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Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia

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ABSTRACT. The abundance, richness and species composition of frog, reptile, bird and mammal faunas varied along an extensive gradient from 470 to 1406 mm annual rainfall, and between three contrasting soil types (clay, loam and sand) in northern Australia. Patterns varied between and within vertebrate classes. In general, the most fertile soils in the highest rainfall sites supported the greatest species richness and abundance, but this association with fertility broke down at lower rainfall sites. Frogs were richest and most abundant at high rainfall sites, especially on clay soils, presumably because these had greatest water availability. Clay soils supported few reptile species, but these were often at relatively high abundance. High rainfall sites supported the richest reptile faunas. On sand and loam soils, bird species richness varied little along the rainfall gradient, but richness declined very substantially on clay soils. This was probably largely due to the far more marked vegetation structural change on clay soils than on other substrates. Few mammals were reported, and no clear trends were associated with either rainfall gradient or soil texture. Turnover in species composition along the rainfall gradient was gradual and limited on sand and loam soils, but far more marked on clay soils. There were few cases of replacements of ecologically comparable species along the gradient. These patterns reflect the disparate history, fragmentation and landscape positioning of clay soil environments, relative to the far more homogeneous eucalypt-dominated vegetation on sand and loam soils. Although comparable studies are lacking on other continents, patterns revealed here may be idiosyncratic due to the virtual monopolisation by eucalypts of the environment across the very extensive rainfall gradient.

KEY WORDS: Australia, birds, diversity, frogs, mammals, rainfall gradient, reptiles, savanna, soil

INTRODUCTION

Biologists have long been intrigued by the richness of tropical ecosystems, and the factors that may underlie geographic variation in diversity. Many recent studies have examined latitudinal variation in animal species richness, typically based on data extracted from coarse-scale distributional maps (Anderson & Marcus 1992, Cogger & Heatwole 1981, Pianka 1966, Rohde 1992). While providing useful broad-scale comparisons across regions, this approach may blur the different components of diversity, especially that of single-site richness (alpha-diversity) with that of the richness attributable to the variety of environments present within a grid cell (beta-diversity), and hence obscure interpretation of the causes underlying diversity patterning. It may also be substantially influenced by variation in sampling effort (e.g. Prendergast *et al.* 1993).

In this study, we investigated variation in alpha-diversity by comparing vertebrate species richness at a series of identically sized and sampled plots placed along a pronounced rainfall gradient (coinciding with a latitudinal span of 5°) in the Australian tropical savannas. These plots were also located to sample variation in soil nutrients, the other main factor underlying variation in the composition, structure and dynamics of tropical savanna vegetation (Skarpe 1992, Solbrig *et al.* 1996, Walker & Menaut 1988). In the relatively unmodified savannas of the Northern Territory, Australia, these two principal variables, as measured by annual rainfall and soil texture, determine much of the vegetation patterning (Bowman 1996, Bowman *et al.* 1993, Walker & Langridge 1997, Williams *et al.* 1996). Although variation in the distribution of some animal groups in this region has been shown to be associated with this rainfall gradient (Whitehead *et al.* 1992), there has been no previous attempt to sample vertebrates across the framework provided by variation in soil texture and rainfall.

In addition to examining patterns of species richness, we also use this framework to explore variation in species composition and turnover, and in vertebrate abundance, across these extensive savanna woodlands, grasslands and tropical open forests. As with richness, broad patterns in the composition of the vertebrate fauna in this region have been described previously (Whitehead *et al.* 1992, Woinarski 1992) from collation of all available records at a coarse scale (1° × 1° cells). This study seeks to confirm or refine such described patterns through a more rigorous sampling procedure.

METHODS

Study sites and sampling procedure

Along the North Australian Tropical Transect (NATT: Koch *et al.* 1995, Williams *et al.* 1996) we sampled vertebrates at five sites, with median annual rainfalls of 472 mm (Kalkarinji), 640 mm (Kidman Springs), 721 mm

