Williams, Stephen E. (1998) ***Spatial patterns of vertebrate biodiversity and assemblage structure in the rainforests of the Australian wet tropics.*** **PhD thesis, James Cook University.**

Spatial Patterns of Vertebrate Biodiversity and Assemblage Structure in the Rainforests of the Australian Wet Tropics

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1998

Submitted for the degree of Doctor of Philosophy
in the Department of Zoology and Tropical Ecology,
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Abstract

This study examined the spatial patterns of vertebrate biodiversity, with an emphasis on mammals, in the Australian Wet Tropics biogeographic region over a range of spatial scales. Regional patterns of diversity were described on the basis of a review and collation of all available data on vertebrate distributions. The highest species diversity of vertebrates was found in sclerophyll habitats (approximately 388 species). Rainforest was considerably less species-rich with about 259 vertebrate species; however, regional endemism was much higher in rainforest (25%) than in the combined sclerophyll habitats (4%). Although there was no consistent latitudinal or altitudinal cline in diversity, there was a consistent turnover in the assemblage composition of vertebrates, both altitudinally and latitudinally. Habitat diversity at the landscape scale was consistently important in explaining the variance in patterns of species richness.

The number of regionally endemic species of vertebrates and the proportion of regional endemics present in each sub-region were both related to the geographic shape and area of sub-regional patches of rainforest. Shape had a more significant influence on regional endemism than area, while area had a stronger influence on species richness. These patterns were similar for all terrestrial vertebrate classes.

Mammal assemblages were examined in more detail: multivariate analyses suggested five different geographically separated rainforest mammal assemblages. The most diverse was found in the central uplands (Atherton Tableland) with a decrease in diversity to the north and south, and with decreasing altitude. The most diverse areas were characterised by large areas of rainforest with a rounder shape (low shape index), high annual rainfall, consistent rainfall in the dry season and a diversity of rainfall regimes.

The combination of rainforest area and shape explained most of the variance ($r^2 = 0.74$) in the patterns of species richness of rainforest mammals. Various measures of habitat diversity were also dependent on area, and a similar degree of the variance in species richness ($r^2 = 0.78$) was explained by using rainforest shape and habitat *diversity variables (rainfall and vegetation diversity) and excluding area. This suggests that the effect of area on the patterns of species richness was primarily due to its positive influence on habitat heterogeneity. Analysis of the mammalian guild structure indicated that it was the number of species within guilds that most strongly affected patterns of species richness, although the number of guilds also had an effect. Most of the variance in species richness could be attributed to three guilds: arboreal folivores, small scansorial and small scansorial folivore-omnivores.*

The results suggest that habitat heterogeneity and patterns of localised extinctions (species sifting) during historical contractions of the rainforest have been extremely important processes in determining regional patterns of vertebrate biodiversity in Australia's wet tropical rainforests.

An investigation of the local-scale patterns of mammal diversity was undertaken on the southern Atherton Tableland. Spotlighting and live trapping were used to examine the relationships between the composition of the mammal assemblage and habitat structure over several spatial scales. The results showed that the structure of the mammal assemblages was closely correlated with vegetation structure. The presence or absence of specific guilds was related to vegetation complexity, although total species richness was not. Local species richness of ground-dwelling mammals was mostly a product of the spatial variability in assemblage structure (^{b}*diversity), which was related to the spatial variability in vegetation structure.*

The effect of spatial scale is crucial to the understanding of the generality of processes which limit or promote biodiversity. Each spatial scale represents a nested hierarchy within the larger scales. The available species pool at a given spatial scale constrains the upper limit of species richness possible at the smaller scales while spatial patterns within a scale are determined by processes acting at that scale. This study examined patterns of diversity over a range of spatial scales and conceptual models are presented which describe the different spatial scales and the variety of processes which act at each spatial scale.

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Dedication

I would like to dedicate this thesis to my daughter Anna. She has been my most loyal and loving supporter for the last eight years. Anna taught me the truth in something that was said by Charles Darwin ..... 'Talk of fame, honor, pleasure, wealth, all are dirt compared with affection'.

Acknowledgements

I would like to thank my family, Yvette and Anna, for making my life happy and for putting up with my absences in the field and the office. It has only been through their support and help that I have been able to complete this thesis, and they have my love and deep gratitude. I would also like to thank my family for their long-term moral support, especially Mum, Dad, Bron, Paula and Jo. I would also like to thank some people who have been special friends and who have helped me in many ways, especially Karl, Jacqui, Danny, Karen L., Ivan, Marc, Richard, Emily, Daniyella (this is not a typo), Karen W. and Martin.

My supervisors have been everthing they should, and much, much more. I would particularly like to thank Helene and Richard for believing in me and trusting me to get the job done despite the numerous distractions that I have been involved in over the last few years. John has taught me so much about the Wet Tropics, the rainforest and the wonderful animals that live there that I could not possibly list them all here, thank you John. I must also thank Richard and Helene for bearing the brunt of many dreary drafts without hardly a complaint. All three have been more like extremely supportive friends than formal supervisors and I have greatly appreciated it.

I would like to give special thanks to the many people and organisations listed in the special reference section (Appendix 5) who made their observations available for inclusion in the chapters on regional patterns of diversity, especially J. Winter, K. McDonald, F.Crome, L.Moore, G.Werren, M.Trenerry, S.Richards and J-M. Hero. Much of this study would not have been possible without their help. In particular I would like to thank John Winter for his enormous contributions in data, time and invaluable discussion.

Thanks to the Department of Zoology and Tropical Ecology, Department of Tropical Environmental Studies and Geography and the Cooperative Research Centre for Tropical Rainforest Ecology and Rainforest for their many faceted support throughout my studies. Thanks also the the Australian Research Council for my APA scholarship.

Australian Geographic also helped with funding, so everyone go out and buy their magazine. I'd also like to thank the Deptartment of Forestry, the Department of Environment and the WTMA for the permits etc. which allowed me to conduct the field studies.

Another special thanks has to go to the Wet Tropics Management Authority (WTMA). Much of the field work was supported by funding from the WTMA and I would like to personally thank Steve Goosem and Arnon Accad for interesting discussions and GIS and database support. Thanks to Alan McIlwee and Ivan Lawler for helping with the preparation of some of the maps, and to Brett and Warwick at CRC-TREM for the vegetation map.

To all of the people who have commented on or discussed various bits of this thesis with me, many thanks: Richard Pearson, Helene Marsh, John Winter, Richard Retallick, Karl Vernes, Jacqui Coughlan, Jiro Kikkawa, Michael Cunningham, Chris Schneider, Craig Moritz, Jean-Marc Hero, Bill Laurance, Nigel Stork, Chris Johnson, Keith McDonald, Francis Crome, Les Moore, Dolph Schluter and Yvette Williams.

Field work in the rainforest is never easy but it was made much easier and more pleasurable by the help and company of many people, many thanks guys: Karl Vernes, Jeff Middleton, Jacqui Coughlan, Eric, James Reiss, Jenny Goldberg, Steve Comport, Stephanie White, Yvette Williams, Lisa Kellogg, Martin Cohen, Caroline Christie, Paula Randall, Frederick Volpi, Christine Schmidt, Niall Connolly, Jane Blackwood, John Winter, Collin, Danny Spence, Les Moore, Bevan, Kirsty, Kylie Freebody and Larry. Field work, especially during the wet season, was made much easier by the tractor shed that I lived in, so thanks to Brian Smith for that privilege. I also appreciated the many hot showers, the food, the company, and the electricity to charge batteries (both mine and the ones for spotlighting) that were provided by John and Helen, Jane Blackwood, Kylie Freebody, Amy Jansen, Jodie Isaacs and Karl Vernes.

On patterns in nature ...

".. causality would be merely a name for something that exists only in our partial and biased mental reconstructings. The pattern which it indexes, however, would be real, but not intellectually apperceivable because the pattern goes everywhere and is everything and cannot be encompassed by finite mind or by anything short of life - which it is."

