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Changes in small mammal assemblage structure across a rain forest/open forest ecotone

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ABSTRACT. The effect of the change in vegetation structure from closed rain forest to tall open forest on the small mammal assemblage was studied by live trapping at three sites where the ecotone was very narrow (<20 m) near the southern end of the Wet Tropics World Heritage Area of Australia. Habitat heterogeneity was significantly higher in the mixed open forest/ecotone area than in the adjacent rain forest. There was a large change in the structure of the small mammal assemblage coincident with the vegetation discontinuity. Although the species richness of small mammals was relatively constant across the gradient, the evenness and diversity of the assemblage declined across the transition from open forest into rain forest and biomass increased, largely due to the high abundance of *Rattus fuscipes* in the rain forest. The results suggest that the species richness of the small mammal assemblage was not determined by the spatial heterogeneity of the vegetation structure. The species composition of the rain forest is probably related to the historical biogeography of the area whereas the species richness of the wet sclerophyll forest is probably due to a mass-area effect from the adjacent large areas of rain forest and dry sclerophyll forest. However, the evenness, and therefore the diversity of the assemblage, was strongly affected by habitat heterogeneity.

INTRODUCTION

Many areas of rain forest in north Queensland are bounded on their western edge by a narrow band (less than 5 km wide) of tall open forest, with mixed casuarina and rain forest elements (Winter 1988). This band of tall open forest, often referred to as wet sclerophyll forest, forms a transitional zone between the rain forest and the extensive xeric woodland to the west of the main dividing range. Often the transition from closed forest to the wet sclerophyll forest

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is very abrupt and can occur over a distance of less than 20 m. Vegetation structure changes completely from a closed and complex canopy with very little ground vegetation to an open sclerophyll canopy with dense shrubs and/or grass. This abrupt change is primarily dependent on the fire regime with frequent fires producing a very narrow ecotone while less frequent fires produce a more diffuse ecotone (Ash 1988, Unwin *et al.* 1985).

There has been considerable controversy over the management of the wet sclerophyll forest in the Australian Wet Tropics, especially with regard to fire. In the absence of fire the adjacent rain forest invades the wet sclerophyll forest. Over the last 50 y rain forest has invaded 70% of the wet sclerophyll forest in the region due to changed fire regimes, and this has raised concerns over the preservation of the habitat and its resident fauna (Harrington & Sanderson 1994). These conservation and management issues highlight the need for ecological data on the wet sclerophyll habitat and fauna.

Relating habitat structure to the structure of faunal communities has been an important issue in ecology, with many studies, including many on small mammal assemblages, attempting to determine relationships between faunal diversity and habitat heterogeneity (August 1983, Braithwaite *et al.* 1978, Braithwaite *et al.* 1985, Hockings 1981, Rosenzweig & Winakur 1969, Winter 1988). It is often easier to determine what factors may be affecting assemblage structure when that structure is changing over a gradient or ecological boundary: Kupfer (1995) identified boundary dynamics as one of the key areas of study in landscape ecology. Examining ecological gradients at a point where they are undergoing a rapid change has several advantages. The amount of sampling required is minimised and since the distances are very small the confounding effects of climate and biogeography can be assumed to be homogeneous over the study area.

This study examined the small mammal assemblage at the rain forest wet sclerophyll forest boundary at three sites at the southern end of the Wet Tropics World Heritage area, to determine the effect of the rapid change in vegetation structure on the small mammal assemblage and to provide basic ecological knowledge for the management of this dynamic habitat boundary.

METHODS

Study sites

Three sites were established on the rain forest ecotone *c.*10 km west of Paluma (19°01′S, 146°07′E) at an altitude of 880 m, in northern Queensland, Australia. The vegetation changes from simple notophyll vine forest to tall open forest dominated by *Eucalyptus grandis* with a blady grass (*Imperata cylindrica*) understorey (Tracey & Webb 1975). Sites were selected where the transitional zone between the rain forest and the wet sclerophyll forest was of similar narrow width (*c.* 20 m) to emphasise the ecological trends, minimize the confounding effects of distance and to reduce logistical problems.