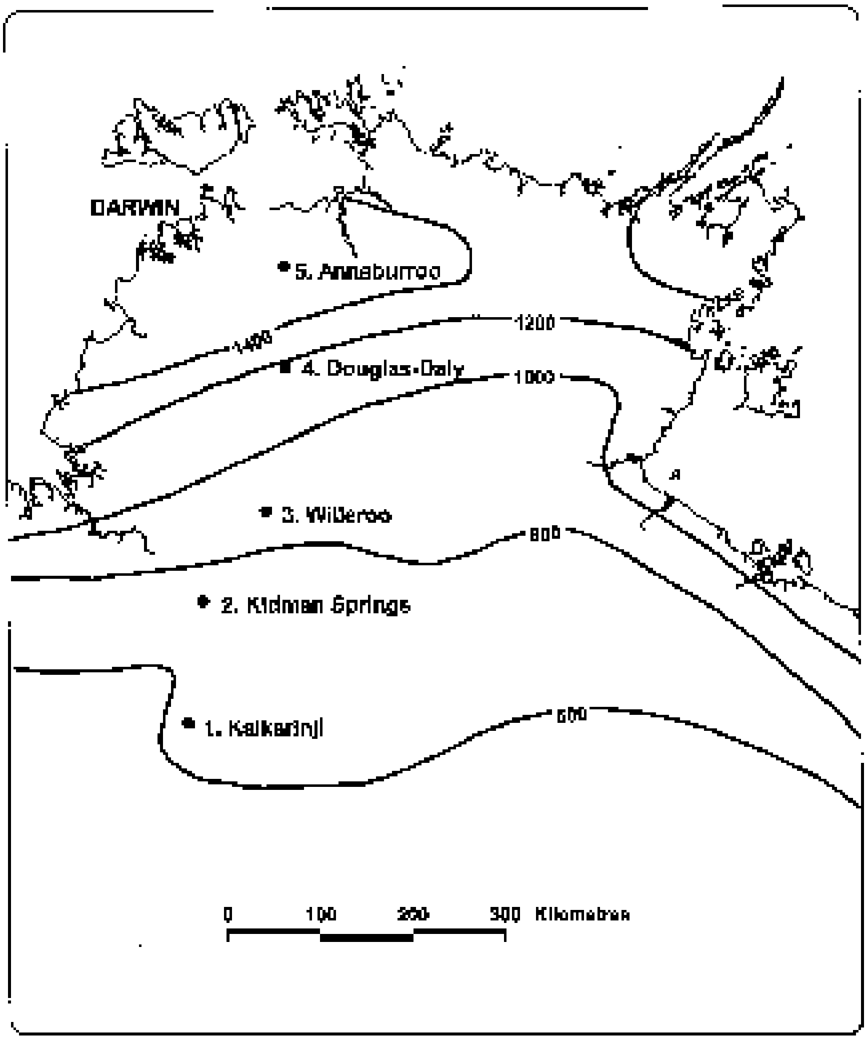

Figure 1. Location of the five sampling sites and isohyets of mean annual rainfall in Northern Territory, Australia.

(Willeroo), 1136 mm (Douglas/Daly) and 1406 mm (Annaburroo), spanning a north–south distance of 520 km and a latitudinal range of 5° (Figure 1). The entire area sampled lies within the monsoon tropics, in which about 90% of the annual rainfall occurs during a short (typically December–March) wet season.

At each site we established two plots in each of three contrasting soil types: clay, loam and sand. These six plots were located within a radius of around 30 km, with at least 1 km between the closest plots. At most sites, the replicate plots of the same soil type were more distant from each other than the mean inter-plot distance. Plots were selected to be representative of extensive savanna and open forests, avoiding riparian areas, patches of monsoon rainforests and rocky topographic features. At each site one plot from each soil type had been selected previously as part of a global examination of savanna plant patterning (Ludwig *et al.* in press).

All plots were 100-m × 100-m. Within each plot we established four pitfall traps (20-l plastic buckets) each with 10 m of driftline fence (for the capture of reptiles, frogs and small mammals). Forty Elliott (aluminium box) traps and eight cage traps (for capture of small mammals and some reptiles) were placed around the perimeter of each plot, and baited daily with a peanut butter, honey and oats mixture. All traps were set over a continuous period of 96 h, and checked three times a day. All plots were searched five times (early morning, late morning, afternoon, and two night), each for 10 min, for reptiles, mammals and frogs. All plots were censused ten times (eight in the day and two at night) for birds. Birds flying over the plot were excluded, unless they were actively hunting. For each species, the total number of individuals seen and caught was tallied to derive a single abundance value for each species in each plot. Species detected from distinctive signs (e.g. faeces, tracks, bones) in a plot, but not seen or captured, were assigned an abundance value of 1. Livestock were excluded from all counts. All plots were sampled in April and May 1997.

Plots were selected to be broadly comparable in disturbance. No plot had been burnt in the 6 mo preceding sampling. All plots were exposed to cattle grazing at low to moderate intensities.

Analysis

For each vertebrate class, the species richness and total abundance of individuals in plots were compared between soil types and rainfall, using generalised linear modelling (Crawley 1993) with a Poisson error distribution. The analysis first considered rainfall, soil type (as a three factor) and rainfall–soil interaction terms within a full model. The model was then re-examined without the interaction term to assess the main effects only. This analysis pathway was also used for examining variation in canopy height, basal area of eucalypts and basal area of non-eucalypts.

We also compared richness and abundance among treatments for the more numerous reptile groups – geckos (Family Gekkonidae), agamids (Agamidae), varanids (Varanidae), skinks (Scincidae) and snakes (Typhlopidae, Colubridae, Boidae and Elapidae) – and for two distinctive and numerous bird foraging groups – nectarivores (honeyeaters and lorikeets) and granivores (doves, button-quail, quail, finches and ground-feeding parrots). Nectarivorous birds are notable in this region for their high mobility and large but often ephemeral contribution to local bird assemblages (e.g. Franklin 1997, Woinarski & Tidemann 1991) in association with variability in nectar availability. To remove the influence of possible local variation in flowering, we also subtracted all nectarivores from our data for total birds, and related the non-nectarivorous bird richness and abundance pattern to annual rainfall and soil types.

We examined habitat specificity of every species recorded from at least five plots, by counting the number of soil types and number of sites from which the species was recorded.

For all species combined, variation between plots in species composition was investigated by ordination using semi-strong hybrid multidimensional scaling within the program PATN (Belbin 1987). Using the Czekanowski similarity index, we also investigated variation in species composition between replicate plots (like-site, like-soil texture), and, for plots on like soil type, between pairs of sites.

The distributions of every species were plotted against variation in annual rainfall and soil texture, and the resulting graphs were inspected for cases of possible mutually exclusive distributions of otherwise ecologically similar species.