John Steinbeck (1958), p.212 *in* "Log from the Sea of Cortez"

Chapter 1: General Introduction

Background

This thesis examines the spatial patterns of vertebrate biodiversity in the rainforests of the Australian Wet Tropics and develops models which describe the determinants of these patterns over a range of spatial scales. There is no doubt about the global importance of biodiversity and understanding the patterns and processes that relate to biodiversity represents one of the greatest challenges to the science of ecology. A huge amount of scientific effort has been invested in publications on the subject of biodiversity over the last 15 years, including thousands of journal papers and many books (Haila & Kouki 1994). The importance of biodiversity is recognised by such monumental efforts as the "Global Biodiversity Assessment" (Heywood 1995), which is a compilation of biodiversity research including the work of over 1000 authors and funded by the United Nations Environmental Program, and the initiation of many global and national biodiversity action plans (Heywood *et al.* 1995). It is widely recognised that tropical rainforests are the largest terrestrial repository of global biodiversity and the inclusion of the Australian Wet Tropics rainforests on the World Heritage listing was primarily based on the recognition of the regions global importance in the preservation of biodiversity.

The Wet Tropics is an ideal location in which to study the determinants of biodiversity for a variety of reasons, including:

1. the region has a unique fauna of global significance with high levels of regional diversity and endemism;
2. the levels of taxonomic and ecological knowledge of the terrestrial vertebrates are better than many other regions of tropical rainforest around the world;
3. there has been considerable research on the long term history of the region, especially with respect to the effects of climate and habitat fluctuation during the Pleistocene glaciations;

4. the habitats and environment of the region have been mapped in detail using GIS technology, making the analysis of spatial patterns of environmental variables possible at a regional scale; and
5. the rainforests within the region are distributed along a series of disjunct mountain ranges, resulting in a number of relatively discrete subregions with differing characteristics. This last feature makes the region ideal to examine spatial patterns and processes relating to biodiversity because the regional biogeography has created a natural experiment where it is possible to compare and contrast the patterns of biodiversity across a range of subregions of varying size, climate, topography and biogeographic history.

Biodiversity, the diversity of life, can be viewed as a concept, a measurable entity or as a socio-political phenomenon which embodies the concern over the degradation of the natural environment (see Gaston 1996 for review). The broad concept of biodiversity has been defined many times; however, considering the complexity of the subject I particularly like the definition that biodiversity is '...the irreducible complexity of the totality of life' (P.H. Williams *et al.* 1994). Within the realm of ecology, and the context within which this study is conducted, biodiversity is predominantly treated as a measurable, albeit complex, entity which is described using four hierarchical dimensions: the diversity of genes, species, ecological functions and ecosystems. The most widely examined aspect of biodiversity, and the primary focus of this study, is species diversity, and in particular species richness. There is considerable evidence that species richness incorporates much of the diversity encapsulated in the other levels of biodiversity (Gaston 1996b). However, species richness should never be considered to be a complete surrogate for biodiversity as high species richness does not always equate with high biodiversity value and the processes which effect species richness may be quite different to those which relate to the other aspects of biodiversity. This study primarily examines patterns of species richness and ecological diversity within various taxonomic and ecological subsets of the vertebrate fauna and relates these patterns to both higher (ecosystem) and lower (genetic) levels of the biodiversity hierarchy.

Few other fields within ecology have received as much attention as the study of the generation and maintenance of patterns of diversity. I will give only a brief summary of the previous work on the causes of diversity as the subject has been comprehensively reviewed many times (e.g. MacArthur & MacArthur 1961; Pianka 1966; MacArthur 1964; Whittaker 1972; 1977; Goodman 1975; McGuiness 1984; Shmida & Wilson 1985; Ricklefs 1987; Wiens 1989a; 1989b; Ricklefs & Schluter 1993a; Rosenzweig 1995; Southwood 1996). Recent reviews on the determinants of diversity (Ricklefs 1987; Wiens 1989; Schluter & Ricklefs 1993; Southwood 1996) emphasise the need for studies of diversity to undertake comparative research on community patterns over a range of spatial scales and to consider the interfaces between the traditional "local" approach (niche theory) and the related fields of evolutionary biology, genetic diversity, phylogeography, biogeography and unique events which may have affected the evolution of the assemblage in question. The production of an integrated theory of the determinants of patterns of diversity requires the integration of all spatial scales and fields of study from genetics to biogeography (Ricklefs 1987).

There has been an increasing awareness that the measurement of diversity is highly dependent on the scale at which it is examined (Whittaker 1972; Ricklefs 1987; Schluter & Ricklefs 1993; Caley & Schluter 1997), and that scale is important over a broad range of ecosystems and taxa, including terrestrial vertebrates (Blondel & Vigne 1993; Morton 1993; Caley & Schluter 1997), fish (Poizat & Pont 1996), vascular plants (Kohn & Walsh 1994; Stoms 1994; Palmer & White 1994), insects (Lawton *et al.* 1993; Pearson & Juliano 1993), mangrove root epibionts (Farnsworth & Ellison 1996) and coral reefs (Karlson & Hurd 1993). Neither local nor regional diversity is independent of the other, although the relative importance of processes varies with the spatial scale in question. Therefore, an understanding of spatial patterns of diversity in any system can only be achieved by sampling across a broad range of spatial scales (Schluter & Ricklefs 1993; Stoms 1994) and, preferably, seeking similar patterns across different taxa. The variability of patterns of diversity with spatial scale is one of the unifying themes of this thesis which examines patterns of diversity in terrestrial vertebrates at the subregional and regional scale, and examines finer scale patterns in the mammal assemblage at the local and landscape scales.

Schluter & Ricklefs (1993) have reviewed current thought and concepts involved in diversity studies and have described seven types of processes which contribute to patterns of diversity:

1. *Local ecological interactions*: Local scale processes such as species-specific response, competition, habitat diversity, predation, disturbance, parasitism and mutualism have been the subject of the majority of studies on diversity (Wiens 1989a). The diversity of a local area depends on the habitat capacity, the habitat area and the length of time over which the environment has been relatively stable (Southwood 1996). Habitat capacity is the product of the both productivity and heterogeneity (Southwood 1996). The relationship between productivity and diversity has been extensively studied with variable results (Southwood 1996). Recently a number of studies have found evidence for a humped relationship between productivity and diversity where diversity is highest at intermediate levels of productivity (Abramsky & Rosenzweig 1984; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993; Rosenzweig 1995). Habitat heterogeneity incorporates both structural complexity and spatial heterogeneity and, in general, there are more species in heterogeneous habitats due to a larger number of available niches (Pianka 1966; Southwood 1996).
2. *Movement of individuals within a habitat* contributing to the spatial and temporal variability in local assemblages.
3. *Movement of individuals between habitats* such as the mass effect (Shmida & Wilson 1985), rescue effects and source-sink dynamics, where local diversity can be increased by the movement of individuals between patches of habitat. Species richness is often inflated by species which are essentially transient vagrants which are incapable of permanent colonisation (Southwood 1996; Gaston 1996).
4. *The spread of taxa within regions* involving the long-term diversification and expansion of taxa between habitats within a region.
5. *Allopatric speciation within the region*, e.g. vicariant speciation (Joseph *et al.* 1995).
6. *The long-term exchange of taxa between regions.* This has had a large effect on the development of the Wet Tropics fauna especially via interaction with New Guinea (see review in Chapter 2).

7. *Unique events* which often cause extinctions thereby reducing the diversity of the region, e.g. paleoclimatic fluctuations (see Chapters 3 & 4).

This study examines patterns associated with all seven process types.

Determination of the processes behind patterns of biodiversity is complex and difficult, both in theory and in practice. Many possible processes need to be considered and there are many biases and confounding influences. Nevertheless, understanding diversity is a vital part of ecology and conservation biology. This study addresses some of the key questions concerning vertebrate biodiversity in the Wet Tropics and diversity theory in general, including:

1. Which environmental factors are related to spatial patterns of diversity and do they vary between taxonomic or ecological groups?
2. Do the processes associated with the spatial patterns of species diversity vary at different spatial scales?
3. Are patterns in local diversity affected by local processes or are they simply a subset of regional diversity and primarily determined by regional scale processes?
4. How are patterns of diversity related to local ecological interactions with habitat structure, within-habitat movements and spatial variability, or between-habitat movements and species turnover?
5. What has been the effect of the biogeographic history of the region?
6. How do the patterns of species richness and ecological diversity relate to known phylogeographic patterns in genetic diversity?
7. Are specific subsets of the fauna, a particular guild for example, responsible for variation in the spatial patterns of diversity?
8. Is there evidence that the spatial patterns of diversity are influenced by either within-habitat or between-habitat dynamics (movements of individuals contributing to the spatial and temporal variability in local or habitat assemblages)?

