

Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example

Brooke L. Bateman^{*,1}, Alex S. Kutt[†], Eric P. Vanderduys[†] and Jeanette E. Kemp[‡]

* School of Marine and Tropical Biology, James Cook University, Townsville, Queensland, Australia 4811

† CSIRO Sustainable Ecosystems, Rangelands and Savannas, Davies Laboratory, PMB PO, Aitkenvale, Queensland, Australia 4814

‡ Queensland Herbarium, Environmental Protection Agency, PO Box 5391, Townsville, Queensland, Australia 4810

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Abstract: This study examined patterns in the species richness and abundance of small non-volant mammals along a tropical altitudinal gradient in north-eastern Australia. We investigated whether a mid-altitudinal peak in diversity was apparent, and if it occurred, whether it was determined by particular environmental conditions. We sampled a small-mammal assemblage at 17 sites distributed along an altitude-environmental gradient from savanna (350 m) to rain-forest vegetation (1000 m). Over four separate occasions (5100 trap-nights) we recorded 17 species of mammal with 416 captures. A positive non-linear relationship between altitude and mammal species richness and abundance was observed, peaking at the 800–900 m range. Many species were distributed across a range of altitudes, while others were strongly associated with particular habitat conditions. There was a distinct reduction in abundance and species richness at low altitudes associated with the less complex vegetation, lower productivity and possible anthropogenic effects. Key findings were: that small-mammal richness peaked towards the summit of the gradient and not at one-half the maximum altitude predicted by the mid-domain effect; contrasting conditions and greatest vegetation juxtaposition had the greatest influence on the patterns recorded; and that local idiosyncratic influences such as habitat factors, land management and historical biogeography are significant.

Key Words: Australia, altitude, gradient, non-volant mammal, species abundance, species richness, tropics

INTRODUCTION

Montane ecosystems are ideal for investigating processes that determine species assemblage along environmental gradients. Altitudinal gradients are particularly important, as there is a strong relationship between changing altitude and changing environmental variables such as climate and vegetation (Körner 2007). Vegetation pattern can exhibit rapid changes over short distances within a single montane system, with corresponding changes in species assemblage (Bullock *et al.* 1995, van Ingen *et al.* 2008). These zones of rapid transition support high concentrations of species, a trend which is especially true in the tropics (Heaney 2001). Therefore these gradients act as natural experiments that can provide key insights into important ecological concepts such as the relationship between environmental heterogeneity and local or regional species diversity (Hutchinson 1959, Shmida & Wilson 1985). However there is only moderate consensus on what factors

explain patterns of diversity along these gradients, despite commonality in biogeography and vegetation pattern observed on different continents (Rowe 2009).

Many studies of assemblages along altitudinal gradients have identified peaks in species richness at mid-altitudes, a phenomenon that occurs across many regions and taxa (Colwell *et al.* 2004, Lacher & Alho 2001, McCain 2004, Nor 2001, Rahbek 1995, 1997, Sanchez-Cordero 2001). In particular, non-volant small mammals often display mid-altitudinal peaks in species richness, especially within tropical systems (Heaney 2001, McCain 2005, Nor 2001). These peaks are predicted to occur at either points of optimal environmental conditions, at mid-domains where species overlap, or locations where distinct vegetation communities occur in close proximity (Currie & Kerr 2008, Lomolino 2001). The mid-domain effect, where species richness is concentrated at mid-altitude due to spatial constraints and hard boundaries, is often cited as influencing patterns of species richness (Colwell *et al.* 2004, McCain 2004). However, such mid-domain effects often coincide with ideal climate position along the gradient or are strongly collinear with environmental gradients (Currie & Kerr

¹ Corresponding author. Email: brooke.bateman@jcu.edu.au

2008, Hawkins *et al.* 2005). More recent studies support the environmental hypothesis, where environmental variables such as climate, topography and productivity drive species patterns (Currie & Kerr 2008, H-Acevedo & Currie 2003, McCain 2007a, 2007b, 2009; Rahbek *et al.* 2007). Although there are varying hypotheses on the underlying cause of the mid-altitudinal peak, a simple universal explanation may be difficult to attain due to local environmental idiosyncrasies such as historical biogeography, regional climate nuances and local anthropogenic impacts (Rowe 2009).

Many climatic patterns along altitudinal gradients are consistent, such as reduction in temperature and radiation with increasing altitude, whereas others such as precipitation, are less predictable (Körner 2007). Many mountain regions display their own unique moisture gradients which interact with local soil nutrient availability and historical fire patterns to create local vegetation patterns (Körner 2007, Lacher & Alho 2001, Webb 1968). Vegetation structure and habitat complexity, as determined by climatic conditions, will have a strong influence on small-mammal community assemblage and thus communities are likely to be in part determined by such climatic gradients (Sanchez-Cordero 2001, Williams & Marsh 1998). There is a well-established link between local and regional species diversity patterns and increasing structural complexity of vegetation (Recher 1969), though in many altitude-gradient studies the effect of climate is often considered more influential (Heaney 2001).

Studies of the pattern of small mammals along gradients within Australian montane systems are lacking in the literature and it is not known whether non-volant small mammals follow this same mid-altitudinal peak pattern. Australian rain forests are an important addition to case studies of altitude patterns as they are very limited in distribution, have a high proportion of endemic species, and contain very sharp gradients from wet rain forest to extensive dry tropical savannas (Bowman 2000). It is necessary to encompass all regions and continents when addressing patterns in global diversity. In particular the tropical rain forest of Queensland has been cited as an excellent candidate for such studies (Colwell *et al.* 2004).

We examined the patterns of small-mammal assemblage along an altitude gradient in tropical Queensland, Australia and investigated key competing hypotheses associated with mountain gradients: (1) there is a mid-altitudinal peak in diversity (species richness and abundance); (2) there is no apparent peak at mid-altitude, but rather species patterns are associated with environmental conditions. We evaluated the distribution of small-mammal species recorded along the gradient, and examine whether there are strong relationships between species diversity patterns and altitude, vegetation type, habitat complexity and/or local effects.