RESULTS

Environmental variation

The soil and rainfall gradients corresponded with marked variation in the vegetation structure and floristics (Table 1, Figure 2). Canopy height decreased down the rainfall gradient, and was generally greater for sand sites than at sites with other substrates. Eucalypts were dominant on sand sites and, to a lesser extent, on loam sites; and their basal area declined down the rainfall gradient. There was a high basal area of non-eucalypts on clay sites at the two highest rainfall sites.

Patterns in vertebrate richness and abundance

A total of 180 species, comprising 17 frogs, 50 reptiles, 97 birds and 16 mammals, was recorded. Illustrative of the relatively intact ecological nature of this area, these tallies included no introduced species.

For the richness and abundance of almost all groups considered, there were significant differences associated with rainfall, soil texture and/or an interaction of these terms (Figure 3, Table 1), with weaker or no significant relationships generally only for the groups with relatively few species and individuals encountered (e.g. snakes, mammals, geckos, agamids, varanids). Over all vertebrates, the most notable feature was that, on clay soils, species richness and abundance declined with decreasing rainfall. There were substantial differences between vertebrate classes in the patterning of richness and abundance in relation to the rainfall and soil texture gradients. Frog species richness and abundance was greatest in plots in the highest rainfall sites, and especially on clay soils there. Reptile species richness varied most substantially between soil types, with notably lower richness on clay soils; but also tended to decrease with decreasing rainfall. Bird species

Table 1. Summary of results of relationships of richness and abundance of taxa with annual rainfall and soil type, using general linear models with a log link function. Values in the table are the change in deviance associated with removing that term from a fuller model.

Variable	Rainfall	Soil type	R × S
df	1	2	2
Species richness			
All species	29.0 ***	3.15 ns	36.2 ***
Birds	9.18 **	1.35 ns	32.8 ***
Reptiles	6.92 **	13.2 **	0.48 ns
Frogs	26.2 ***	9.22 **	6.06 *
Mammals	1.46 ns	0.30 ns	1.90 ns
Geckos	0.02 ns	4.83 ns	3.89 ns
Agamids	0.05 ns	3.96 ns	1.12 ns
Varanids	4.55 *	0.63 ns	0.56 ns
Skinks	6.05 *	3.76 ns	1.40 ns
Snakes	0.13 ns	4.01 ns	7.35 *
Granivorous birds	1.89 ns	1.55 ns	5.77 ns
Nectarivorous birds	1.72 ns	2.89 ns	11.0 **
Non-nectarivorous birds	7.45 **	0.84 ns	23.2 ***
Abundance			
All species	101 ***	5.73 *	321 ***
Birds	0.59 ns	63.4 ***	159 ***
Reptiles	55.9 ***	14.0 ***	2.49 ns
Frogs	312 ***	233 ***	160 ***
Mammals	5.36 *	4.74 ns	7.27 *
Geckos	3.24 ns	12.8 **	8.01 *
Agamids	0.36 ns	6.88 *	0.98 ns
Varanids	6.24 *	0.55 ns	1.08 ns
Skinks	60.7 ***	3.71 ns	6.87 *
Snakes	0.47 ns	4.32 ns	9.16 *
Granivorous birds	68.5 ***	83.6 ***	149 ***
Nectarivorous birds	0.00 ns	25.0 ***	42.5 ***
Non-nectarivorous birds	0.67 ns	50.1 ***	122 ***
Eucalypt basal area	13.3 ***	32.1 ***	0.54 ns
Non-eucalypt basal area	32.5 ***	6.16 *	2.58 ns
Canopy height	27.9 ***	9.45 **	2.15 ns

Asterisks indicate the significance associated with a χ^2 test on the change of deviance (with degrees of freedom as indicated): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

richness and abundance showed little variation across the rainfall gradient for sand and loam soils, but a substantial decline on clay soils. Few mammals were recorded, and the only clear pattern involved a peak in richness and abundance (particularly on clay and loam soils) at the site with second highest rainfall.

Within classes, individual taxonomic or ecological groups often showed highly individualistic responses to rainfall and soil variation. For example, within reptiles, varanids showed a decline along the rainfall gradient but no significant variation in richness or abundance related to soil texture; gecko species richness showed no significant variation, but the number of individuals was least on clay soils; agamids were also least abundant on clay soils; there