Terminology

There is considerable variation in the terminology associated with studies on diversity and assemblage structure. Therefore, to avoid confusion, I will define the terms and the context in which they are used in this study:

1. species composition refers to the specific species present in a defined locality;

2. assemblage structure is the combination of the species composition and their relative abundances;
3. species richness is the number of recognised species, and
4. species diversity indices are a combination of species richness and relative abundances. There are a large number of diversity indices (Magurran 1988); however, the most commonly used index, and the one used in this study, is the Shannon-Weaver information index (Wiens 1989a).

Most analyses concentrate on species richness as the biological interpretation of diversity indices is ambiguous at best (Wiens 1989a). Endemism refers to the proportion of species at a locality which are endemic to the Wet Tropics biogeographic region; no other meaning of the term endemic will be used here. Whittaker (1972) describes an hierarchical system of spatially nested diversity measures from local (alpha) diversity up to regional (epsilon) diversity. The application to specific spatial scales is often difficult and different for different organisms. Point diversity for bacteria is obviously at a completely different spatial scale from that of vertebrates. This study describes six spatial scales, some of which are intermediate to those described by Whittaker (1972). Table 1.1 summarises the spatial scales, diversity measures and terminology used in this study (this table is also available in the foldout at the back of the thesis for easy reference).

Approach of this study

Since there are so many factors associated with the generation and maintenance of diversity, it is extremely difficult to objectively choose appropriate processes to test experimentally. Consequently, the approach used in this study was to examine many variables and to extract meaningful conclusions from the observed patterns. The analytical methodology uses a broad, "top down" approach and uses comparative and correlative multivariate pattern analysis to generate hypotheses, rather than to test specific factors. This type of approach has often been criticised by advocates of a strict Popperian approach to science based on hypothesis-testing. However, the trend towards the belief that experimental manipulation and the testing of specific hypotheses is the only way to "do good science" has been heavily criticised as actually inhibiting the development of an integrated science of ecology (Gould 1993; Weiner 1995; Lawton 1996). "To do science is to search for repeated patterns" (MacArthur 1972 quoted in

Lawton 1996). Ecologists must face the fact that ecology is a science which depends on both the here-and-now and the profound influence of history, which combined with the multitude of possible causal processes, often precludes the opportunity for manipulative experimentation on specific factors. In the words of S.J. Gould (1993), "If the evidence be sufficient, the explanation can be as rigorous and confident as anything done in the realm of experimental science...no apologies needed". Holistic, "top down" (hypothesis generating) and reductionist "bottom up" (hypothesis testing) approaches should not be seen as an antagonistic dichotomy but as equally valuable and complementary.

There are two main approaches used in this study. The first deals with regional scale patterns (Chapters 2, 3 & 4) and the second with local/landscape patterns in the mammal assemblage only (Chapter 5).

The regional analyses predominantly use comparative pattern analysis based on the species present in 23 subregions within the Wet Tropics biogeographic region. These data represent a compilation of information on vertebrate from published records, museum databases, unpublished reports and the unpublished data of many biologists working in the Wet Tropics. A summary of these data is presented in Chapter 2 within a general review of the state of knowledge on vertebrate biodiversity within the Wet Tropics (published in Williams *et al.* 1996). The taxonomic and distributional data on each species is included in Appendices 1-4. The patterns of regional species richness are analysed in a number of taxonomic and ecological subsets in conjunction with a variety of environmental and climatic factors. Patterns of endemism were particularly interesting and the analyses implicated historical extinctions as one of the main processes structuring patterns of vertebrate endemism (Chapter 3). Regional scale patterns of mammal diversity and assemblage structure are presented in Chapter 4 where I show that most of the variation in mammal species richness is explained by variability within three guilds and that extinctions at the subregional scale have probably had a greater impact on rainforest mammals than any of the other vertebrate groups. There is also strong evidence that habitat heterogeneity plays a vital role in spatial patterns of species richness at both the regional and local scale (Chapters 3, 4, & 5).

Local scale patterns were examined on the southern Atherton Tableland where there is the highest mammal diversity in the region, and possibly within Australia (Chapter 5). The emphasis in this chapter is the local interactions between mammal assemblage structure and habitat structure. Examination of trends in mammal assemblage structure across the gradient in vegetation structure from rainforest to open forest is used to elucidate mammal/habitat relationships within a relatively small area where it can be assumed that confounding effects due to history and biogeography are minimal. The results discussed in Chapter 5 show that on a local scale there is a very strong link between vegetation structure and mammal assemblage structure, and that small mammal diversity is closely related to spatial variation in assemblage structure and the spatial heterogeneity of the vegetation structure.

Table 1.1: Definitions and terminology describing diversity and the various spatial scales

Abbreviations: MAS - mammal assemblage structure; s.d. - standard deviation. See methods in Chapters 2 and 5 for full explanations of the sampling methods. Literature terminology is a summary of the terminology describing diversity referred to in Whittaker 1972; 1977; Wiens 1989a; Schluter & Ricklefs 1993).

Sample Type	**Spatial Scale (estimated area of influence)**	**Terminology in this study**	**Equivalent terms in literature**	**Scale of Influence within mammal assemblage structure (MAS)**
Individual trap	(100 m^2)			individuals and their movements
Trapping grid	POINT (0.3 - 1.7 ha)	sample	internal alpha	individuals - coexisting in an area where interaction probable within normal foraging movements
Spotlight segment	POINT (0.4 - 1.0 ha)	sample	internal alpha	individuals - coexisting in an area where interaction probable within normal foraging movements
Site	LOCAL (2 - 8 ha)	local diversity (alpha diversity)	alpha diversity or within-habitat diversity	local assemblage with spatial variation in structure - populations may inter-relate but not really at the scale of individuals.
Spatial variability within a site	LOCAL (2 - 8 ha)	spatial variation in MAS within a site	internal beta diversity	local scale spatial variability in MAS and dispersal movements of individuals within a habitat
Spatial variability between sites	LANDSCAPE (within approx. 5000m)	between-habitat variation in MAS	beta diversity or between-habitat diversity	movements between habitats (mass effects), dispersal movements, variation in MAS across habitats
Study area (local mammal studies)	LANDSCAPE (~2500 ha)	landscape (gamma diversity)	landscape (or gamma) diversity	landscape scale of different assemblages - mixing dependent on species vagility and habitat specificity
Sub-regional (22 defined subregions of the Wet Tropics)	SUB-REGION (1000 - 170 000 ha)	subregional diversity	landscape (gamma) - regional (epsilon)	area of mixed habitats with similar biogeography, history & available species pool within the constituent habitats
Wet Tropics Region	REGION (~900 000 ha)	regional diversity	epsilon diversity	biome species pool - mixed with other regions over geological time - sub-regions within region have differing effects of biogeography

Chapter 2: Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge[1]

Introduction

This study is the first broad examination of the patterns in distribution and biodiversity of the terrestrial vertebrates of the Australian Wet Tropics. This chapter reviews and summarises current knowledge of the distribution of the terrestrial vertebrate fauna collated from a wide range of published and unpublished sources. The collated data form the basis for some preliminary analyses of the patterns of vertebrate species richness in this chapter and detailed regional analyses in Chapters 3 and 4.

For the purpose of this study the Wet Tropics is defined as the biogeographic region between Mount Elliot (25km south of Townsville) and just north of Cooktown (Figure 2.1). The region extends from the coast to the western edge of the wetter sclerophyll forests (approx. between the 1000mm and 1500mm annual rainfall isohyet), where the forests give way to more open, drier woodlands (Tracey 1982). This is a biologically defined area and includes land under a variety of tenure types, including the Wet Tropics World Heritage Area (WTWHA) (for descriptions of the region refer to Webb and Tracey 1981; Keto and Scott 1986; Bell *et al.* 1987; Webb 1987; Winter *et al.* 1987a; Winter *et al.* 1987b; Mackey *et al.* 1989; Winter *et al.* 1991a & b; Werren 1993).