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Sampling design

Two transects 400 m long and 100 m apart were established at each of three sites running across the ecotone. On each transect at sites 1 and 2, 11 traps were arranged at each of five grids which were positioned at 100-m intervals across the gradient with the ecotone bisecting the centre of the middle grid. Each grid consisted of nine Elliott (type A) traps and two wire-cage traps (45 cm × 20 cm × 15 cm), set out in a 40 m × 40 m grid (3 × 3 rows of traps, each 20 m apart) with the two wire cages on opposite sides of the grid.

Site 3 differed from the others. The grids were positioned along a transect 400 m long which went from wet sclerophyll forest, through a narrow (80-m wide) riparian corridor of rain forest, crossed more wet sclerophyll forest and then went into the main rain forest block. Trapping grids were therefore situated in open forest, rain forest, open forest, ecotone and rain forest along the transect. This site acted as a test for any trends observed in the main sites, since any habitat-associated trend should oscillate twice along the transect.

Live trapping was conducted on four field trips: in September and November 1989, and in January and March 1990. The traps were baited with a mixture of rolled oats and vanilla essence. Each site was trapped for three consecutive nights during each trip. Experimentation showed that three nights of trapping with this grid design was sufficient to catch a representative sample of both species and individuals (Williams 1990). Several individuals of *Uromys caudimaculatus* were caught at two grids; however, individuals of all other species were trapped at one grid only, so the grids were relatively independent. Each animal trapped was weighed and individually marked by either a numbered monel metal fingerling tag in both ears (*Rattus fuscipes*, *R. lutreolus*, *Melomys cervinipes*, *Antechinus flavipes*, *A. stuartii*) or by tattooing the ear pinna (*Uromys caudimaculatus*, *Isoodon macrourus*). The number of animals known to be alive (KTBA), calculated as the number of individuals caught at each grid over each block of three nights of trapping was used as an index of relative abundance of each species. This index of abundance is not affected by the variable trappability of each species as recaptures are not included. Spotlighting was conducted to record some species that were not trapped; however, only trapped species are included in the analyses to maintain standardised sampling effort. A biomass index was calculated from the cumulative weights of each individual KTBA at each grid (grams per grid) for each three-day sampling period.

Habitat structure was assessed by measuring seven structural attributes of the vegetation at each at each trap point in every grid (30 × 9 locations). Vegetation structure was measured by visually estimating the density of foliage in four vertical strata (ground cover 0–1 m; low shrubs 1–2 m; shrubs 2–5 m; canopy >5 m) using a modified Braun-Blanquet scale (0 – absent; 1 – present; 2 – common but less than 5%; 3 – 5–25%; 4 – 25–50%; 5 – 50–75%; 6 – 75–100%). Projected foliage cover (total canopy cover) was estimated by taking 10 vertical sitings in a circle 1 m from each trap site using a telescopic rifle scope

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and scoring if the crosshairs were on vegetation or sky. Canopy height was measured with an inclinometer and the number of tree stems above 3 m in height were counted in a 10-m radius at each trap station. A number of other habitat features were scored on an ordinal scale at each grid to obtain a measure of life-form and habitat diversity (see Appendix for list of measured variables).

All observed trends in relative abundance and biomass were tested using analysis of variance (ANOVA). The squareroot of the number of individuals of each species of small mammal known to be alive (KTBA) at sites 1 and 2 was the response. The model use sites (1 and 2), times (field trips 1 to 4) and position on the gradient (1=200 m into open forest, 2=100 m into open forest, 3=ecotone, 4=100 m into closed forest, 5=200 m into closed forest) as the main effects with two transects as replicates. A repeated-measures design was used since samples over time at the same grids were not independent. Some species did not have sufficient sample size to allow the use of this design and simpler but less powerful models were used (e.g. pooling both transects or pooling over time). Polynomial contrasts were used to confirm that significant differences were due to a systematic trend across the gradient.