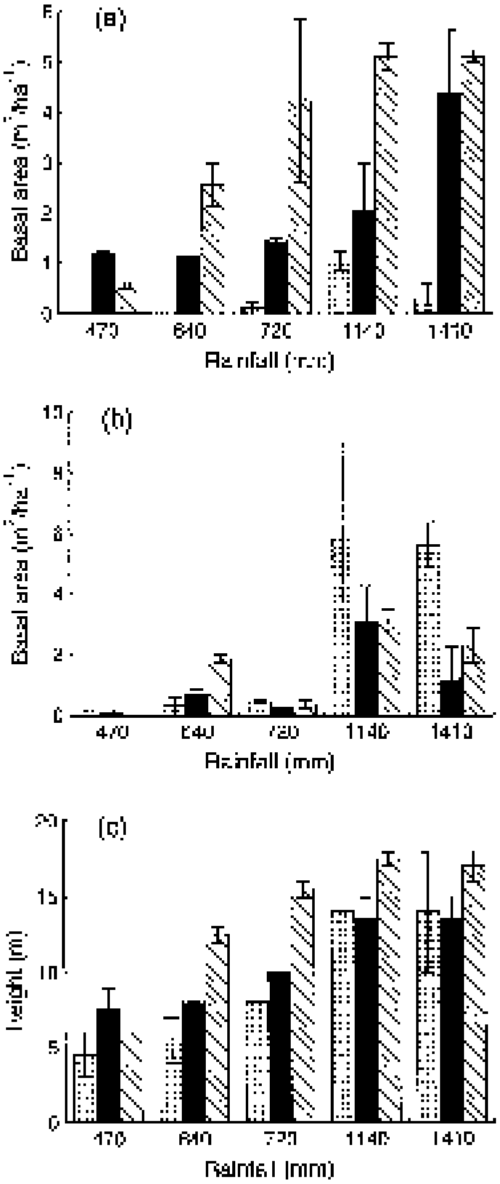

Figure 2. Variation along the rainfall gradient and across the three soil types in (a) basal area of eucalypts, (b) basal area of non-eucalypts, and (c) canopy height. Lightly shaded (dotted) columns represent clay soils; dark filled columns represent loam soils; hatched columns represent sand soils. Bars represent ± SE.

were no significant relationships between snake species richness or abundance and either rainfall or soil type; and skink species richness and abundance declined along the rainfall gradient (Table 1; Figure 4). The removal of nectarivores from tallies for all bird species resulted in very little change in the relationship with rainfall or soil type (Table 1).

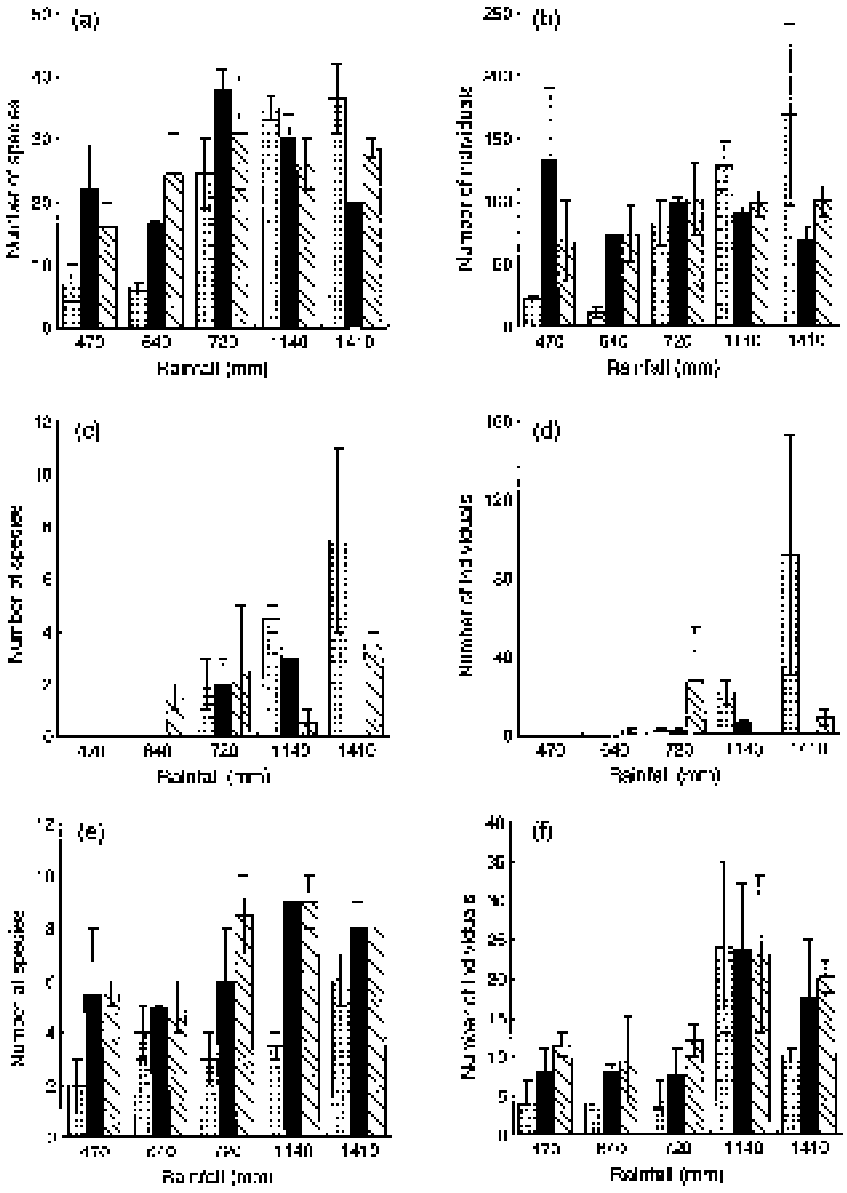

Figure 3. Variation in richness and abundance of vertebrate taxa in relation to variation in annual rainfall and soil texture. (a) richness of all vertebrates, (b) abundance of all vertebrates, (c) richness of frogs, (d) abundance of frogs, (e) richness of reptiles, (f) abundance of reptiles, (g) richness of birds, (h) abundance of birds, (i) richness of mammals, and (j) abundance of mammals. Conventions as in Figure 2.