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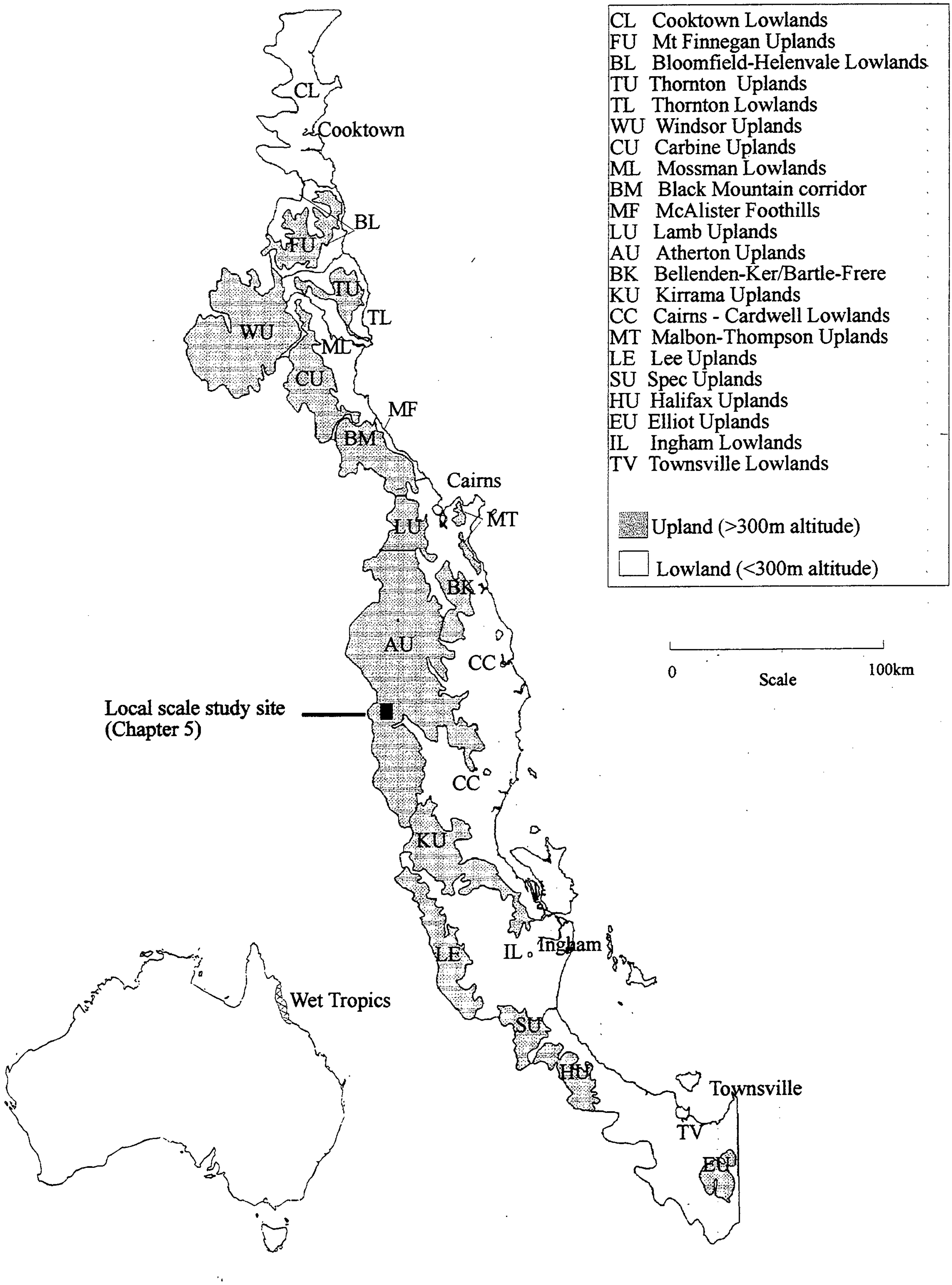
[1] This chapter has been published as a review article:
Williams, S.E., Pearson R.G. & Walsh P.J. 1996. Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. *Pacific Conservation Biology* **2**: 327-62

Figure 2.1: Faunal subregions within the Wet Tropics (modified from Winter et al. 1984).



Global context

Tropical rainforests are the most diverse terrestrial biome (Wilson 1988; Winter 1991; Joseph *et al.* 1995). It is estimated that although tropical rainforest covers only 7% of the earth's surface, it contains over half of the world's species (Wilson 1988). There are about 783 000 ha of tropical rainforest in the Australian Wet Tropics which represents about 0.09% of the total rainforest in the world (Wilson 1988; Winter *et al.* 1987; Goudberg & Bonell 1991). Although this is a very small proportion of the world's rainforest, the Australian Wet Tropics are of global importance as recognised by World Heritage Listing. Webb (1987) stated that the Australian Wet Tropics is one of the 'most significant regional ecosystems in the world' as a key to understanding the origins of angiosperms, past climatic sifting and in understanding links with temperate Australia, Asia, and South America. The Australian Wet Tropics are of great scientific interest due to their latitudinal spread, the highest concentration of primitive angiosperms in the world (Keto & Scott 1986) and high levels of faunal endemicity (Winter *et al.* 1987).

These factors make the Wet Tropics internationally important. High levels of diversity coupled with high levels of endemicity are especially important to the conservation of biodiversity (Gentry 1992) and are vital as evolutionary 'hot spots' as discussed by Myers (1988). Understanding these evolutionary hot spots of ongoing evolution is vital to managing and preserving biodiversity as, in the words of Soule and Wilcox (1980), 'Death is one thing: an end to birth is another'. Ecologists in the Wet Tropics have the unique advantage of having available a globally significant area of protected tropical forest in a developed nation (with the capacity to finance ecological research) where it should be possible to elucidate the determinants of biodiversity.

National context

The Wet Tropics is the most diverse biogeographic region in Australia (Keto & Scott 1986; Bell *et al.* 1987; Nix 1991; Werren 1993). Although the Wet Tropics covers only 0.1% of Australia (Keto & Scott 1986; Winter *et al.* 1987) it contains approximately

30% of the Australian terrestrial vertebrate fauna, including 78 species which are regional endemics. This is despite the fact that a significant proportion of the tropical rainforest has been cleared (estimates vary from 20% by Winter *et al.* (1987) to over 60% by Webb & Tracey (1981)). Most of the remaining tropical rainforest is now protected by World Heritage listing and is managed by the Wet Tropics Management Authority (WTMA).

Regional context

Specific knowledge of the vertebrates of the Wet Tropics is patchy and highly variable within and between taxonomic groups and geographic areas. The distributions of mammals are probably the best documented, followed by frogs, birds, and reptiles (in that order). It is unlikely that there are many new species of vertebrates to be described. There are several microhylid frogs currently being described (S. Richards and A. Dennis, pers. comm.); there are some recent taxonomic reviews which have changed the specific status of some animals (e.g. Leaf-tailed Geckos , Couper *et al.* 1993); and there is some taxonomy which needs to be examined (e.g. the specific status of Coppery Brushtail Possum *Trichosurus vulpecula johnstoni* and the Yellow-bellied Glider *Petaurus australis reginae*). However, these minor variations will not have major impacts on the overall patterns of vertebrate diversity in the region.

Nix (1991) describes the Wet Tropics as an archipelago of mesotherm islands which are separated by dry and/or warm barriers. He examined the distributions of endemic vertebrates by grouping species on the basis of climatic variables describing known points of occurrence. This climatic analysis produced five distinct groups of endemic vertebrates (Table 2.1), which particularly emphasize the importance of altitudinal zonation in describing the distribution patterns of rainforest endemics.

There has not been any comprehensive analysis of the patterns of vertebrate diversity in the Wet Tropics. All previous studies have examined only a subset of the vertebrate fauna, either a particular taxon (e.g. rainforest frogs, McDonald 1992) or a particular ecological group (e.g. vertebrates endemic to the region, Nix and Switzer 1991).

Congruence of patterns between taxonomic groups provides stronger evidence for causal biogeographic influences than a pattern for a single taxon, an important reason for the holistic approach used in this study.

Table 2.1: Groups of endemic vertebrates as defined by climatic analysis by Nix (1991).