The change in the abundance of *R. fuscipes* between the three trap positions within the ecotonal grid spanning the transition from closed to open forest at sites 1 and 2 was examined using a Friedman two-way non-parametric ANOVA due to the inequality of variances. The main factors were as follows: (a) positions (n=3) across the ecotone (traps 1, 2, 3 were classified as closed forest; 4, 5, 6 as ecotone; 7, 8, 9 as open forest); and, (b) grids (n=4, one on each transect at each of sites 1 and 2).

The MRPP statistic which is analogous to a multivariate analysis of variance (Zimmerman *et al.* 1985) was used to measure the significance of the change in small mammal community structure across the gradient from open forest to closed forest at sites 1 and 2.

RESULTS

Habitat

The density of the ground cover decreased from 40% in the open forest to almost zero within the closed forest while canopy density increased from 35% to almost 100% (Figure 1a). Foliage density of the shrub layer (1–5 m) peaked at 60% on the rain forest edge (Figure 1a), producing the dense thickets characteristic of this ecotone. Stem density increased from open forest to rain forest and was most variable on the closed forest edge (Figure 1b).

Trends in habitat heterogeneity based on the Shannon index of diversity were calculated using all of the habitat variables (Figure 1c), and by using a simplified variable list: canopy height, tree density (number of trees per 100 m^2), and the stratified foliage densities at 0–1, 1–2, 2–5 and >5 m

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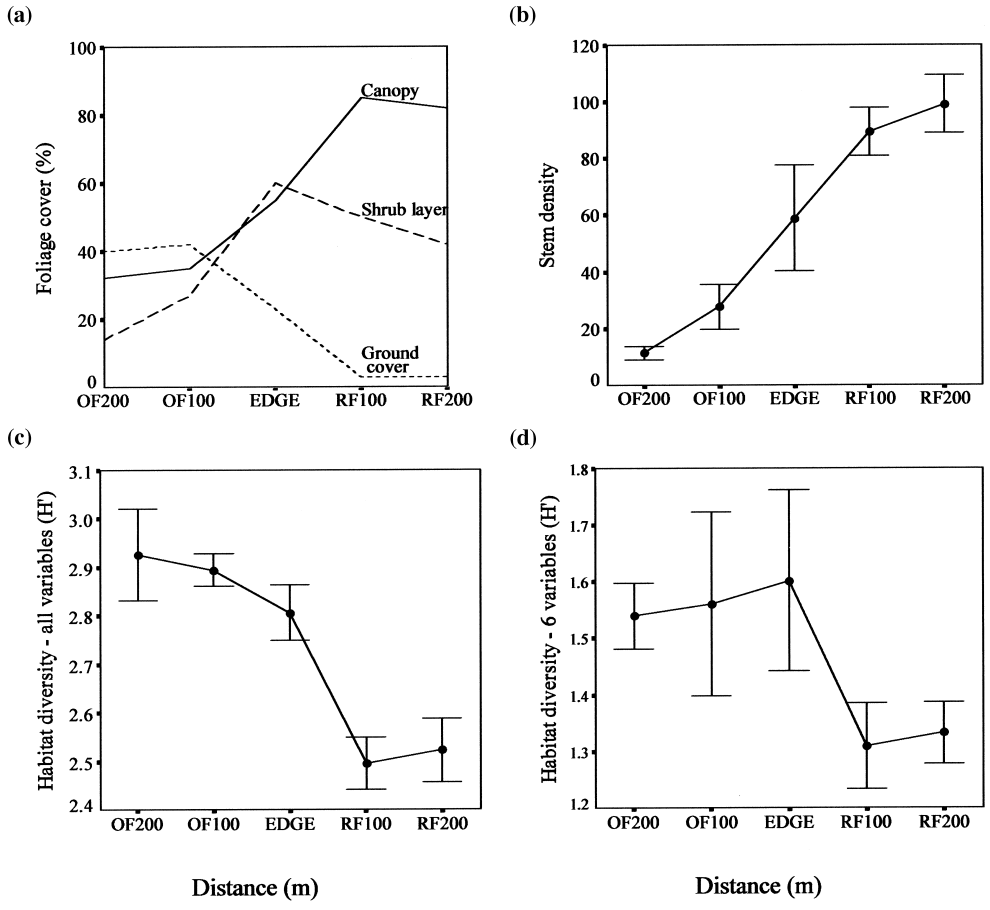