METHODS

Study area

The study sites are located on Mt Lewis (16°30'S, 145°12'E) in tropical north-eastern Queensland. The property was operated as a pastoral lease for many years, but has been owned and managed for conservation (as the Brooklyn Sanctuary) by the Australian Wildlife Conservancy since 2004. The sites occur along an altitudinal gradient that ranges from a plateau of open savanna woodlands (300 m) to upland (>1000 m) tropical rain forest to the east. Rainfall varies from typical tropical savanna rainfall of <600 mm y⁻¹ to the west through to >3000 mm y⁻¹ at upland sites (van Ingen *et al.* 2008, Webb 1968). Climate data derived from ANUCLIM software indicate that annual mean temperature ranges between ~22 °C at the base of the mountain to ~19 °C at the top, with rainfall seasonality (coefficient of variation of mean monthly precipitation) varying from ~115 to ~80 correspondingly (ANUCLIM, version 5.1, Fenner School, Australian National University).

There were 17 sampling sites located along the altitudinal gradient on two adjacent ridgelines; ten sites were located on a walking track that follows a ridgeline. These ten sites encompass a vegetation and altitudinal gradient from 620 m to 1000 m (Figure 1). Seven sites were located along an adjacent ridge; these seven sites encompass the entire accessible portion of this ridgeline, a gradient from 350–700 m (Figure 1).

Sample sites were located on the ground with reference to vegetation mapping for the region (Sattler & Williams 1999) and physical reconnaissance. Sites were located within a mapped vegetation polygon, and where possible, at least 500 m from each other and at least 200 m from the nearest obvious ecotone or edge between vegetation types. In two cases where the pattern in vegetation change was rapid, the edge of one quadrat was only 300 m from the start of the next. Sample sites were 100 × 100 m in size and marked by three permanent steel fence posts at 0, 50 and 100 m points that run down the ridgeline. Two reflective tags were placed on trees at 50 m on both sides and perpendicular to the 0 m mark which is labelled with a large reflective tag and site number. Sites were grouped into Broad Vegetation Groups as allocated to vegetation mapping units by the Queensland Herbarium (Accad *et al.* 2008). Brief vegetation descriptions based on the quadrats and the number of sites sampled in each type are presented in Table 1.

Mammal sampling

Small mammals were sampled over a 6-d, five-night period on four separate occasions (May 2006,

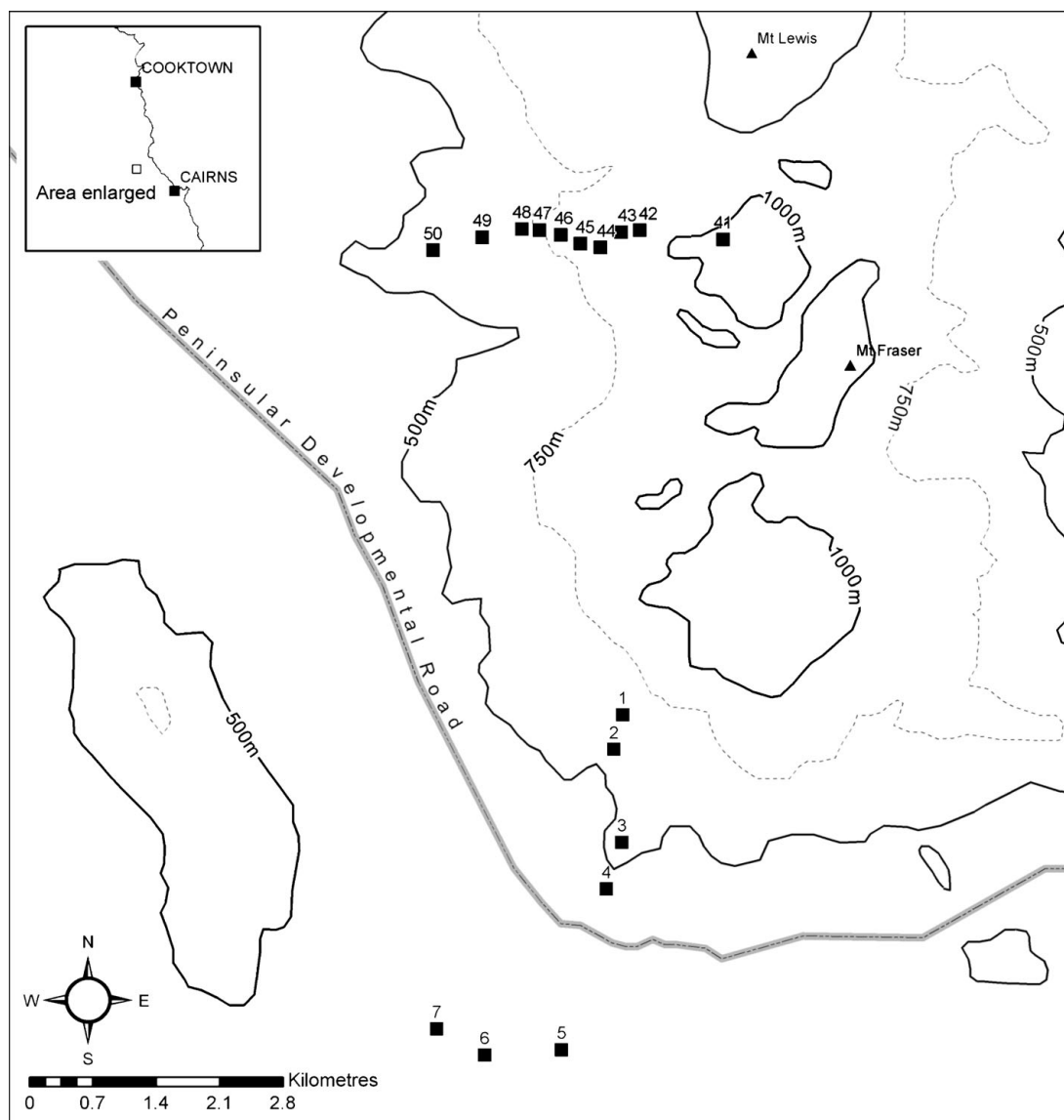


Figure 1. Location of sites and gradient sampled, and location of Brooklyn Station in Queensland.

