.3	0.14	0.16
Meranoplus sp A (*diversus gp*)	2							0.92	0.07	0.92	0.0	0.0	0.0	0.14	1.83
Melophorus sp A (*aeneovirens gp*)	18	29	1.487	-0.631***	-0.008**		-0.476***	**5.17**	**2.29**	**5.0**	**2.23**	0.14	0.0	0.0	0.0

CRYPTIC, SPECIALIST PREDATORS, *Myrmecia? varians, Cerapachys varians, Cerapachys* sp B (*fervidus* gp), HOT CLIMATE SPECIALISTS *Meranoplus* sp B (*diversus gp*), DOMINANT DOLICHODERINAE *I. mayri*, SUBORDINATE CAMPONOTUS *Calomyrmex* sp A, *Camponotus* sp A (*subnitidus* gp), *Camponotus* sp B (*novaehollandiae* gp), *Camponotus* sp C (*rubiginous* gp), *Camponotus* sp D (*discors* gp), *Camponotus* sp E (*discors* gp), *Camponotus* sp F (*discors* gp), *Camponotus* sp G (*subnitidus* gp), *Polyrhachis* sp C (*gravis gp*), *Polyrhachis* sp E (*inconspicua gp*), *Polyrhachis hookeri*

Chapter 6. General conclusions.

The tropical savannas of northern Australia are in some ways enigmatic landscapes: seemingly constant expanses of treed and treeless plains that cover vast areas of the continent but environmentally in a state of flux. A capricious climate (short resource boom followed by long term bust) coupled with widespread ecological connectivity is the foundation of the tropical savanna character (Woinarski 1999). The pattern of its flora and fauna are tightly in tune with these resource vagaries. This illusion of plentiful and limitless environment lured explorers and settlers (Bennett 1928; Smith 1994; Ash *et al.* 1997; Holmes 1990). However a failure to perceive and understand the climatic inconsistency has plagued the viability of pastoralism in tropical savannas for decades (Ash *et al.* 1997), consequently creating serious problems of landscape degradation (Holmes 1990; Winter 1990).

Tropical savanna landscapes are often considered to be “intact”, largely because of the limited extent of habitat destruction through clearing and a general belief that the impacts on fauna by pastoralism are benign or very localised (Kirkpatrick and Lavery 1979; McKenzie 1981; Curry and Hacker 1990; Whitehead *et al.* 2000; Read 2002). There is now substantial evidence that a range of factors, including grazing or fire management, has compromised landscape health in many areas (Woinarski *et al.* 1999; Whitehead *et al.* 2000). Post-European mammal extinction and avifauna disarray (e.g. granivorous birds) are recognised examples of this (Burbidge and McKenzie 1989; Franklin 1999; Lunney 2001). Though the concept of “ecological health” is nebulous (Whitehead *et al.* 2001) it does reflect a current growing concern that the *status quo* of resource use is not only unsustainable, but also economically very costly (Allen Consulting Group 2001). There is a current appreciation that functioning of tropical savanna systems are possibly at the cusp of a period of further serious decline (Woinarski *et al.* 2000).

Conservation management in tropical savanna requires regional strategies rather than those concentrating on small, discrete refugia (Woinarski 1999b). As such land-use decision-making and management in tropical savanna environments need to understand broadscale patterns and processes. The joint history of pastoral enterprise and conservation planning in Queensland has, in this respect, been poor. For example very little preliminary ecological research or structured regional conservation planning was conducted in the Brigalow Belt prior to the onset of development of this bioregion in the 1970's (Gordon 1984; Covacevich *et al.* 1998; Sattler and Williams 1999). The lack of accurate distributional data for the North-west Highlands and Gulf Plains (see chapter 2) further emphasises the parlous state of ecological knowledge for tropical savannas in Queensland.

For these reasons the research framework and survey strategy followed in this study of the Desert Uplands bioregion, is a suitable approach to accruing knowledge for large biogeographic regions in a manner that is both useful for exploring ecological patterns and for incorporating in practical land management and conservation planning. Four key research questions were posed in this thesis, utilising a research framework proposed for rangelands (James *et al.* 1995; Fisher 2001). The survey also examined the relative influence of a number of determinants of ecological patterning (Ricklefs and Schluter 1993), namely the biogeographic shadow covering the composition of the bioregional species pool, the relationship between regional fauna assemblage and habitat heterogeneity, and local-scale interactions with landscape process. In very brief summary this research identified:

- *What is the zoogeographic context of the Desert Uplands?* The Desert Uplands is a cohesive biogeographic unit, with a distinct alliance with neighbouring coastal regions, but also faunal affinity to the wider arc of tropical savanna bioregions across northern Australia. Evidence of species replacement and isolation between coastal and inland faunas confirms its position on a number of biogeographic boundaries.

- *What are the patterns of distribution and composition in relation to the environment?* The vertebrate fauna assemblages of the Desert Uplands exhibit a high fidelity to particular habitats and environmental extremes (e.g. hummock and tussock grasslands), whereas other assemblages are indistinct, in particular those in an interconnected suite of *Acacia* and *Eucalyptus* woodlands. This group, though the most species-rich, is characterised by having a core assemblage that varies in abundance between different types, according to relatively subtle environmental gradients (e.g. comparatively minor changes in substrate, ground and canopy cover dominance).