Figure 1. Changes in the vegetation structure across the rain forest ecotone at Paluma sites 1 and 2 (Error bars are 95% confidence intervals): (a) trends in foliage density of the canopy (>5 m), shrub layer (1–5 m) and ground cover (<1 m); (b) stem density measured by the number of trees (>3 m high) per 100 m^2; (c) Shannon index H′ based on all habitat variables; (d) Shannon index H′ based on six structural attributes of vegetation. Position on the ecotonal gradient is indicated by: OF200 – open forest grids 200 m from the rain forest edge; OF100 – open forest grids 100 m from the rain forest edge; EDGE – grids on the rain forest/wet sclerophyll forest boundary; RF100 – grids 100 m into the rain forest; RF200 – grids 200 m into the rainforest.

(Figure 1d). The inclusion of all of the variables to obtain habitat diversity indices is problematic due to the inclusion of different variable types. The simplified variable set only utilises quantitative variables directly pertaining to the vegetation structure and is therefore easier to interpret. Habitat heterogeneity decreased across the gradient from open to closed forest (Figure 1c,d). When it was based on vegetation structure only, habitat heterogeneity peaked on the ecotone, although not at a significantly greater value than the open forest (Figure 1d). Both variable sets clearly show that the open forest has a greater habitat heterogeneity than rain forest.

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Mammal assemblage

The small mammals exhibited three patterns of distribution: *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* occurred right across the transition (Figure 2a); *Uromys caudimaculatus* and *Antechinus stuartii* were restricted to the closed forest (Figure 2b); and, *Rattus lutreolus* and *Isoodon macrourus* were observed in the open forest only (Figure 2b). Several non-standardised spotlighting censuses and other incidental observations indicated that the red-legged pademelon (*Thylogale stigmatica*) and the long-nosed bandicoot (*Perameles nasuta*) were associated primarily with closed forest, although both species were observed in shrubby areas in the open forest. Therefore, the total observed species richness of small mammals was seven species in both open forest and rain forest.

R. fuscipes, *R. lutreolus*, *M. cervinipes* and *U. caudimaculatus* all exhibited a significant change in abundance across the ecotone (Figure 2, Table 1). *I. macrourus* was also very close to showing a significant change (P=0.067) despite the small number of captures. The significant difference in the mean abundance of these species across the ecotone was due to a systematic trend across the gradient (Table 1: polynomial contrasts). Although data for both *Antechinus flavipes* and *A. stuartii* were insufficient to allow statistical testing, these data suggest that *A. flavipes* occured across this gradient and *A. stuartii* was confined to the rain forest (Figure 2b). This is consistent with data from other areas in northern Queensland (S.E. Williams, unpubl. data; A.Watt *pers. comm.*).