Group	Description
1	highly adapted to cool, wet uplands
2	similar to group 1 but occur over a wider altitudinal and temperature range
3	confined to uplands in the northern part of the Wet Tropics
4	low altitude group
5	confined to summit regions of highest mountains

Mammals

Spatial and altitudinal distributions of rainforest mammals over the Wet Tropics are relatively well known (Winter *et al.* 1984; Winter 1988; Winter 1991a; 1991b; 1991c; Winter *et al.* 1991a; Van Dyck 1991; Nix and Switzer 1991). Nevertheless range extensions continue to be reported, e.g. *Uromys hadrourus* (Winter *et al.* 1984; Winter and Moore 1995); *Sminthopsis leucopus* (Van Dyck 1985; Laurance 1989) and *Antechinus godmani* (McDonald 1991); the recent rediscovery of the Mahogany Glider (*Petaurus gracilis*) (Van Dyck 1990); and the discovery of populations of an undescribed *Pseudomys sp.* and *Leggadina lakedownensis* in the Mount Spec Uplands (M. Cermak, pers. comm.).

Two sub-regions of mammalian faunal assemblages in tropical rainforest have been proposed by Winter *et al.* (1984): a northern sub-region (Thornton Peak Range, Finnegan Range and the surrounding lowlands) and a southern sub-region (from the northern end of the Atherton Tableland south to Townsville), with an overlap zone including the Carbine Range and Windsor Tableland (Figure 1). The centres of these two sub-regions (Thornton Uplands and Atherton Uplands respectively), separated by the lower altitude rainforest of the Black Mountain Corridor, have been cited as the focal points of mammalian diversity in the Wet Tropics (Winter *et al.* 1984; 1991a).

Patterns in diversity have been largely attributed to altitudinal preferences (uplands have higher diversity), dispersal from New Guinea and the fluctuations in the size of rainforest refugia over the last 25 000 years (Schodde and Calaby 1972; Winter 1988; Winter 1991a). Endemic rainforest specialists are considered to be 'relict species of a once more widespread community' which are now primarily restricted to upland, cooler rainforest (Winter 1988;1991a; Nix 1991).

Birds

Broad distributions and habitat preferences of most rainforest birds of the Wet Tropics have been well documented (Kikkawa 1968; 1974; 1976; 1982; 1988; 1991a;1991b; Kikkawa and Pearse 1969; Kikkawa and Williams 1971a;1971b; Schodde and Calaby 1972; Kikkawa *et al.* 1981; Crome and Nix 1991; Blakers *et al.* 1984; Simpson and Day 1996; Driscoll and Kikkawa 1989; Ingram and Raven 1991). However, data detailing the distributions of individual species within the region are very patchy. Specific sites with full species lists are rare except at research sites and in areas popularly frequented by bird watchers. This results in very detailed species lists for a few localities (e.g. near Townsville, Cairns and on the Atherton Tableland) and poor records for much of the region.

There are two sub-provinces within Cape York peninsula that have quite distinct rainforest bird assemblages (Kikkawa *et al.* 1981). The assemblages north of Cooktown have a strong affinity with the lowland rainforest assemblages in New Guinea, whereas there are high levels of regional endemism in the upland rainforest south of Cooktown (the Wet Tropics) (Kikkawa *et al.* 1981). Many of the upland endemic species are considered to be relicts of either an older connection with the upland fauna of New Guinea (e.g. most endemic birds) or from an older, cool temperate, Australian fauna (Kikkawa *et al.* 1981). Present upland rainforest in the Wet Tropics is a refugium and an 'epicentre of evolution for low vagility animals' (Kikkawa *et al.* 1981). In contrast, the lowland rainforest of the Wet Tropics has a higher affinity with the Cape York rainforests with dispersal from the north being a more important process than the vicariance inferred by a 'pattern of overlap among closely related species' in upland bird assemblages (Kikkawa *et al.* 1981). Recent genetic analysis of some rainforest birds (Joseph and Moritz 1994) suggests that vicariant evolution in historical rainforest refugia has been an important influence on the bird fauna, although the effects of this history have been more complex than previously thought, resulting in different patterns in different species. Genetic analysis also suggests that the time of important vicariant events is variable between species and much longer ago than the late Pleistocene contractions (Joseph and Moritz 1994).

Sclerophyll habitats on Cape York, including those within the Wet Tropics, are primarily Australian in origin and there is very little evidence of dispersal of sclerophyll birds from New Guinea. The patterns of dispersal in the sclerophyll habitats of Cape York are the opposite to those in rainforest, that is, there have been a number of Australian forms which have migrated north into the sclerophyll forests of New Guinea in contrast to rainforest species which have migrated from New Guinea into Australia (Kikkawa *et al.* 1981).

The distributions of birds which are endemic to the rainforest of the Wet Tropics (13 species) were reviewed by Crome and Nix (1991). There are many other species which have part or most of their range in the Wet Tropics, and there are a further ten subspecies restricted to the region (Crome and Nix 1991). Of the 13 endemic species, nine are restricted to the uplands, with the remaining four being widespread in the Wet Tropics (Crome and Nix, 1991). Crome and Nix (1991) re-emphasise the close links between New Guinea and the rainforest of the Wet Tropics (all 13 endemic species have close relatives in the highlands of New Guinea).

Reptiles

Reptile distribution patterns, although reasonably well known on a broad habitat scale, are not as well documented as those of the other vertebrate groups. This is largely due to the problems involved in sampling reptiles: records are usually opportunistic and, therefore, so is the knowledge of habitat preferences and distributions. The Wet Tropics is part of the Torresian biogeographic zone and has many representatives of recent invasions of species from the north (Cogger and Heatwole 1981). The Wet Tropics consists of a mixture of old endemics (Gondwanan origin) and recent invaders from the New Guinea (Cogger and Heatwole 1981; Kikkawa *et al.* 1981). The origins of the Wet Tropics reptiles are further discussed by Covacevich *et al.* (1982) in a review of the rare frogs and reptiles of Cape York Peninsula. Latitudinal ranges of these rare species are given on the basis of collection details from museum specimens.

Covacevich (in press) reviews the rainforest reptile zoogeography of the Wet Tropics. About 50 species of reptiles had been recorded in rainforest at the time of her review. Of these, 29 species are rainforest specialists with 20 species being endemic to the region, making the level of reptile endemism in the Wet Tropics the highest of all Australian rainforests (Covacevich, in press). However, levels of diversity are low in comparison to rainforest reptile diversity in South America or South-east Asia (Cogger and Heatwole 1981). Covacevich (in press) summarises the biogeographic history of the Wet Tropics and discusses the influence of old gondwanan reptile groups and more recent influences from Asia and New Guinea. She then gives broad latitudinal ranges and an assessment of the conservation status of each species of rainforest reptile, but does not detail specific distributions in most cases. Czechura and Covacevich (1985) identified seven species of reptiles within the Wet Tropics whose habits are unknown. These species are mostly very restricted in their distribution, often to a specific location e.g. *Bartleia jigurru* in boulder fields on the summit of Mount Bartle-Frere. This species belongs to a group of skinks primarily associated with temperate localities and represents an example of a relict species which has survived in the cooler 'temperate' rainforest on the summit of Mount Bartle-Frere (Schuster 1981; Covacevich 1984; Covacevich and McDonald 1991a; 1991b).

The most up-to-date review of the reptiles of the Wet Tropics is a report to the Wet Tropics Management Agency by Covacevich and Couper (1994). The report includes maps of the distribution of each species, and the collection location for all specimens currently held by the Queensland and Australian Museums. Most of the information in previous reviews by Covacevich (Covacevich *et al.* 1982; Covacevich and McDonald 1991a; 1991b; 1993; McDonald *et al.* 1991) is contained and updated in this report. Covacevich and Couper (1994) name 166 species of reptiles which have been recorded in the Wet Tropics. It should be noted, however, that the area covered by their report includes considerable areas to the west of the Wet Tropics region, which have been excluded from my study. This results in the discrepancy between the 166 species mentioned by Covacevich and Couper and the 131 species listed here. Covacevich and Couper 1994) and Covacevich and McDonald (1991) list 18 species of reptile which are obligate rainforest species and are confined to the Wet Tropics. Endemism is not as high in the drier habitats of the region, although generally there is less known about the species in these drier habitats (Covacevich and Couper 1994).