November 2006, April 2007 and November 2007). Trapping occurred within the 100×100 -m quadrat, and comprised five baited treadle cage traps (three $300 \times 300 \times 600$ -mm and two $200 \times 200 \times 400$ -mm treadle traps) and ten baited Elliott ($100 \times 100 \times 300$ -mm aluminium box) traps. The cages were placed at 0, 50 and 100 m ridgeline markers, with two additional cages placed perpendicular and on either side to the 0-m cage, 50 m from this point. The Elliott traps were placed at 10-m intervals, along the perpendicular arm, running down either side of the ridge line. Elliott and cage traps were baited with peanut butter, honey, oats, vanilla or pistachio essence; alternative traps were also baited with dog biscuits. One cage trap at each site was baited with chicken to target *Dasyurus* spp. (quolls). Traps

were checked in the morning between 06h00 and 10h00. Each animal trapped was identified and released. In this study we were concerned with differences in the relative abundance (*sensu* Martin & McIntye 2007) of mammal species along the altitudinal and vegetation gradient, and not absolute counts such as 'known to be alive' estimates; thus we did not undertake mark-capture measurements.

Common names, scientific names and authorities for fauna follow Clayton *et al.* (2006). Scientific names and authorities for plants follow Bostock & Holland (2007). However, there is some uncertainty regarding the species of *Sminthopsis* (Dasyuridae). Preliminary genetic analyses of specimens collected at high- and low-altitude sites, were in conflict with morphological characteristics of the species. Until this can be satisfactorily resolved we

Table 1. The description of the broad vegetation groups sampled along the altitudinal gradient. Broad vegetation groups follow naming protocols of Accad *et al.* (2008). The broad floristic description of each habitat is as follows: RFE = Complex notophyll vine forest and ecotone woodland of *Eucalyptus grandis*, with understorey rain-forest elements, WTOF = *E. resinifera*, *E. reducta*, *Corymbia intermedia*, *Syncarpia glomulifera*, *Allocasuarina torulosa* and *Banksia aquilonia* tall open forest, DOF = *Eucalyptus reducta*, *E. portuensis*, *E. tereticornis*, *Corymbia intermedia*, *C. citriodora*, *C. stockeri* open forest, DOW = *Eucalyptus cullenii*, *E. portuensis*, *Corymbia stockeri* low open woodland and DAW = *Eucalyptus platyphylla* and *E. leptophleba* open woodland.

Site	Habitat	Altitude (m)	Altitude Band
B41	Rain forest and ecotone (RFE)	1000	>900
B42		940	
B43	Wet tall open forest (WTOF)	890	800–900
B44		870	
B45		850	
B46		810	
B47		780	
B48	Dry open forest (DOF)	740	700–800
B49		700	
B01		680	
B02	Dry open woodland (DOW)	650	600–700
B50		620	
B03		550	
B04		550	
B05		350	
B06		350	
B07		350	

will refer to the two morphotypes as *Sminthopsis* sp. A (high-altitude species) and *Sminthopsis* sp. B (low-altitude species), though the putative species for each is *S. murina*.

Vegetation sampling

Structural and habitat variables were measured following the methods outlined in Neldner *et al.* (2004) sampled along the 100-m transect line running perpendicular to the ridge line. Canopy heights and crown cover for each stratum were measured using a line intercept method (Neldner *et al.* 2004). A 100-m tape was laid down and the vertical projection onto the tape of the start and finish of each crown by species and strata was recorded. A vertical sighting tube was used to ensure that crown intercepts were vertically projected. The total length of crown was divided by the total length of the tape to give an estimate of percentage crown cover. Height of each stratum was measured using a clinometer and measurements were taken at the 0-, 50- and 100-m points of the 100-m tape and averaged. The ground cover (% live vegetation cover, rock cover) was visually estimated using five 1-m² quadrats placed at the 35-, 45-, 55-, 65- and 75-m marks of the tape. Site score represents the average of the five quadrats.

Analysis

For grouping and analysis of the data, we selected altitude bands over broad vegetation types. From convention, studies of mountain gradients are generally couched in the language of changes along altitude, and altitude is a convenient corollary of environmental gradients. To reconcile the use of altitude bands as representative of the environmental gradients, we tested via Spearman rank correlations the relationship between altitude, broad vegetation group category (numbered 1–6, with 1 the uplands vegetation group, and 6 the lowland vegetation group) and vegetation structural measures. We also tested the strength of the altitude band and broad vegetation groups to categorize variation in mammal assemblage via analysis of similarity (ANOSIM) (Primer version 6.1.11, Primer-E Ltd). ANOSIM tests a priori categorization of multivariate data by non-parametric permutation applied to the underlying similar matrix. The larger output value R (rank similarities) the greater the separation of replicates between groups. We used fourth-root transformed Bray–Curtis similarity matrices derived from the mammal abundance data.

We investigated the adequacy of our sampling effort via sample-based (observed) rarefaction curves and estimate-based rarefaction curves (Chao2 estimates). We plotted the number of observed species and estimated species per altitudinal band (300, 500, 600, 700, 800 and 900+ m) against the number of trapping days consecutive over the four survey periods (1–20 d), using the module DIVERSE in Primer. If the curves approached the asymptote, those sites were considered sufficiently sampled. To account for variation among altitudinal bands, observed species accumulation curves were compared against the non-parametric randomization estimator Chao2 (McCain 2004) also using DIVERSE in Primer.

The relationship between altitude and the total abundance of small mammals, abundance of selected species (*Melomys cervinipes*, *Melomys burtoni*, *Rattus fuscipes*, *Dasyurus hallucatus* and *Zyomys argurus*) and total species richness (pooled over all four sampling periods), were examined via generalized linear modelling (Crawley 1993) testing linear, non-linear and polynomial distributions (STATISTICA, version 6. StatSoft, Inc., www.statsoft.com). For each comparison we tested whether the linear, non-linear or polynomial fit best represented the relationship by examining the resultant residual sum of squares (linear regression), or percentage deviance explained (non-linear and polynomial regression). The percentage deviance explained is the difference between the model with the explanatory term included (e.g. altitude), against the model with the explanatory variable excluded.

The altitudinal distribution of each small-mammal species recorded was examined using weighted

maximum–minimum, mean and standard error range plots, weighting each distribution by total abundance for each species at each altitude. Weighting adjusts the contribution of individual cases (e.g. altitudes) within the range plots in proportion to the values of a selected variable (e.g. abundance of mammal).