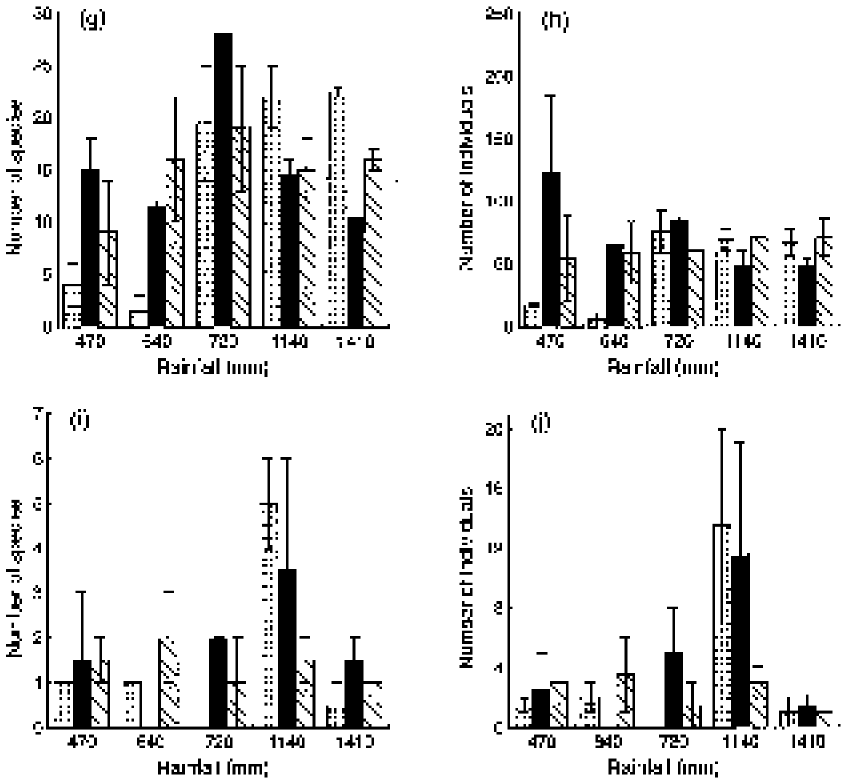

Figure 3. *Continued.*

With plots combined across soil types (Table 2), the total richness of birds, reptiles and frogs showed a distinct decrease down the rainfall gradient. Combined across sites, there were more species of frogs, but fewer species of reptiles, recorded from clay plots.

Individual species

Most of the 51 species recorded from at least five plots occurred widely across the rainfall gradient and, particularly, across soil types (Figure 5).

Species composition

An ordination of all plots by their vertebrate species composition (Figure 6) illustrated the influence of both the rainfall gradient and soil texture in determining species composition. Clay plots were notable in exhibiting the greatest amplitude on the first axis of this ordination. Most sand plots were comparatively tightly clumped, suggesting relatively homogeneous species composition. A comforting feature of the ordination is its generally close placement of replicate plots (same site, same soil type) to each other.

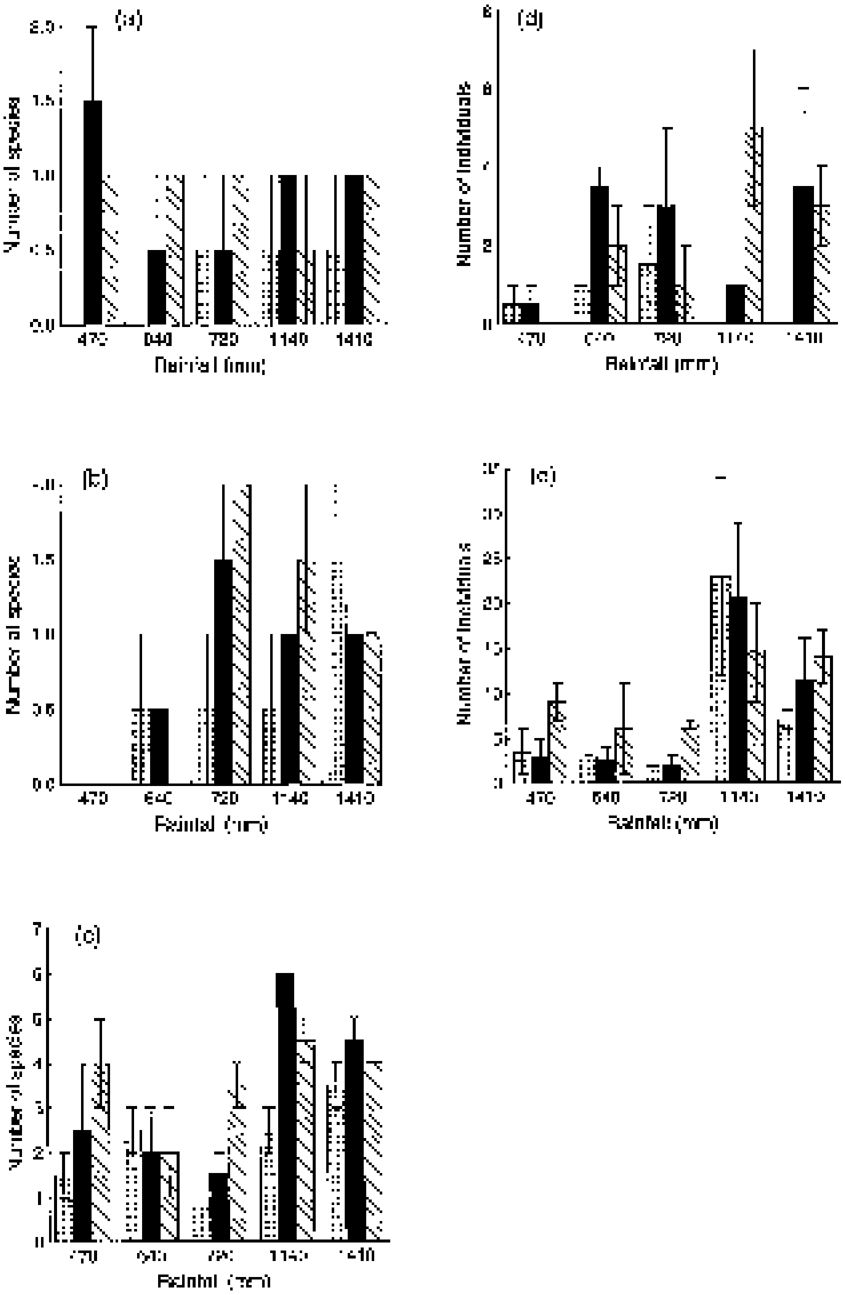

Figure 4. Variation in richness and abundance for some reptile groups. (a) richness of agamids, (b) richness of varanids, (c) richness of skinks, (d) abundance of geckos, and (e) abundance of skinks. Conventions as in Figure 2.