- *How might these patterns influence conservation planning in the region?* Regional ecosystems, the base conservation-planning unit in Queensland, have broad correspondence with fauna composition. However conservation planning driven primarily by protection of regional ecosystems of conservation significance will not protect species-rich sites or sites with a high abundance of species. Conservation planning in the Desert Uplands must also take into account targeted planning for species-rich areas, unique but species-poor areas and species of conservation significance.

- *What is the impact upon biodiversity of pastoralism, in particular cattle grazing and fire patterns?* Fire and grazing have a significant, and often interacting influence on the abundance of a number of fauna species and guilds in the *Eucalyptus similis* vegetation community. For vertebrate taxa, the grazing effects were quite marked, though there were a number of notable increaser and decreaser fire and grazing effects for many species and guilds.

What then are the implications of this research both in regards to the value and efficacy of broad-scale bioregional survey in Queensland's tropical savannas for conservation planning, and the contribution to land management policy in vast, largely intact biotic systems? At least in Queensland, bioregional inventories have been uncommon in the savanna rangelands (Chapter 2 and 3). Elsewhere such data has been utilised to not only elucidate the biogeographic and biological patterns of savannas biota (Chapter 3), but also to recognise that conservation planning in these areas require strategies concomitant to its geographical scope (Chapter 3, 4). In the Northern Territory, this work underpins a philosophy to planning that recognises interconnected environmental pattern and stark temporal variation (Woinarski 1999). Long term research has also presented a intricate dilemma that may otherwise be masked from consideration: guilds of species widespread species across savanna rangelands and those with restricted distribution in small well protected have both seemingly suffered a declines in abundance reserves (Franklin 1999; Woinarski *et al.* 2000). As yet the causes are proving difficult to tease out, but likely relate to changes in multiple aspects of land management (Franklin 1999). This suggests that there is still much information regarding the ecological function of wildlife in savannas yet to be discovered. The survey of the Desert Uplands has demonstrated that a similar foundation of data is achievable Queensland. However the discovery of new species and exceptional range extensions indicate that there is still a large amount of knowledge to be gleaned regarding the composition and patterns of native plants and animals (Chapter 3). Though land classification, such as regional ecosystem mapping, is a simple strategy for rapidly trying to capture a comprehensive and representative protected area estate, it is clear that such surrogates are not perfect for species and groups are poorly known, restricted, and temporally or environmentally fickle. Landscape-based proxies cannot be considered conservation planning cure-alls, and as such they are no substitute for hard data (Chapter 4).

Biodiversity protection has generally believed to lie in the realm of comprehensive reserves systems that collect the representative range of examples of native wildlife and ecosystems (JANIS 1997). However reserves are generally incapable of capturing the essence of pervasive natural systems like tropical savannas, and often cannot ensure integrity of ecological process and population viability in perpetuity. Instead native plant and animal conservation must operate in parallel to the geographic and climatic scope of tropical savannas (Woinarski 1999). The majority of rangelands lie outside the formal reserve system. For example, grazing beef cattle represents 97% of the geographic extent of land use the Desert Uplands. Therefore the concept of “off-reserve conservation” has become in vogue, and this applies to the development of management strategies that promote biodiversity conservation across all rangelands without detracting from the economics of pastoral systems (Hale and Lamb 1997, Fisher 2001). While there is widespread recognition of this imperative amongst many land managers and natural resource management agencies, there is still a poor understanding of how to achieve this (Fisher 2001). Reported strategies include: management of total grazing pressure according to land capability (Ash *et al.* 1997), undertaking wet-season spelling (Ash *et al.* 1997), using of fire more effectively (Landsberg *et al.* 1998), redistributing the arrangement of water-point distribution (James *et al.* 2000), fencing out cattle from areas of high conservation value (Lavery *et al.* 1997), control of threatening processes such as weeds (Crowley and Garnett 2000), using grazing land management to improve land condition (Ash *et al.* 2002) and education packages to promote the concepts of environmental sustainability (Dorricot *et al.* 1998).

There is a rising tide of goodwill among landholders to biodiversity concerns and many of the strategies identified above have a distinct benefit to economic viability as well as wildlife (Landsberg *et al.* 1998). However there is still slow acceptance that there is a negative relationship between some aspects of grazing land management (e.g. proliferation of water points) and biodiversity consequences (pers. obs.). Coupled with this is the lack of incentive to consider nature conservation, despite community expectations that this should occur (Productivity Commission 2001, 2003). Therefore there needs to be an appropriate policy context (sympathetic taxation systems, property tenure certainty, other incentives), within government to ensure biodiversity conservation is accepted as part of the core business of agriculture (Productivity Commission 2001, 2003). Recent discussion regarding changes to Queensland leasehold tenure conditions indicate there is some strong will by governments to make an environmental duty of care a proviso of renewal, but also rewarding compliance with on-going certainty (Queensland Government 2003a, b). But perhaps now it is the accumulation of ecological information, and the capacity to interpret and apply this data to pastoral land management systems, that is lagging. This is certainly the case in Queensland. Future tropical savanna research needs to focus on how pastoral management influences the patterns of biota, and which strategies best promote biodiversity and landscape health within the framework of a system whose primary aim is cattle-grazing and not nature conservation (e.g. James *et al.* 2000).

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Appendix 1.

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Appendix 2.

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Appendix 6.

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