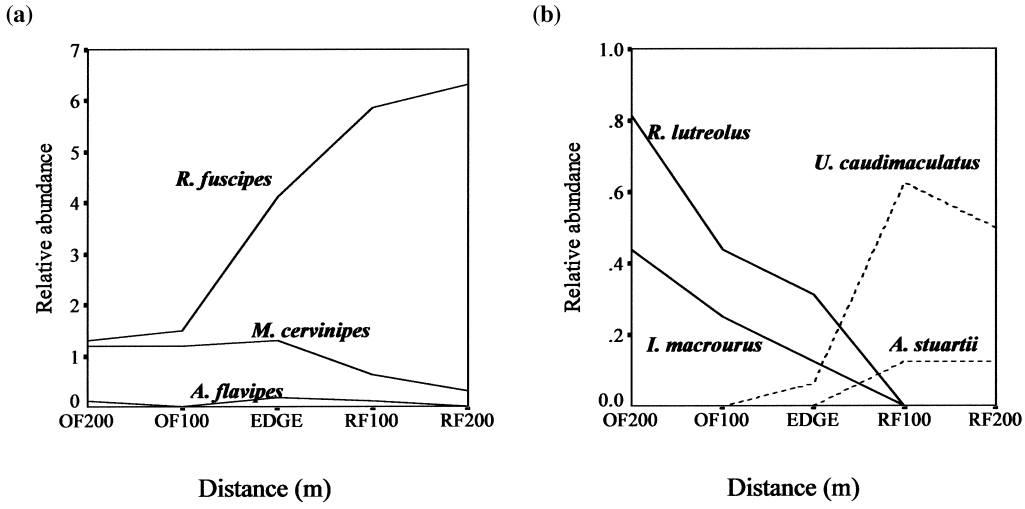


Figure 2. Changes in the relative abundance of small mammals across the ecotone. Trends in the small mammal diversity have been calculated by pooling results over all sampling times, and then taking the means of analogous gradient positions at both sites. Error bars are not shown to reduce clutter on the figure, but significance tests of the trends are shown in Table 1. (a) The number of individuals known to be alive (KTBA) of small mammal species occurring across the entire gradient; (b) the number of individuals known to be alive (KTBA) of small mammal species whose distribution is delimited by the ecotone. Abbreviations for grids are the same as for Figure 1.

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Table 1. Results of analysis of variance models to test for significant changes in the abundance ($P \leq 0.05$) of small mammal species and small-mammal biomass with position across the ecotonal gradient at Paluma (POS), at the two sites (SITE) and over the four field trips (TIME) with two replicates (transects) at each site.

Species/attribute	ANOVA model	Factor	F	df	P
R. fuscipes	POS × SITE × TIME	POS	16.3	4, 10	0.0002
		POS × TIME	2.3	12, 30	0.0356
	polynomial contrasts	linear	58.3	1, 10	0.0000
R. lutreolus	POS × SITE × TIME	POS	3.9	4, 10	0.0367
		SITE × TIME	3.9	3, 30	0.0179
	polynomial contrasts	linear	14.7	1, 10	0.0033
M. cervinipes	POS × SITE × TIME	POS	7.3	4, 12	0.0033
	polynomial contrasts	linear	21.5	1, 12	0.0006
U. caudimaculatus	POS × SITE × TIME	POS	6.5	4, 12	0.0051
	polynomial contrasts	linear	10.1	1, 12	0.0080
I. macrourus	POS × TIME	POS	3.7	4, 20	0.0201
	(SITES POOLED)	TIME	3.7	3, 20	0.0294
Biomass	POS × SITE × TIME	POS	5.7	4, 10	0.0116
		SITE	13.0	1, 10	0.0048
		POS × TIME	5.6	4, 10	0.0124
		SITE × TIME	17.0	1, 10	0.0020
		SITE × POS × TIME	8.1	4, 10	0.0035
	polynomial contrasts	linear	16.2	1, 10	0.0024

Changes in the species composition and relative abundance of most species (Figure 2 a,b) indicated a very significant overall change in community structure across the gradient from open forest to closed forest at sites 1 and 2 which was supported by the MRPP test (MRPP statistic = –4.701; n = 4 for each of five gradient positions; P = 0.0003). All of these changes in small mammal assemblage structure occurred over a distance of less than 100 m (Figure 2). The abruptness of the ecotonal change was further illustrated by the significant change in the abundance of *R. fuscipes* between three trap positions (only 20 m apart) in the four edge grids spanning the transition from closed to open forest (Friedman's statistic H = 9.66, df = 2; P = 0.0093).