Table 2. Counts of total species richness for each soil type, combined across sites, and for each site, combined across soil types.

		Total number of species			
		Frogs	Reptiles	Birds	Mammals
Site	(rainfall)				
1	(472)	0	15	33	4
2	(640)	3	13	33	4
3	(721)	7	19	51	5
4	(1136)	10	21	44	8
5	(1406)	14	22	47	4
Soil texture					
Clay		9	36	56	8
Loam		6	29	62	12
Sand		14	23	62	8

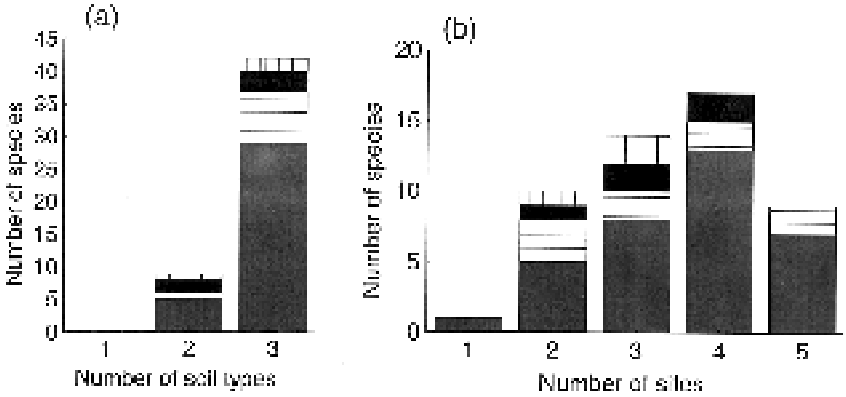

Figure 5. The frequency distribution of species across (a) soil types, and (b) sites. The lightly-filled segment of each bar represents birds; the section marked by horizontal lines represent reptiles; dark-filled section represents frogs; and the section marked by vertical lines represents mammals.

For both birds and reptiles, there was a strong web of similarities between all sand plots and between all loam plots, suggesting relatively little, and gradual, turnover in species composition for these soil types along the rainfall gradient (Figure 7). In contrast, for clay soils there was far more marked disjunction in species composition along the rainfall gradient.

Species replacement

There were only two examples suggestive of replacements of ecologically similar species along either of the two gradients (Figure 8), and even one of these includes some overlap at one site.

DISCUSSION

The species richness, abundance and composition of terrestrial vertebrates in this region were significantly associated with the two gradients of rainfall and

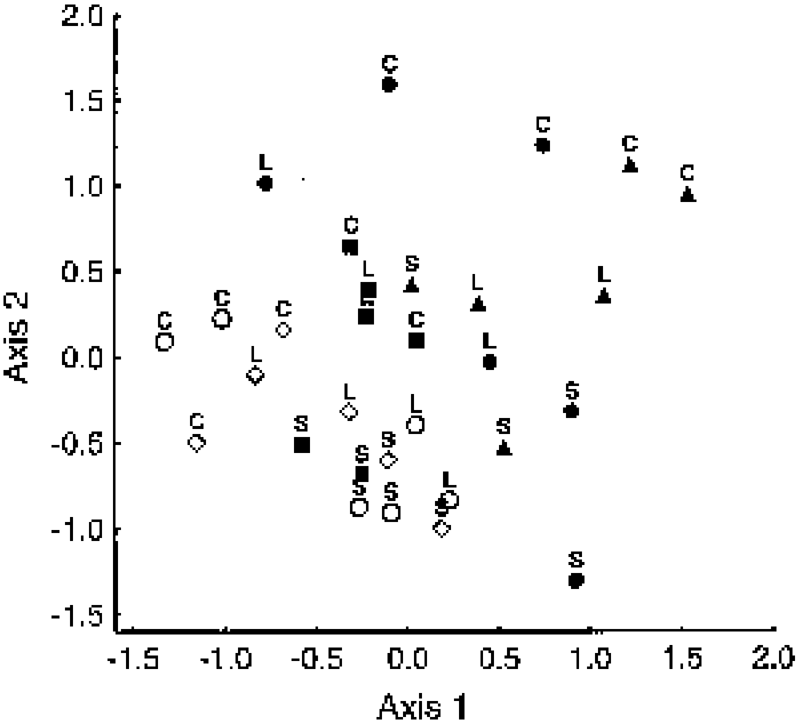

Figure 6. Ordination of all plots sampled, by their similarity in vertebrate species composition. Clay plots are marked C, loam plots L and sand plots S. Filled circle, site 1 (lowest rainfall); filled triangle, site 2; filled square, site 3; open diamond, site 4; open circle, site 5 (highest rainfall).