The variation in the mean abundance and richness of all species across the altitude bands, were examined using non-parametric (Kruskal–Wallis) one-way analysis of variance. We also tested variation of individual species abundance (data pooled across the four sample periods) for all small mammals recorded in more than three sites, and variation in habitat complexity (cover and height) also using non-parametric ANOVA.

Two-dimensional ordination using semi-strong hybrid multi-dimensional scaling (SSHMDS) derived from Bray–Curtis association (dissimilarity) indices were used to investigate variation in the assemblage composition (Belbin 1991). Three-dimensional ordination was forsaken due to low improvement in the stress, and the increase in complexity of the interpretation of the pattern sites for little gain in clarity. Ordinations used range-transformed total abundance data pooled over the four sampling periods. No clustering was undertaken; rather we used the altitude bands as the group classification, recognizing that this is strongly correlated to vegetation and habitat change along the gradient (ANOSIM Global $R = 0.74$).

Principal axis correlation (PCC) was used to examine the correlation between environmental 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 1993). The resultant output identifies the direction of best fit and a correlation coefficient. A Monte Carlo randomization technique (MCAO) using 999 permutations was undertaken to test the statistical significance of the correlation coefficient of each vector (Belbin 1993). We tested the vegetation cover and height measures as environmental vectors to examine which were strongly correlated to the ordination pattern.

RESULTS

There was strong correlation between altitude and broad vegetation group ($R = 0.98$), canopy cover ($R = 0.59$), subcanopy cover ($R = 0.49$), shrub cover ($R = 0.76$), canopy height ($R = 0.79$) and subcanopy height ($R = 0.75$). The a priori categorization of the small-mammal assemblage using altitude bands was strong (Global $R = 0.74$) as it was for broad vegetation groups (Global $R = 0.65$). These results reinforce our contention that altitude is a strong surrogate for environmental variation along the gradient, and variation in the mammal assemblage

composition. Subsequent analysis used altitude bands for grouping sites, recognising that this is in effect an environmental gradient.

Species accumulation curves for all altitudinal bands were all approaching the asymptote suggesting the sampling effort per site was adequate and suitable to examine patterns of species richness along the gradient. However the Chao2-estimated species richness suggested that for the 800-m band, the species richness was potentially underestimated compared with the samples for the other altitude band (Figure 2).

The relationship between species richness and altitude was best characterized by a non-linear relationship (per cent deviance explained = 41%) (Figure 3a), as was the relationship between abundance and altitude (per cent deviance explained = 91%) (Figure 3b). Investigation of the pattern between individual abundance and altitude indicated a strong non-linear relationship between the rodents *M. cervinipes* and *R. fuscipes* and altitude (percent deviance explained = 88% and 66% respectively) (Figure 4a), and moderate polynomial relationships between *D. hallucatus* (32%), *M. burtoni* (20%) and *Z. argurus* (36%) (Figure 4b).

Seventeen species of mammal representing three families (Dasyuridae, 5 species; Peramelidae, 2 species; Muridae, 10 species) were recorded from 416 captures and 5100 trap-nights along the altitudinal gradient (Table 2). The most abundant species were *M. cervinipes*, *M. burtoni*, *R. fuscipes* and *Z. argurus*. The least abundant were *Parameles nasuta*, *Rattus sordidus* and *Rattus leucopus*. Five species were restricted to one altitude, though two of these (*R. leucopus* and *R. sordidus*) were represented only by a single capture (Figure 5). The remaining 11 species occupied sites over a range of altitudes with *M. cervinipes*, *M. burtoni*, *R. fuscipes*, *Isoodon macrourus*, *D. hallucatus* and *Pseudomys delicatulus* being the most cosmopolitan species, distributed between 200–300 m of altitude (Figure 5).

The distribution of species across the altitude bands, indicated that the most species-rich vegetation (total pooled data for all four surveys) was the 800-m band (11 species), followed by 700-m (7 species) and the > 900-m and 600-m bands (6 species). The total abundance, also pooled data for all four surveys was clearly highest in the 800-m (156 captures) and > 900-m bands (128 captures) (Table 2). Mean site abundance was highest in the > 900-m band (64.5 ± 2.5) and lowest declining steadily to the dry alluvial woodland (5.7 ± 0.7). Sites in dry open woodland and dry alluvial woodland had the lowest species richness (2.0–2.6) and mammal abundance was also low (3.5 and 5.7 respectively, Table 2). There was significant variation in species abundance across the altitude bands for five species; *M. cervinipes* ($H = 14.8$, $P = 0.01$) and *R. fuscipes* ($H = 15.1$, $P = 0.009$) most abundant in the high-altitude sites; *Z. argurus* ($H = 11.3$,