The species richness of small mammals was relatively constant across the ecotone with only a slight decrease in the mean species richness from open to closed forest (Figure 3a). However, small mammal diversity, as measured by evenness and the Shannon index (H′) decreased steadily across the gradient from open forest to closed forest (Figures 3 b,c respectively). The decrease in the diversity index is primarily due to the decrease in evenness. The index of biomass indicated that there was a trend of increasing biomass of small mammals from open forest to rain forest (Figure 3d). This was mainly due to the high abundance of *R. fuscipes* in the rain forest.

Verification of trends

All of the trends presented above for sites 1 and 2 showed the same relationship to habitat at site 3. Both autecological trends of species abundance and

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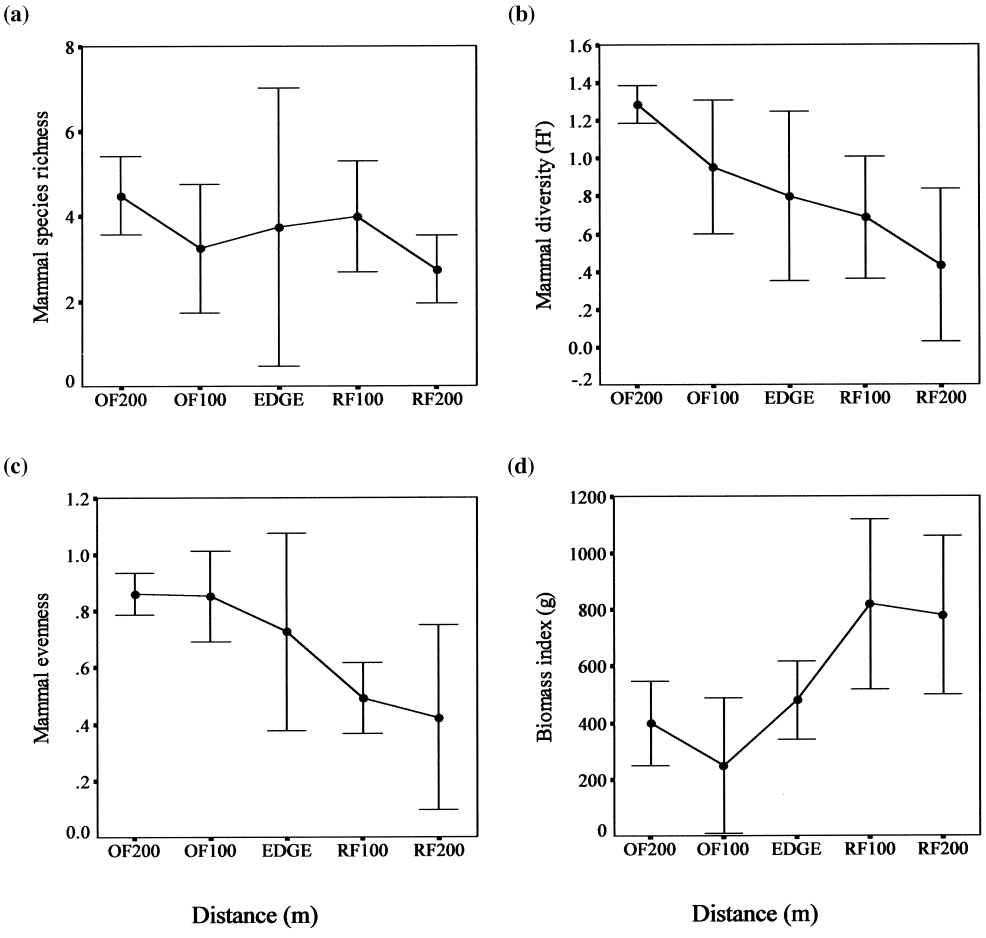


Figure 3. Changes in small mammal assemblage structure across the ecotone: (a) species richness of small mammals; (b) Shannon index (H′) of small mammal diversity; (c) evenness of small mammals; and (d) small mammal biomass. Abbreviations as for Figure 1.

changes in the community closely followed the fluctuating changes in habitat (e.g. parallel trends in habitat and mammal diversity and the opposite trend in mammal biomass, Figure 4).