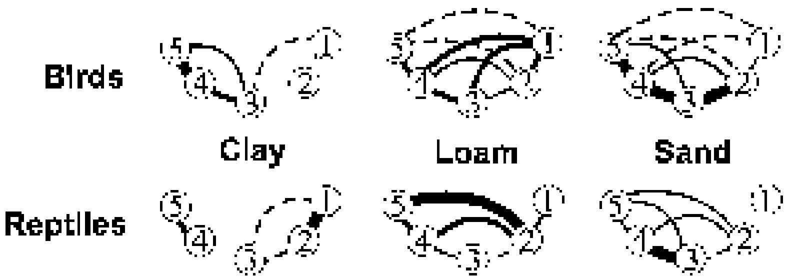

Figure 7. Constellation diagrams showing similarity in species composition beween pairs of sites on like soil types. Sites are numbered from 1 to 5, as in Figure 1. Separate diagrams are presented for birds and for reptiles, and for each of the three soil types. Widest lines signify similarity index (SI) > 50, second widest 50 > SI > 40, third widest 40 > SI > 30, narrowest 30 > SI > 20, and dashed lines shown indicate SI < 20.

soil texture, previously shown to underly vegetation patterning. These relationships contrasted between and within vertebrate groups, underlining the futility of searching for an all-encompassing functional explanation for all vertebrates. However, before resorting to particular explanations on a case-by-case basis, we note some general features that affect all relationships.

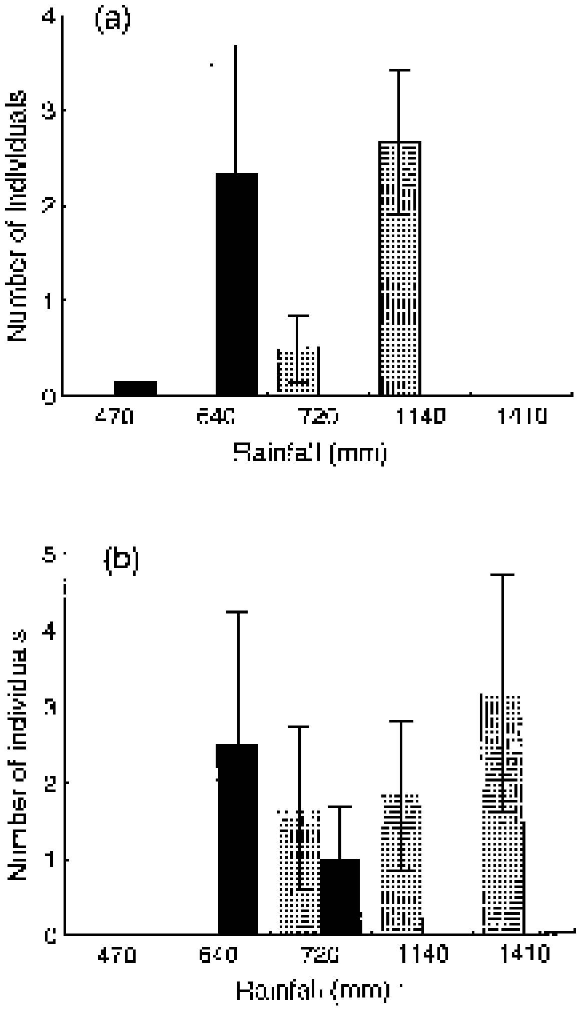

Figure 8. Examples of 'replacements' of ecologically similar species along the rainfall gradient. (a) Two small skinks, *Menetia maini* (dark columns) and *M. greyi* (paler columns); (b) two small insectivorous/nectarivorous birds, the rufous-throated honeyeater *Conopophila rufogularis* (dark columns) and white-throated honeyeater *Melithreptus albogularis* (paler columns). Bars represent ± SE.

While the rainfall gradient considered is gradual and uncomplicated, spatial variation in soil textures is far more complex. At some sites, there were only relatively small isolated areas of one of the soil types (e.g. sandy soils at site 4), hence the fauna recorded from plots of that soil type at that site may be unrepresentatively poor and unusually similar to that of the site's more spatially dominant soil types.

In this region, soil type is often associated with landscape position, and hence any association between vertebrate distribution and soil type is not necessarily related to some intrinsic feature of the soil. Thus, most clay plots sampled were on plains, often exposed to seasonal flooding. In contrast, most loam sites were on upland areas. Consistent with previous findings (Williams *et al.* 1996), the vegetation differed substantially with soil texture, with clay plots notably distinct in supporting a higher proportion of non-eucalypt woody vegetation and generally woodlands of relatively low stature. There was also a notable disjunction in the landscape history of clay soils along the rainfall gradient. Clays at the highest rainfall sites are very recent (<10 000 y at the highest rainfall site: Chappell & Thom 1986) and hence nutrient-rich; those at the lower rainfall sites are considerably older and less rich (Stewart 1970).

The association of landscape position with soil type may explain much of the variation in frog abundance, with the largest number of frogs recorded from plots at the margin of seasonally inundated floodplains (clay soils at the highest rainfall site). The decline in frog species richness and abundance down the rainfall gradient is consistent with previous Australian studies based on less intensive sampling (Tyler 1994), and comparable studies in other tropical areas (e.g. Daniels 1992). However, our gradient did not extend quite far enough south to include the extensive sandy Tanami Desert, where very high abundances of arid-adapted frogs have been recorded (Morton *et al.* 1993). No species from this distinctive frog fauna was recorded from our lowest rainfall site.