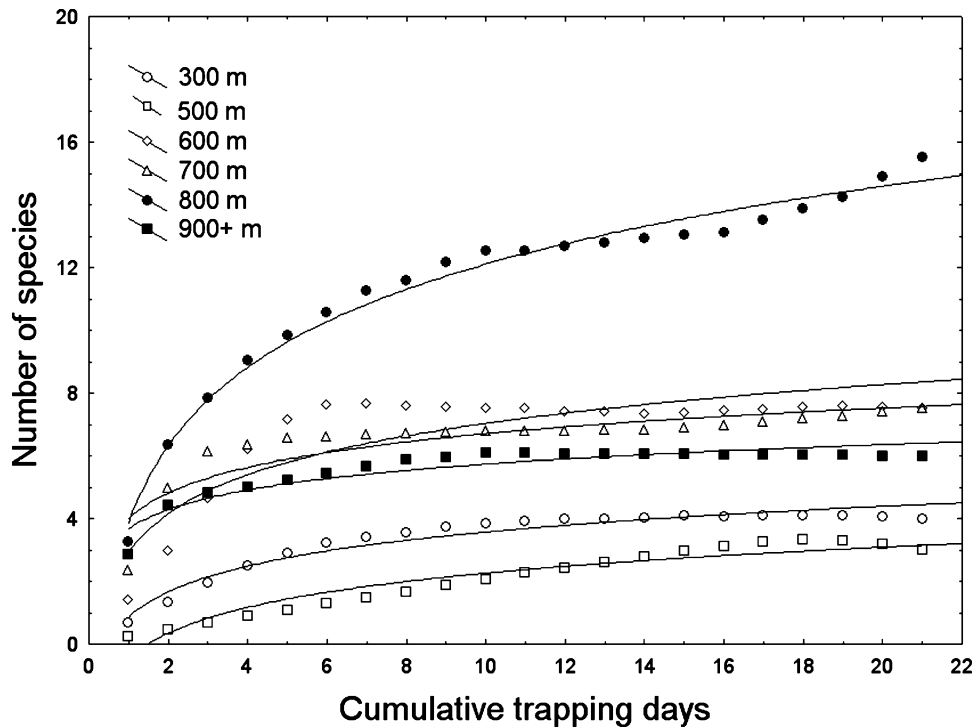


Figure 2. Estimated species accumulation curves (Chao 2) for the small-mammal species richness across six altitudinal bands. Cumulative trapping days are the four survey periods assessed combined in sequence.

$P = 0.04$) and *D. hallucatus* ($H = 10.7$, $P = 0.05$) in the mid-altitude sites and *Mus musculus* ($H = 15.8$, $P = 0.007$) in the low-altitude sites (Table 2).

The change in structure and dominant vegetation composition up the altitudinal gradient was from woodland dominated by two to three *Eucalyptus* spp., through diverse myrtaceous (*Eucalyptus*, *Corymbia*, *Banksia*) forest (dominated by 6 spp.), to rain forest at the top of the mountain (Table 1). In terms of habitat structure and complexity, there were significant changes in canopy and subcanopy height from the low-altitude sites (16.3 m for canopy, 7.0 m for subcanopy) to the >900-m band (28.5 m for canopy, 16.5 m for subcanopy) (Table 2). Canopy and subcanopy cover was highest in the > 900-m and 800-m bands (68–64.5% for canopy, 28.5–23.5% for subcanopy), declining sharply down the gradient to 38.7% (canopy) and 7.0% (subcanopy) at the bottom (Table 2). Shrub cover was significantly higher in the 700-m, 800-m and > 900-m bands. Ground cover and height did not vary markedly along the gradient, but rock cover was significantly higher in the 600-m and 700-m bands.

Environmental vector fitting on the ordination (not illustrated) suggested that there were strong relationships between the small-mammal composition with canopy height ($r^2 = 0.57$), subcanopy height ($r^2 = 0.60$), rock cover ($r^2 = 0.43$), and canopy cover ($r^2 = 0.40$). The gradient for canopy height, subcanopy height and canopy

cover broadly followed an axis of change from low-altitude to high-altitude sites (which also represents the shift from dry open woodlands through to the wet tall open forest and rain forest). The rock-cover gradient runs perpendicular to these axes, and identifies a mid- to low-altitude zone of rock outcropping (600–700 m).

DISCUSSION

In this study, we found that richness of small non-volant mammals peaked towards the summit of the gradient and not at one-half the maximum altitude predicted by the mid-domain effect (Currie & Kerr 2008, McCain 2005). Such skews in richness peaks towards higher altitudes are indicative of climatic influences which are often associated with changes in vegetation (McCain 2005). Peak richness occurred at the point of optimal environmental conditions (high productivity and structural diversity) and the zone of rapid transition between distinct vegetation communities.

The altitudinal gradient of this study is situated on the western fall of the upland wet tropical region and provides a zone of rapid transition from dry savanna woodlands at lower altitude, through to high-rainfall areas with true rain forest on the mountain tops (Harrington & Sanderson 1994, Webb 1968). Temperature, precipitation, productivity and vegetation

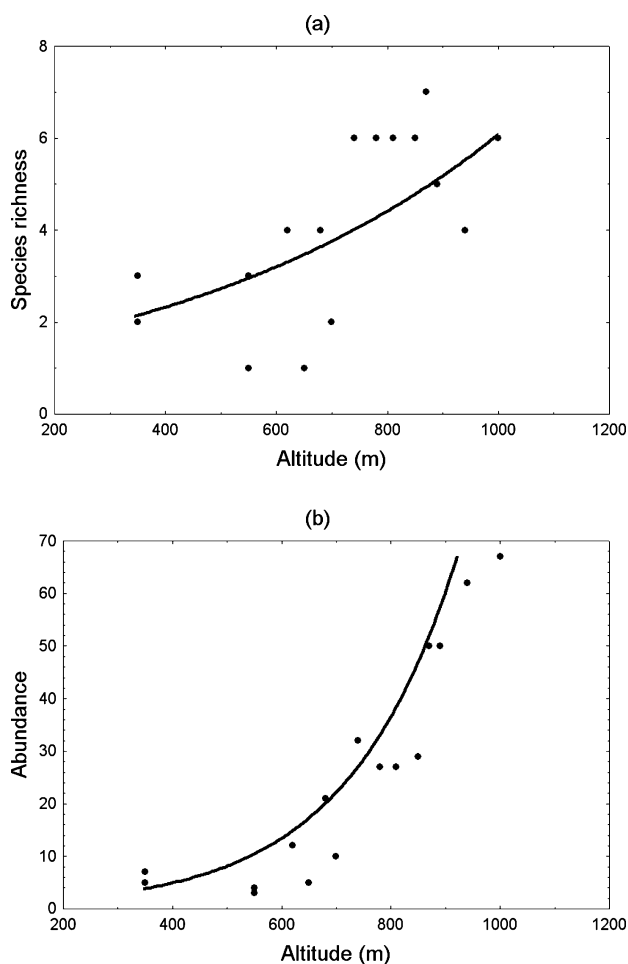


Figure 3. The relationship between the distribution of total mammal abundance (pooled over the four surveys) and species richness across the altitude gradient as identified via generalized linear modelling. Relationship with species richness ($y = e^{(0.21 + (0.0016x))}$) (a). A normal distribution with a log-link function was used. Relationship with abundance ($y = e^{(-0.40 + (0.005x))}$) (b). A normal distribution with a log-link function was used.