Covacevich and Couper (1994) found that the areas of highest reptile diversity in the region are (in descending order) the Bellenden Ker Range/southern Lamb range (includes some sclerophyll areas), Bloomfield, Mt Lewis/Mt Spurgeon/Windsor Tableland, Ravenshoe/Tully Falls, Kuranda, Paluma and Cardwell . They also found that there is lower diversity in the sclerophyll forests in general than in the rainforest, with the highest open forest diversity being found in the 'Mareeba area and in areas to the near west of Mt Carbine, Ravenshoe and Townsville'.

Frogs

Distributions of rainforest frogs have been relatively well documented throughout the Wet Tropics (Covacevich *et al.* 1982; Covacevich and McDonald 1991a; 1991b; Ingram and Longmore 1991; McDonald 1992; Covacevich and McDonald 1993; Richards *et al.* 1993). McDonald (1992) presents the most comprehensive review to date of the patterns of distribution and diversity of rainforest frogs. Since that report was published there have been dramatic declines in abundance in a number of species of Wet Tropics frogs (Richards *et al.* 1993) in a similar manner to some more southern rainforest frogs (Czechura and Ingram 1990). Four species (*Litoria nyakalensis, L. lorica, Taudactylus acutirostris, T. rheophilus*) cannot presently be found despite intense survey work (R. Alford, K. McDonald, S. Richards, J-M. Hero, A. Dennis, pers. com.). Three other species (*Litoria nannotis, L. rheocola, Nyctimystes dayi*) have severely declined in upland areas (above 300m) throughout their previous ranges (Richards *et al.* 1993). *Litoria nannotis* has been observed recently at several localities at higher altitudes (600-700m) in both wet sclerophyll forest and in rainforest (J-M Hero pers. comm.; unpublished data).

The Wet Tropics contains the most diverse rainforest frog assemblage in Australia with very high levels of regional endemism (McDonald 1992). McDonald (1992) cites the Atherton Uplands, Carbine Uplands and Thornton Uplands as core areas of high rainforest frog diversity. High diversity areas were 'characterised by high rainfall, granite parent rock and high altitude' with uplands having, in general, the highest diversity (areas above 600m and above 1000m are particularly important). McDonald suggests that the lower diversity in some southern uplands may be due to smaller area of rainforest, altitudinal range, disjunct distribution of rainforest or, in some areas, insufficient searching. The highest diversity in the lowlands is in the northern lowlands (Thornton, Daintree, Cape Tribulation lowlands) (McDonald 1992).

What is known about the determinants or processes underlying the patterns in vertebrate biodiversity in the Wet Tropics?

A recurring theme in many papers which consider the distribution of vertebrates in the Wet Tropics is the influence of historical climate and habitat changes (Winter *et al.* 1984; Winter 1988; 1991a; House and Moritz 1991; Nix and Switzer 1991; Hopkins *et al.* 1993; Walter and Paterson 1994; Joseph *et al.* 1995; Hopkins *et al.* 1996). The relative importance of dispersal, vicariance and ecological determinism as influences on current patterns of distribution has been the subject of ongoing debate in biogeographical literature (e.g. Endler 1982a,b,c; Winter 1988). Genetic studies of several Wet Tropics vertebrate species support the hypothesis that vicariance has been a source of speciation (House and Moritz 1991; Moritz *et al.* 1993; Joseph and Moritz 1994; Joseph *et al.* 1995). However, Winter (1988) points out that any present distribution and, therefore, any patterns in assemblage structure, will almost certainly be affected by both current ecological factors and historical events.

Latitude has traditionally been cited as an important determinant and/or correlate with diversity gradients. The generality of this hypothesis has come under increasing criticism in recent years (Kikkawa *et al.* 1981; Pianka and Schall 1981; Ridpath 1985; Smith *et al.* 1994). Ridpath (1985) suggests that general patterns are more difficult to distinguish in the tropics because of much higher temporal variability and spatial patchiness, and that diversity in the tropics is likely to depend more on rainfall and seasonality than on latitude.

Habitat heterogeneity (vegetation, landform, elevation, etc.) is almost invariably related to faunal diversity at some scale. Heterogeneity has been cited as an important factor in the Wet Tropics for a number of taxa (e.g. birds - Kikkawa *et al.* 1981, Williams 1994; mammals - Winter *et al.* 1984, 1988, Williams 1990; frogs - McDonald 1992; insects - Kitching 1994).

Anthropogenic fragmentation of natural habitats, with the subsequent increase in edge effects, can have large impacts on the assemblage structure of vertebrates (House and Moritz 1991; Laurance 1990; 1991a; 1991b; 1994; Laurance and Yenson 1991; Malcolm 1994; Murcia 1995). Rainforest mammal assemblages decline in diversity and the relative abundances of generalist species to core rainforest species can also change in fragmented rainforest (Laurance 1990; 1994). Natural disturbance can either increase or decrease diversity depending on the intensity and frequency of the disturbance (Connell 1978; House and Moritz 1991; Williams 1990).

Overlap zones, where habitats or regions of vicariant evolution meet, have also been suggested as a reason for high levels of local diversity. Winter (Winter *et al.* 1984; Winter 1988) has suggested that the high diversity of mammals in the Carbine Range is due to an overlap of distributions between the two major centres of diversity, the Atherton sub-region and the Thornton sub-region; that is, an overlap zone on a subregional spatial scale. Ecotonal areas often have high diversity due to the overlap of two distinct habitats each with its own fauna, that is, a high beta-diversity at an overlap zone on a landscape scale (e.g. Rainforest / Wet sclerophyll ecotone on the western edge of the rainforest – Williams 1990; Williams & Marsh in review; Chapter 5).

What is not known about vertebrate biodiversity in the Wet Tropics ?

Patterns of diversity or endemism have only been examined superficially for a few groups of vertebrates in the Wet Tropics and there has been very little research on the possible determinants of these patterns. Most discussion has been intuitive and suggestive of possible processes involved in determining vertebrate biodiversity in the Wet Tropics, rather than quantitative analysis of the patterns of diversity and environmental parameters. The most comprehensive analyses prior to this study have been by Winter *et al.* (1984) and Winter (1988) on mammals, McDonald (1992) on frogs and the papers incorporated in Nix and Switzer (1991) on rainforest endemics. Even in these papers there is only superficial treatment of the possible causes of the patterns described. Reports on the effects of vicariance by House and Moritz (1991), Moritz *et al.* (1993), Joseph and Moritz (1994) and Joseph *et al.* (1995) appear to be the only papers which really consider the processes behind some of the patterns of diversity. There has been little analysis of the possible environmental influences on diversity.

Detailed knowledge of the distribution of many species, especially reptiles, is incomplete. Areas with difficult access still have not been surveyed in great detail (e.g. Finnegan and Thornton uplands). There has been no holistic analysis of the distribution of any terrestrial vertebrate group in the Wet Tropics, nor any comparison of the patterns between taxa or between important groups within each taxon (e.g. comparing the patterns of total diversity, rainforest assemblage diversity and endemic diversity of a group). Congruence in these patterns may be important in forming hypotheses on the determinants or causal processes behind the patterns. Factors which may be important in determining diversity will almost certainly vary between different subsets of the fauna, and this variation needs to be examined in order to separate factors which promote diversity in general, and factors which are important to specific sub-sets of the vertebrate fauna (e.g. a specific taxon, specific ecological guild or level of endemism).

Methods

Geographic definition of subregions

The Wet Tropics was divided into 23 subregions (Figure 2.1) based on the sub-regions defined by Winter *et al.* (1984) and adopted by McDonald (1992). The level of detailed knowledge on vertebrate distributions is not adequate to allow an analysis based on point locality data. Analysis based on these large subregions is the finest resolution possible with current levels of knowledge. These subregions are primarily defined by the biogeographically distinct upland (above 300m) blocks. The western edges of the subregions are less well defined. The 300m contour was used where practical, but in some subregions the altitude remains well above 300m to the west of the main mountain ranges. In these cases, the edge of the subregion is defined climatically at approximately the 1500mm annual rainfall isohyet. A refinement of these subregions using a combination of the previous scheme, altitudinal zones, and vegetation types has been developed by Winter *et al.* (1993), but this scheme has the disadvantage that the current knowledge of detailed distributions of the fauna is inadequate to enable analysis at the finer level of resolution. The original scheme (Winter *et al.* 1984) was adopted for this study with some minor changes: the Atherton Uplands was split into the Lamb Uplands (LU), Atherton Uplands (AU), Bellenden Ker/Bartle-Frere Uplands (BK) and the Kirrama Uplands (KU) to enable more detailed analysis of this large area (Figure 2.1). Each subregion contains a diverse assortment of habitats; however, this thesis primarily deals with rainforest. These subregions were chosen as the basic unit for the analyses for two reasons. Firstly, the subregions represent relatively discrete biogeographic units with the rainforest in each sub-region being separated either by intervening sclerophyll forests, low altitude river gorges or, at the very least, low altitude gaps which would have been significant sclerophyll barriers during recent glaciations (Nix & Switzer 1991). Secondly, current distributional data were inadequate to compile species composition data at a finer spatial resolution than the subregions used here.