Variation in reptile species richness and abundance is more complex, with the patterns for all reptiles built up from often contrasting patterns for individual reptile families. The most striking feature of reptile patterning was the low species richness (but not total abundance) on clay soils, a pattern determined largely by variation for skinks and agamids. Clay environments are more starkly seasonal than those on sand and loam soils, being often waterlogged in the wet season and cracking in the dry season. Relatively few reptile species appear to tolerate this seasonality, but those that do often occur at high density. In the lower rainfall areas, the reptile species composition on clay soils is also notably distinct from that on adjacent soil types, and from that of the clay soils of markedly different evolution at higher rainfall sites (Horner & Fisher 1998). In contrast, for sand and for loam soils, there is far more continuity and similarity in reptile species composition down the rainfall gradient. Although not as pronounced as the relationship with soil type, reptile richness declined down the rainfall gradient, a pattern most evident for skinks and, less so, varanids. This relationship has been reported previously for varanids and all reptiles, based on overlap of species distribution maps (Cogger & Heatwole 1981), but many previous studies have emphasised the remarkably high diversity of reptiles in Australia's sandy deserts (e.g. Morton & James 1988, Pianka 1981). As with frogs, our transect did not extend far enough south to include the extensive hummock grasslands on sands with which this rich and distinctive arid-adapted reptile fauna is closely associated.

Bird species richness generally declined down the rainfall gradient, consistent with previous studies based on generalised overlap of species distribution maps (Blakers *et al.* 1984). This decline was most marked for clay soils, which were the richest plots at the high rainfall sites, but the least rich sites at the low rainfall sites. As with reptiles, the bird species composition on sand and on loam soils showed far more continuity and similarity down the rainfall gradient than did that on clay soils. These patterns may reflect a more direct relationship (well documented elsewhere: Recher 1969) between bird species diversity and vegetation structure (as measured here by canopy height and basal area) rather than a response to soil texture or rainfall *per se*.

Few mammals were recorded during this survey. While the total abundance declined weakly down the rainfall gradient, the highest rainfall site had anomolously few mammals. Decline in mammal richness down the rainfall gradient was reported by Woinarski *et al.* (1992) based more generally from surveys in this region.

Australian soils are typically infertile (Milewski 1981) and local and regional variation in this fertility has been invoked as a major determinant of the richness and abundance of a broad range of temperate Australian animals (e.g. Braithwaite *et al.* 1984, Recher *et al.* 1996, Woinarski *et al.* 1997). This study provides only limited and equivocal support for such linkage in tropical Australia. The most fertile environments considered here were the clay soils at highest rainfall. These supported the most rich and abundant vertebrate fauna (although this pattern was not consistent across vertebrate classes). The extraordinary productivity of, and density of vertebrates in, these environments has been documented previously by Madsen & Shine (1996). However, in the less productive lower rainfall sites, clay soils supported fewer vertebrates than the even more impoverished sand and loam soils. This disparity may be due to the recent origins of the high rainfall clay soils, which renders them unusually productive. It may also be influenced by vegetation patterning: the higher rainfall clay sites supported open forests, but the lower rainfall clay sites supported little woody vegetation, and hence were probably below a habitat suitability threshold for a very broad range of primarily arboreal vertebrates. In contrast, the low rainfall sand and loam sites retained a more extensive cover of low open woodland.

The observed decline in vertebrate species richness down the rainfall gradient parallels, and is probably partly explained by, that reported for plant richness (Bowman 1996, Woinarski *et al.* 1996) and vegetation structural complexity (Figure 2). Trends in vertebrate richness may also be partly due to greater productivity in higher rainfall areas. However, the most striking feature of the pattern in vertebrate richness and abundance is its very limited variation on sand and loam soils, despite the extent of the rainfall gradient and its associated large variation in vegetation structure. In part, this limited variation in vertebrate richness down the rainfall gradient on sand and loam soils is due to the retention of many species throughout the gradient. Change in vegetation on these soils along this gradient is essentially subtle variation within virtually continuous eucalypt open forests and woodlands. These dominate the landscapes of northern Australia (comprising 77% of the 5.2×10^5 km^2 land area in the Northern Territory north of 18° S: calculated from Wilson *et al.* 1990), allowing vast ranges for the many vertebrate species associated with them. This lack of environmental disjunction in the eucalypt-dominated woodlands and open forests is also reflected in the very few clear cases of replacements of ecologically comparable species along the rainfall gradient spanned.

Our sampling design focused attention on broad gradients, and in doing so some important components of landscape diversity were excluded. Heterogeneity in this system is provided mainly in the interstices, where soil texture, topographic feature or water availability breaks up the eucalypt-dominated matrix. A series of recent studies (Gambold & Woinarski 1993, Woinarski 1993, Woinarski & Fisher 1995, Woinarski & Gambold 1992, Woinarski *et al.* 1988, 1992) has demonstrated that these relatively small areas of rainforests, riparian vegetation, sandstone escarpments and plateaux, and *Acacia* woodlands hold faunas which generally contrast far more with their eucalypt-dominated surrounds than the variation reported here within the dominant environments across very extensive rainfall and soil gradients.

The relative homogeneity in species composition, and very limited decline in richness, down the rainfall gradient for sand and loam soils may be an idiosyncratic Australian phenomenon controlled by the near ubiquity of eucalypt-dominated forests and woodlands in this region. Comparable studies along similar tropical transects on other continents (e.g. Koch *et al.* 1995) are needed to determine whether this eucalypt domination distorts or dampens a more general larger response of vertebrates to extensive rainfall gradients.

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