cover have been shown to influence patterns of species richness (H-Acevedo & Currie 2003, Williams & Middleton 2008) and richness often increases with increasing precipitation and humidity (Nor 2001, O'Brien 1998). In tropical regions, such as north-east Australia, species richness may be limited by precipitation (H-Acevedo & Currie 2003, Nor 2001) and variation in productivity is influenced more by rainfall patterns, in particular precipitation seasonality, than temperature (Williams & Middleton 2008 and references therein). The savannas of this region are characterized by high seasonality of precipitation, and decreasing precipitation seasonality is observed with increasing altitude towards the wet-forest habitats (Williams & Middleton 2008, Woinarski *et al.* 2005). The increasing precipitation, decreasing precipitation seasonality, structural complexity and mammal diversity

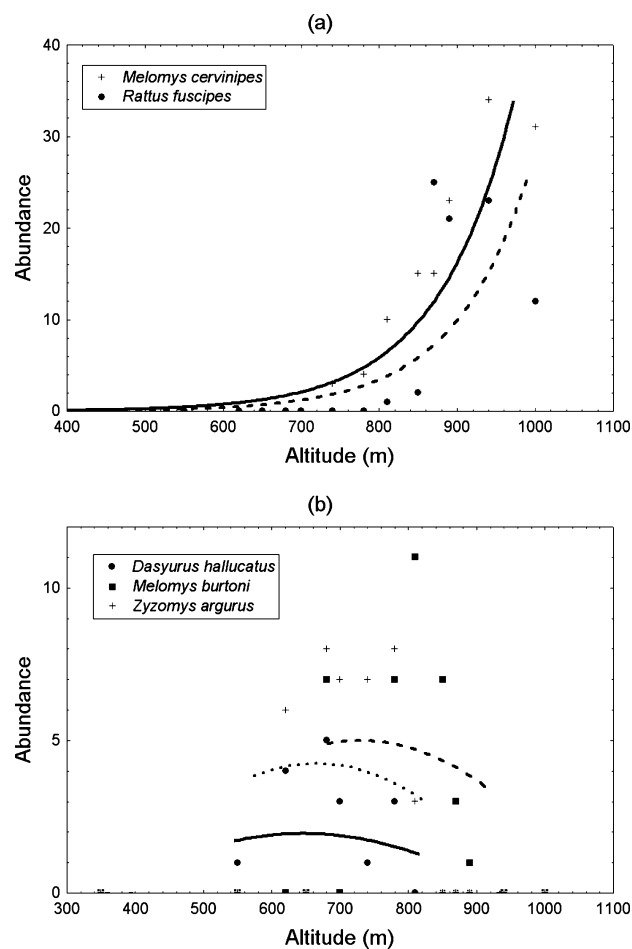


Figure 4. The relationship between the distribution of total mammal abundance (pooled over the four surveys), for selected species across the altitude gradient as identified via generalized linear modelling. Relationship with *Melomys cervinipes* (solid line) ($y = e^{(-6.4 + (0.01x))}$) and *Rattus fuscipes* (dashed line) ($y = e^{(-7.2 + (0.011x))}$) abundance (a). A Poisson distribution with a log-link function was used. Relationship with *Dasyurus hallucatus* (solid line) ($y = -7.8 + 0.03x - 0.000023x^2$), *Zyzomys argurus* (dotted line) ($y = -17.6 + 0.07x - 0.000049x^2$) and *Melomys burtoni* (dashed line) ($y = -18.6 + 0.06x - 0.000044x^2$) abundance (b). A polynomial distribution was used.

of the high-altitude habitats from this study is consistent with previous studies in the Australian wet tropics region (Williams & Marsh 1998). The small-mammal assemblage described here, appears to support the environmental hypothesis that predicts peak richness where climate is the most favourable rather than a geographic or mid-domain effect (Currie & Kerr 2008). This is consistent with other recent studies where climate has been shown to be an important influence on species diversity patterns (H-Acevedo & Currie 2003, McCain 2007a, 2007b, 2009). Species abundance also increased with increasing altitude, a typical relationship where high abundance is strongly related to high productivity, in this case associated with rain-forest vegetation (Williams *et al.* 2002).

Table 2. Species richness, abundance and habitat measures and individual species abundances for altitude bands. n = number of sites that a species was recorded. Data tabulated are the mean scores \pm SE. Other data are totals. Variation in mean site richness, abundance, habitat measures and species was examined using non-parametric analysis of variance (Kruskal–Wallis). H is the test statistic for this ANOVA.