DISCUSSION

The vegetation discontinuity was correlated with a large change in the small mammal community. There was a very significant change in community structure at the vegetation boundary, both in terms of species composition and relative abundances (Figure 2). These changes occurred over a very short distance. The habitat preferences of the species at this site show four types of distribution patterns: rain forest specialist (*U. caudimaculatus* and *A. stuartii*);

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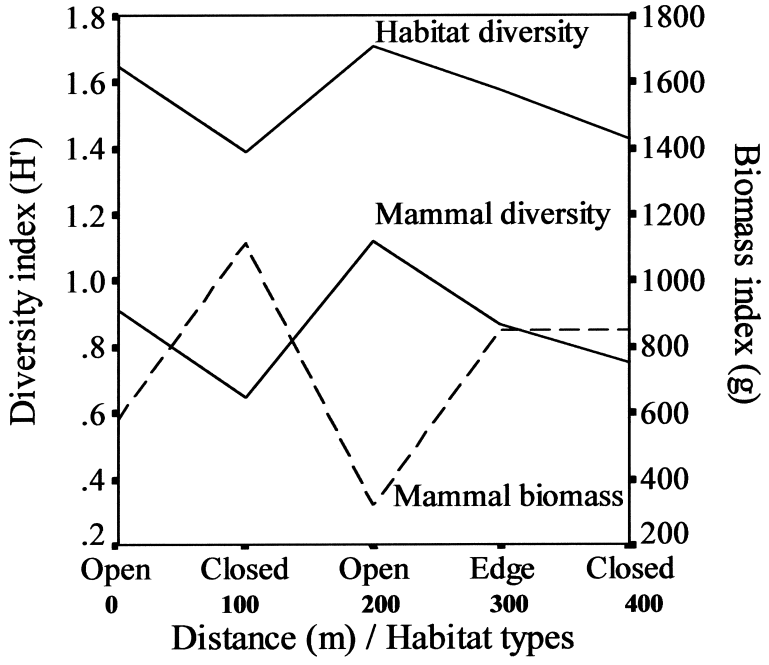


Figure 4. Trends in mammal diversity, habitat diversity and mammal biomass across alternating habitat types at Paluma site 3 (see methods for description of site 3). (Diversity is expressed by the Shannon index H′).

rain forest semi-dependent (*R. fuscipes*, *P. nasuta* and *T. stigmatica*); forest generalist (*M. cervinipes* and *A. flavipes*); and open forest specialist (*R. lutreolus* and *I. macrourus*) (Figure 2 a,b). This agrees with the classifications suggested by Winter *et al.* (1991).

Several studies have shown that terrestrial trapping produces a biased estimate of assemblage structure dependent on the relative arboreality of the constituent species (Laurance 1992; Malcolm 1990, 1991). Although the results presented here are based only on terrestrial trapping the patterns are probably not unduly biased for several reasons. In this study area, the mammal assemblage is relatively species-poor, especially with respect to arboreal species. The low species richness of the study area is ostensibly due to extinctions due to severe contractions in the area of rainforest during the Pleistocene (Williams 1997, Williams & Pearson 1997). Additionally, as part of a pilot study, tree-trapping and spotlighting were tested and were shown to provide little additional information (Williams 1990).

Habitat heterogeneity was significantly higher in the mixed open forest/ecotone area than in the adjacent rain forest (Figure 1 c,d). The gradient of habitat diversity also suggested that the edge of the vegetation discontinuity was more similar to the open forest than the rain forest. This is not surprising

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considering the relative homogeneity of the rain forest with its constant closed canopy and lack of ground vegetation.

Mammal diversity (H′) steadily declined across the transition from open forest into rain forest (Figure 3c), whereas biomass underwent a steady rise. These trends are also apparent at site 3 (Figure 4). It appears that the relative homogeneity of the rain forest has resulted in the proliferation of one species, *R. fuscipes* (Figure 2a), and this factor is a major contributor to the decrease in community evenness (Figure 3c) which is in turn responsible for the decline in the diversity index. Since the distance involved in this study was only 400 m, it is unlikely that confounding effects associated with distance are significant. In addition, the oscillation of the trends at site 3 confirms the habitat/small mammal community relationships presented above for sites 1 and 2 (eg. Figure 4).