Compilation of distribution data

Data were collated on the vertebrate species present within each of the 23 subregions from a wide range of sources, including published fauna surveys, ecological papers, published monographs on the Wet Tropics, unpublished internal reports from the CSIRO, the Queensland Department of Environment and Heritage, James Cook University, the Wet Tropics Management Authority, records of the Queensland Museum, CSIRO records, records of expert amateurs and the personal records of a number of professional biologists currently working in the Wet Tropics. These sources are listed in the special references section in Appendix 5. Any records which were uncertain were excluded. The data were presence/absence records; however, since there are large differences in the amount of sampling which has occurred in each subregion, some predicted presences were included to remove some of the bias caused by a highly variable sampling intensity. These predictions were made with the consultation of the relevant experts (mammals - John Winter; birds - Francis Crome and Les Moore; reptiles - Keith McDonald; frogs - Keith McDonald, Steve Richards, Jean-Marc Hero) currently working in the region, based on their knowledge of the species involved, definite sightings in adjacent areas and the habitats present. Only species with a very high likelihood of occurrence in a particular subregion were given a “P” (probable) rating. Predictions of species occurrences which had a higher degree of uncertainty were assigned an “L” rating (likely to occur) or excluded. All of the analyses in this chapter have used definite records and “P” rated species, and analyses have been conducted only on subsets of the data with minimal predicted occurrences. Overall 11% of the records are predicted, dropping to 9% in rainforest species. Analyses were tested with and without predicted records without any significant differences. “L” rated species were excluded. The results of this exercise, a species-by-subregion occurrence matrix, are presented in Appendices 1-4. Species which are primarily distributed in drier, more western regions and which occur only on the edge of the Wet Tropics have been indicated in the appendices and tables as “edge species”. Data were collated for offshore islands but are excluded from all analyses because of the confounding factors associated with the diverse and widely spread islands along the Queensland coast.

Environmental data

Information describing the environmental characteristics of each subregion were compiled, including: total rainforest area, the length of the rainforest perimeter within each subregion, rainforest area broken down by structural vegetation types and altitude, rainforest shape (see below), vegetation diversity, altitudinal diversity, latitude (centre of subregion), latitudinal range (from northern to southern tips of each subregion), annual rainfall, the number of different rainfall regimes (average annual rainfall), rainfall consistency (indexed by mean monthly rainfall during the driest quarter) and minimum temperature (mean minimum temperature of the coldest quarter). Rainfall and temperature variables were taken from Nix 1991. Shannon-Weaver diversity indices were used to calculate spatial diversity of structural vegetation types (vegetation diversity) and altitudinal diversity. The data used were the number of vegetation types and their respective area within each subregion, calculated from 1:100 000 vegetation maps (after Tracey and Webb 1975; Tracey 1982) using the ARC/INFO GIS system of the Wet Tropics Management Authority.

Shape Index

Shape is defined as the areographic shape of the habitat, and can be quantified by the shape index (SI) (Patton 1975) which is dimensionless and is both theoretically and, in this study, empirically independent of area (log SI *vs* log Area, $r = 0.0780$, $P = 0.730$, $n=22$). It is important that shape is independent of area in order to separate the effects of shape and area to avoid collinearity in multiple regression models. The shape index is a measure of the degree to which a shape differs from circular ($SI = 1.0$ for a circle; $SI>1.0$ for all other shapes). The index was calculated from the area (RFAREA) and perimeter length (P) of rainforest within each of the 22 sub-regions:

$$\text{Shape Index (SI)} = \frac{P}{2\,(p\ \mathrm{RFAREA})^{0.5}}$$

The area of rainforest, rainforest shape index, species richness of endemic vertebrates (total and by class) and proportion of endemism within rainforest for each of the sub-regions are presented in Chapter 3. Estimates of rainforest area and perimeter length were calculated from 1:100 000 vegetation maps (after Tracey and Webb 1975; Tracey 1982) using the ARC/INFO GIS system of the Wet Tropics Management Authority. This scale of measurement (1:100 000) only measures deviations in the scale of hundeds of metres, which is appropriate in this study since the scale of changes in species distributions is of this order (e.g. edge effects - Laurance 1991b). Measurement at a finer scale (tens of metres) would produce very high shape indices due to small scale fuzziness at the rainforest boundary which would not be approriate to a regional analysis. Perimeter values do not include boundaries where there was continuous upland rainforest between two adjoining sub-regions - that is, the perimeter lengths only include boundaries with non-rainforest habitats.

Multiple regression analysis

The relationships between the patterns of vertebrate species richness and environmental variables were examined using multiple regression techniques. Environmental variables which were strongly collinear were removed from the analyses. Bats and water birds were excluded from the analyses due to insufficient data on bats and the fact that water birds are dependent on a specific resource (water bodies) which is largely independent of rainforest. The subregion of Mount Elliot (EU) was removed from these analyses as a complete set of environmental variables was not available for this subregion. Multiple regression modelling (backward removal), with species richness as the dependent variable and the same set of ten environmental factors as the independent variables was carried out for the total species richness of rainforest vertebrates and for mammals, birds, reptiles and frogs separately.

Results

At least 610 terrestrial vertebrate species occur in the Wet Tropics, as it is defined in this study (Table 2.2). Excluding introduced species (15) and edge species (29) leaves 566 species which make up the terrestrial vertebrate fauna of the Wet Tropics biogeographic region. This represents 28% of the entire Australian terrestrial vertebrate fauna and includes 95 mammal, 311 bird, 111 reptile and 49 frog species. There is a substantial degree of regional endemism (12%), although this is highly variable between taxonomic groups (4% - 43%) (Table 2.2).

Table 2.2: Summary of overall vertebrate diversity and numbers of species endemic to the Wet Tropics.

Percentages of species and families in parentheses = percentage of the total number of species/families in Australia. Levels of endemism are expressed as the number of species endemic to the Wet Tropics region and regional endemism is the proportion of species which are restricted to the Wet Tropics region. Edge species are species which primarily occur in adjacent regions and which only occur on the edge of the Wet Tropics region (see text).

	No. of Species (% Aust. Total)	No. of Introduced Species	No. of Edge Species	No. of Families (% Aust. Total)	No. of Endemic Species (% Regional Endemism)
Mammals	109 (45%)	9	5	25 (88%)	13 (12%)
Birds	316 (43%)	5	-	69 (83%)	13 (4%)
Reptiles	131 (21%)	-	20	12 (100%)	27 (21%)
Frogs	54 (28%)	1	4	5 (100%)	23 (43%)
Total	610 (30%)	15	29	115 (85%)	74 (12%)

Twenty-three percent of all species within the region (143 species) should be regarded as Very Important Species (VIS) (Table 2.3) in a conservation sense: that is, they have a Rare and Threatened ranking and/or are endemic to the Wet Tropics biogeographic region (specific and/or sub-specific) (see Appendices 1-4 for full species lists).

Table 2.3: Summary of the number of species by conservation status.
Very important species (VIS) are those species or sub-species which are either endemic to the region and/or have a rare and threatened status in Cogger *et al.* (1993), Garnett (1992), Ingram and Raven (1991) or *Queensland Nature Conservation (Wildlife) Regulation 1994.* Restricted endemics are Wet Tropics endemics which have very small distributions within the Wet Tropics, usually confined to a single subregion. Numbers of rare and threatened species in table follow the *Queensland Nature Conservation (Wildlife) Regulation 1994* (E - endangered, V - vulnerable, R - rare). VIS (%) is the percentage of species in the region which are listed as VIS.