Factors	n	300–499 m	500–599 m	600–699 m	700–799 m	800–899 m	>900 m	H	P
Number of sites		3	2	3	3	4	2		
Richness		4.0	3.0	6.0	7.0	11.0	6.0		
Abundance		17.0	7.0	38.0	69.0	156.0	129.0		
Mean site species richness		2.6 \pm 0.3	2.0 \pm 1.0	3.0 \pm 1.0	4.7 \pm 1.3	6.0 \pm 0.4	5.0 \pm 1.0	9.6	0.09
Mean site abundance		5.7 \pm 0.7	3.5 \pm 0.5	12.7 \pm 4.6	23.0 \pm 6.6	39.0 \pm 6.4	64.5 \pm 2.5	14.1	0.02
Canopy height (m)		16.3 \pm 0.7	8.5 \pm 0.5	13.7 \pm 2.4	16.7 \pm 0.3	23.8 \pm 3.5	28.5 \pm 6.5	13.7	0.01
Subcanopy cover (%)		9.3 \pm 4.7	11.0 \pm 0.0	22.3 \pm 6.2	21.3 \pm 14.4	54.5 \pm 11.7	48.0 \pm 38.0	6.4	0.27
Subcanopy height (m)		7.0 \pm 1.0	4.0 \pm 1.0	5.0 \pm 0.6	8.0 \pm 0.0	13.5 \pm 3.7	16.5 \pm 1.5	12.9	0.02
Shrub cover (%)		0.0	1.5 \pm 0.5	8.3 \pm 3.3	15.7 \pm 2.2	17.8 \pm 6.6	12.5 \pm 2.5	11.1	0.05
Shrub height (m)		1.0 \pm 0.0	1.35 \pm 0.2	0.39 \pm 0.3	0.8 \pm 0.2	1.3 \pm 0.2	1.3 \pm 0.5	4.9	0.42
Ground cover (%)		38.6 \pm 7.8	46.0 \pm 2.0	20.7 \pm 7.5	16.7 \pm 6.7	40.0 \pm 7.5	32.5 \pm 22.5	6.6	0.25
Ground cover height (m)		0.6 \pm 0.0	0.2 \pm 0.4	0.3 \pm 0.0	0.23 \pm 0.0	0.4 \pm 0.1	0.8 \pm 0.5	8.6	0.12
Rock cover (%)		0.0	4.0 \pm 0.0	18.0 \pm 8.7	20.0 \pm 7.6	9.3 \pm 4.3	2.0 \pm 0.0	11.3	0.04
Dasyuridae									
<i>Antechinus adustus</i>	1	0.0	0.0	0.0	0.0	0.0	2.5 \pm 2.5		
<i>Antechinus flavipes</i>	4	0.0	0.0	0.0	0.0	1.3 \pm 0.9	1.5 \pm 0.5	10.2	0.07
<i>Dasyurus hallucatus</i>	6	0.0	0.5 \pm 0.5	3.0 \pm 1.5	2.3 \pm 0.7	0.0	0.0	10.7	0.05
<i>Sminthopsis</i> sp. A	3	0.0	0.0	0.0	0.3 \pm 0.3	1.0 \pm 0.7	0.0	5.3	0.38
<i>Sminthopsis</i> sp. B	1	1.0 \pm 1.0	0.0	0.0	0.0	0.0	0.0		
Muridae									
<i>Melomys burtoni</i>	7	0.0	0.0	2.3 \pm 2.3	8.3 \pm 5.2	5.5 \pm 2.20	0.0	9.4	0.09
<i>Melomys cervinipes</i>	8	0.0	0.0	0.0	2.3 \pm 1.2	15.7 \pm 2.7	32.5 \pm 1.5	14.8	0.01
<i>Mus musculus</i>	3	3.6 \pm 0.9	0.0	0.0	0.0	0.0	0.0	15.8	0.007
<i>Pseudomys delicatulus</i>	3	0.3 \pm 0.3	0.5 \pm 0.5	1.7 \pm 1.7	0.0	0.0	0.0	4.0	0.54
<i>Pseudomys gracilicaudatus</i>	6	0.7 \pm 0.7	2.5 \pm 0.5	0.7 \pm 0.3	0.0	0.25	0.0	8.9	0.11
<i>Rattus fuscipes</i>	6	0.0	0.0	0.0	0.0	12.3 \pm 6.3	17.5 \pm 5.5	15.1	0.009
<i>Rattus leucopes</i>	1	0.0	0.0	0.0	0.0	0.0	1.0		
<i>Rattus sordidus</i>	1	0.0	0.0	0.0	0.0	0.75	0.0		
<i>Uromys caudimaculata</i>	4	0.0	0.0	0.0	0.7 \pm 0.7	0.3 \pm 0.3	9.5 \pm 6.5	10.3	0.06
<i>Zyomys argurus</i>	6	0.0	0.0	4.7 \pm 2.4	7.3 \pm 0.3	0.8 \pm 0.8	0.0	11.3	0.04
Peramelidae									
<i>Isoodon macrourus</i>	6	0.0	0.0	0.3 \pm 0.3	1.7 \pm 0.9	1.0 \pm 0.4	0.0	7.6	0.17
<i>Perameles nasuta</i>	1	0.0	0.0	0.0	0.0	0.25 \pm 0.25	0.0		

Unlike other gradient studies, there was no clear evidence of any major point of species disjunction (Lacher & Alho 2001, van Ingen *et al.* 2008), and, instead a gradual overlap and replacement of species was observed. The key point of change was where the savanna and rain-forest vegetation were adjacent, and these transition zones between dry and wet forests tend to be sources of diversity due to increased landscape complexity (Lacher & Alho 2001, Lomolino 2001). Such richness peaks at transition zones are common in tropical altitudinal gradients of small non-volant mammals, and often occur where communities from adjacent zonal habitats overlap in species ranges (Heaney 2001, Lomolino 2001, Nor 2001, Rickart 2001, Sanchez-Cordero 2001). This suggests that species diversity along the gradient in this study is not only a function of local conditions within one vegetation type, but also of neighbouring resources in adjacent types. A mass effect occurs where there are marginal habitat patches that are suitable yet suboptimal, which allows temporal and spatial variation in habitat occupation (Williams

et al. 2002). The rapid transition of habitat types along altitudinal gradient only enhances this effect.

Outside tropical environments, patterns of mammal composition through conifer forest to desert, indicated that temporal and habitat variation was as influential as altitude change (Kelt 1999). This suggests that, despite some universal patterns associated with altitude gradients, there are regional idiosyncratic influences on mammal pattern such as biogeography, landscape context, level of disturbance, and habitat extent and structural diversity of the transect in question. We found this to be the case in our study too; that is the strong relationship between saxicolous small-mammal species (*D. hallucatus*, *Z. argurus*) and rock cover within the 600-m and 700-m altitudinal bands. In this case substrate, not vegetation type, was influential on species pattern. Local habitat variation within gradient can control assemblage pattern, quite apart from altitude, climate or vegetation change (Kelt 1999).

The sudden depletion of the mammal assemblage below 600 m is partly influenced by the occurrence of