The productivity theory of diversity suggests that diversity should increase with productivity (Connell & Orians 1964). However, many recent studies have found that diversity is highest at intermediate levels of productivity (see review by Rosenzweig & Abramsky 1993). Pianka (1966) in his review of species diversity gradients states that there is often an inverse relation between species diversity and standing crop (which is usually related to productivity). While this study has not directly measured productivity, it seems likely that the assumed higher productivity of the rain forest is correlated with a higher small mammal biomass. However, the biomass is dominated by one species (*R. fuscipes*) which results in lower small mammal diversity. The results of this study tentatively support the hypothesis of Rosenzweig & Abramsky (1993); that is, that habitat heterogeneity decreases at higher levels of productivity resulting in a decrease in biotic diversity.

Habitat diversity and small mammal diversity both increased across the gradient from rain forest to wet sclerophyll forest and these data could be taken as support for the theory of habitat heterogeneity as a major affect on diversity. However, the species richness of small mammals does not vary across the gradient despite the significant changes in the spatial heterogeneity and vertical complexity of the vegetation. Williams (1997) and Williams & Pearson (1997), in a biogeographic analysis of spatial patterns of vertebrate biodiversity, hypothesised that regional patterns of mammalian species richness in the rain forests of the Australian Wet Tropics have been largely determined by fluctuations in rain forest area during the Pleistocene and the resultant patterns of localised extinctions: a sifting effect. This suggests that the species composition within the rain forest is predominantly determined by historical biogeography and that at a local scale, within a given sub-region of the Wet Tropics, the vegetation structure is only affecting the relative abundances of each species.

Of the seven small mammal species recorded in the wet sclerophyll forest, five are primarily associated with rain forest (*Rattus fuscipes*, *Melomys cervinipes*, *Perameles nasuta*, *Thylogale stigmatica* and *Antechinus flavipes*) and one species is

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widespread in dry forests (*Isoodon macrourus*). In this assemblage one species only (*Rattus lutreolus*) is restricted to wet sclerophyll forest. Further studies have shown that all five species that are primarily rain forest species are not found beyond the narrow band of wet sclerophyll forest (S. E. Williams, unpubl. data). It seems probable that species richness within the wet sclerophyll forest is primarily due to a mass-area effect (Shmida & Wilson 1985) where rain forest species are also utilising what may be a sub-optimal habitat, and that the relatively high evenness of the wet sclerophyll assemblage is promoted by high habitat heterogeneity rather than any real increase in species richness. Therefore, in this assemblage it seems that habitat heterogeneity does not significantly influence species richness but does have a significant influence on the spatial patterns of species abundance and assemblage evenness.

The results of this study suggest that one of the striking features of the wet sclerophyll forest is the high degree of spatial habitat heterogeneity. The abruptness of the change in small mammal assemblage structure at the ecotone highlights the close relationship between these species and the vegetation structure and suggests that effective management of the faunal assemblage could be achieved by careful management of the habitat structure. Management should aim at maintaining the habitat heterogeneity of the wet sclerophyll forest, as any management regime which reduces the habitat diversity would probably result in a decrease in the diversity of it's small mammals.

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Appendix: Environmental attributes measured at each grid (30 locations) using an ordinal scale of abundance at each grid: 0 – absent, 1 – rare, 2 – occasional, 3 – common.

Eucalyptus grandis	Mosses/liverworts	Logs
Syncarpia glomulifera	Buttressed trees	Litter coverage
Allocasuarina torulosa	Strangler figs	Litter depth
Banksia integrifolia	Fire scars	Canopy gaps
Other eucalypts	Free water	Vegetation discontinuity
Grasses	Palms	Disturbance
Sedges	Ferns	Slender vines
Woody lianes	Tree ferns	Epiphytes

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