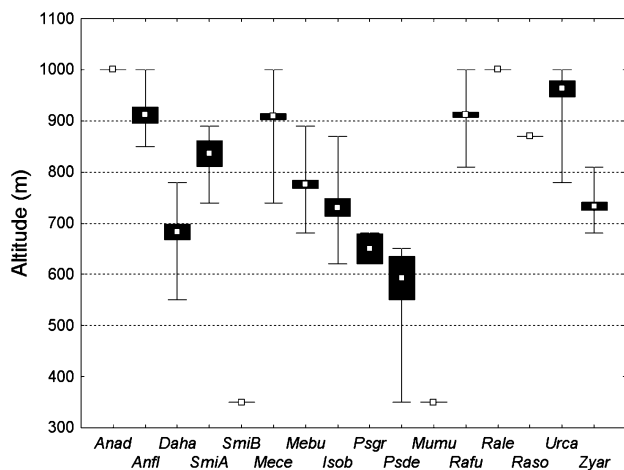


Figure 5. The mean, SE and range of altitudinal distribution of each small-mammal species recorded in this study. Each distribution is weighted by total abundance; that is weighting adjusts the contribution of individual cases (e.g. altitudes) within the range plots in proportion to the values of a selected variable (e.g. abundance of mammal). Species codes are as follows: *Anad* = *Antechinus adustus*, *Anfl* = *Antechinus flavipes*, *Daha* = *Dasyurus hallucatus*, *SmiA* = *Sminthopsis* sp. A, *SmiB* = *S.* sp. B, *Mebu* = *Melomys burtoni*, *Mece* = *M. cervinipes*, *Mumu* = *Mus musculus*, *Psde* = *Pseudomys delicatulus*, *Psgr* = *P. gracilicaudatus*, *Rafu* = *Rattus fuscipes*, *Rale* = *R. leucopes*, *Raso* = *R. sordidus*, *Urca* = *Uromys caudimaculata*, *Zyar* = *Zyzomys argurus*. *Perameles nasuta* was recorded from a single individual from a single site and as such is not illustrated.

feral predators and the historical poor management of Australian rangelands (Johnson 2006, Kutt & Woinarski 2007). Some species unrecorded in this study (the rodents *Rattus tunneyi*, *Mesembriomys gouldi* and the dasyurid *Planigale maculata*), might have been absent for reasons of natural rarity, or reduced abundance due to range contractions in north-eastern Australia caused by land management (Braithwaite & Brady 1993, Braithwaite & Griffiths 1996, Kutt & Woinarski 2007). Where *R. tunneyi* occurs in high numbers, it is easily caught by the methods utilized in this survey, so its absence from the transect at low altitudes is probably a factor of land management (Braithwaite & Griffiths 1996). On the other hand *M. gouldi* is an arboreal rodent that is extremely trap-shy; its absence might be a trapping artefact. Similarly the very small dasyurid *P. maculata* is widely distributed and disturbance-tolerant but more readily recorded through pitfall trapping (A. Kutt pers. obs.). Other species captured at higher altitudes on this transect that should occur in the lower-altitude savanna woodlands (*M. burtoni*, *P. gracilicaudatus*, *D. hallucatus*, *I. macrourus*) were absent, and this is a function of species-specific effects (i.e. ingestion by *D. hallucatus* of cane toad and its fatal toxin; Burnett 1997), or broader land-management impacts on these species (Woinarski *et al.* 2001).

The two species recorded in the dry open and alluvial woodlands *P. delicatulus* and the introduced *M. musculus*, are adapted to disturbed sites being able to persist

in sites with sparse ground cover (*P. delicatulus*) or highly modified environments (*M. musculus*) (Braithwaite & Brady 1993, Kutt & Woinarski 2007). From a global perspective, lowland and upland sites on altitude gradients tend to be the most disturbed montane communities, and thus species poor (Nogues-Bravo *et al.* 2008, Rahbek 1995). This modification of habitats alters natural diversity patterns along such gradients, making it more difficult to discern any patterns in diversity which may exist (Nogues-Bravo *et al.* 2008). Similarly the low-altitude sites on the gradient, and the associated low species richness may simply be a function of low environmental suitability and productivity (i.e. low rainfall, simple structural diversity) (Rowe 2009), which is compounded by poor land management (Kutt & Woinarski 2007).

This study examined sites from 300 m to 1000 m, omitting sites between 1000 m and 1250 m (the peak of this mountain range) as well as sites within the 400-m altitudinal band. Recent work has shown that omission of part of any gradient can allow for observations of only an element of the true pattern (Nogues-Bravo *et al.* 2008). It is generally accepted that peaks of species richness are expected to occur between 1000 and 2500-m, and beyond a certain altitude, there is a decrease in habitat heterogeneity and in most cases a decline in mammal species richness resulting in a mid-altitude peak in species richness (Heaney 2001, Mena & Vázquez-Domínguez 2005). This is the case for most mountains that have longitudinal montane gradients (<300 m to >1900 m) (Goodman & Rasolonandrasana 2001, Mena & Vázquez-Domínguez 2005, Rahbek 1997). Regardless, the maximum potential height of Mt Lewis (our study area) is only 1250 m and the minimum at 300 m. As the study site is considered to be a small site (100–1000 km²) and Mt Lewis is a small mountain (<1250 m), what variation does present is most likely a factor of vegetation type and biotic interactions rather than altitude and climate at such a scale, and such mountains are expected to have little variation in species richness (Heaney 2001, Hortal *et al.* 2008, Körner 2000). As the regions of the gradient left out of this survey display consistent vegetation characteristic to the sites sampled within this survey we are confident the range we encompassed will reflect true species patterns of this mountain.

CONCLUSION

In this study, we found a peak in species richness of small non-volant mammals towards the summit of the altitude gradient at the point of optimal environmental conditions and greatest vegetation juxtaposition. With increasing altitude, the steep gradient caused a gradual overlap and

replacement of species and increasing species diversity was observed. We suggest that our study identifies a more typical ecological concept; that is there is a relationship between local habitat, resource heterogeneity and species richness supporting the environmental hypothesis rather than a mid-domain effect. Similarly species richness was influenced by local effects, such as the relationship between certain species (e.g. saxicolous) and habitat resources (e.g. rock outcrop), and a combination of anthropogenic effects and low primary productivity (e.g. lower rainfall) at the lowest altitude sites.

We support the contention that, despite some universal patterns associated with altitude gradients, there are regional idiosyncratic influences on mammal pattern such as biogeography, landscape context, level of disturbance, and habitat extent and structural diversity of the transect in question. However our study only provides one example from Australia, and it is imperative that more such studies are conducted in other transect and in different environmental conditions (e.g. alpine Australia), to observe how altitudinal and environmental gradients vary both regionally and across taxa. These natural experiments that provide data on how species patterns change with changing climate (e.g. reduced rainfall, increased temperatures and rainfall seasonality) and landscape effects (e.g. fire frequency) will provide significant information with respect to the resilience or adaptability of fauna patterns to changing global environmental conditions.

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