	VIS	Endemics	Restricted endemics	Endemic subspecies	E	V	R
Mammals	37(22%)	13	3	4	2	3	17
Birds	42(11%)	13	0	10	3	5	10
Reptiles	38(30%)	31	7	n/a	-	2	17
Frogs	26(48%)	21	9	n/a	7	-	12
Total	141	78	19		12	10	56

A breakdown of the diversity of each major taxonomic group into broad habitat types (as defined in Winter 1991b) is given in Table 2.4. The drier sclerophyll forests form the largest habitat category (1283000 ha) within the Wet Tropics region. They also contain the largest diversity of terrestrial vertebrates with about 388 species (Table 2.4). However, this vegetation category is very broad, and includes a wide variety of habitats from dry sclerophyll woodlands to Melaleuca forests and swamps. There are approximately 259 species of vertebrates which occur in the 783000 hectares of rainforest in the Wet Tropics (Table 2.4), which is considerably less than in the sclerophyll forests. This pattern is consistent among taxa. The wet sclerophyll forest forms a narrow band on the western edge of the Wet Tropics rainforest. This habitat is very rich in vertebrate species with at least 227 species of vertebrates in only 72000 ha. This high diversity is largely due to this habitat being an overlap zone or ecotone between rainforest and dry sclerophyll. There are only five species of vertebrates which are largely confined to wet sclerophyll in the Wet Tropics: Fluffy Glider (*Petaurus australis*), Northern Bettong (*Bettongia tropica*), Swamp Rat (*Rattus lutreolus),* White-browed Scrubwren (*Sericornis frontalis*) and Eastern Yellow Robin (*Eopsaltria australis*); and only one of these (*Bettongia tropica*) is endemic to the region.

Table 2.4: Number of species of each taxon within each habitat type in the Wet Tropics.
(CF - closed forest, WS - wet sclerophyll forest, DS - dry sclerophyll (combined OF+W), OF - open forest, W - woodland, G - grassland, RK - rocky outcrops, CV - caves, FW - freshwater, MAR - marine, MAN - mangroves, STI - frogs which breed in still water, RUN - frogs which breed in running water). Introduced species excluded.

	CF	WS	DS	OF	W	G	RK	CV	FW	MAR	MAN	STI	RUN
Mammals	51	43	71	67	49	13	8	9	3		8		
Mammals (ex bats)	28	25	35	30	31	12	8	1	2		3		
Birds	112	107	174	138	141	48	3		73	17	63		
Reptiles	65	61	108	96	89	24	27	1	16	4	14		
Frogs	31	16	35	33	30	20	1		30		2	27	15
Total	259	227	388	334	309	105	39	10	124	21	87		

A breakdown of the numbers of endemic species in each habitat is given in Table 2.5. Although the dry sclerophyll forests contain the highest overall diversity there is low degree of endemism in these habitats (4%). In contrast, the rainforest fauna includes 66 species which are found only in the Wet Tropics biogeographic region. This means that 25% of the rainforest species are endemic to the region.

Table 2.5: The number of endemic species which utilize each major habitat in the Wet Tropics.
(CF - closed forest, WS - wet sclerophyll forest, DS - dry sclerophyll (combined OF+W), OF - open forest, W - woodland, G - grassland, RK - rocky outcrops, CV - caves, FW - freshwater, MAR - marine, MAN - mangroves, STI - frogs which breed in still water, RUN - frogs which breed in running water). (% - refers to the level of regional endemism in each habitat type) (no endemics in marine - MAR, grassland - G, caves - CV)

	Total	CF	WS	DS	OF	W	RK	FW	MAN	STI	RUN
Mammals	13	10	2	2	2	1	1				
Birds	13	13	4								
Reptiles	31	24	9	8	7	5	6		2		
Frogs	21	19	2	3	3	1	1	5		2	6
Total	78	66	17	13	12	7	8	5	2		
% regional endemism		25	7	4	4	2	21	4	2		

Spatial patterns of regional diversity

Very Important Species

The central uplands (AU, LU, KU, BK) and the Carbine Uplands (CU) contain a high diversity of important species with 98, 79, 76, 68 and 74 species respectively (Table 2.6). Frogs, in particular, have high levels of endemism and a large proportion of species which are rare/threatened; thus 48% of the frogs are very important species.

Table 2.6: Subregional characteristics and species richness.
The total area (ha), area of rainforest (RFAREA) (ha), number of important conservation species (VIS) and species richness (by taxonomic group) for each subregion (subreg): subregional codes are defined in Figure 2.1): RFMAMM - rainforest mammals, RFBIRD - rainforest birds, RFREPT - rainforest reptiles, RFFROG - rainforest frogs. Introduced species are excluded. Numbers are approximate as predicted occurrences are included (refer text and appendices).

SUBREG	AREA	RFAREA	VIS	MAMMALS	RFMAMM	BIRDS	RFBIRD	REPTILES	RFREPT	FROGS	RFFROG
CL	155561	4400	37	29	12	164	76	76	29	23	7
FU	53592	28090	55	26	17	85	75	45	33	19	15
BL	59473	14390	50	30	16	129	73	57	29	27	17
TU	31528	23770	58	22	19	62	59	28	22	22	20
TL	56887	31570	55	27	19	118	82	45	32	23	18
WU	183864	25620	65	37	23	113	81	58	30	28	18
CU	75625	39430	74	40	24	111	90	53	31	32	21
ML	73155	35380	47	25	17	145	85	45	32	25	17
BM	67012	34360	62	30	20	171	102	48	29	31	20
MF	8112	1060	29	17	11	161	86	41	24	18	10
LU	36259	20824	79	45	27	178	103	54	35	26	20
BK	32484	29260	68	26	24	119	95	30	27	18	17
AU	356778	170489	98	48	28	228	108	80	46	37	23
KU	101033	59093	76	45	27	166	94	61	40	28	19
CC	445200	157030	70	29	18	208	100	75	42	38	22
MT	8801	6192	44	18	17	79	69	14	14	13	11
LE	73413	36580	35	31	18	131	83	9	8	9	9
SU	29655	16780	52	27	17	167	98	31	27	14	11
HU	37723	12140	43	23	14	134	90	30	24	12	9
EU	22128	3500	16	14	9	80	56	22	16	4	3
IL	241044	17780	44	26	15	174	80	42	19	30	15
TV	268193	3879	41	32	12	192	72	74	27	25	8
IS	57438	11150	38	15	8	168	93	43	23	5	4

Mammals

Mammal diversity is generally higher in the upland subregions (Table 2.6), with a mean species richness of 30.9 compared to a mean of 26.9 in the lowland subregions; however, this difference is not statistically significant (1-way AOV, df=1, F=1.00, p=0.3334). This upland/lowland pattern is stronger in the diversity of rainforest mammals (mean species richness = 20.3 species in uplands versus 15.0 in lowlands, AOV df=1, F=6.25, p=0.0212). Diversity is highest in the central uplands, centred on the Atherton Tablelands, which has 48 species. Mammal diversity tends to decrease to the north and south, and with decreasing altitude. There are eight species exclusively recorded from lowland subregions and 12 species which are found exclusively in the uplands in the Wet Tropics region.

Birds

In general the diversity of terrestrial birds is higher in the lowlands (mean species richness per subregion = 161 species) than in the upland subregions (mean species richness per subregion = 130 species), but this difference is not statistically significant (1-way AOV, df = 1, F = 2.78, p = 0.11). The Atherton Uplands have the highest diversity (228 species); however, this includes many species which are primarily lowland species. This high total probably reflects the large amount of sampling effort on the Atherton Tablelands leading to the inclusion of rare visitors to the upland area. Removing the Atherton Uplands from the comparison leaves a significant difference between the diversity of upland subregions (mean = 123 species) and lowland subregions (mean = 162 species) (AOV, df = 1, F = 5.61, p = 0.0286). The diversity of rainforest birds in lowland and upland subregions is very similar with mean species richness of 81.8 and 85.9 species respectively (AOV df = 1, F = 0.4453, p = 0.5122).

Reptiles

Records of reptiles are patchy and patterns are difficult to interpret. Accurate distribution records and knowledge of the habitats used by each species are also poor, making it difficult to decide whether or not to include unusual records or records of species which are considered to be primarily western species of drier habitats (edge species). Identification is often difficult which can lead to erroneus distribution data. The Atherton Uplands has the most diverse reptile assemblage (both total and rainforest), the Cooktown Lowlands have the second highest species richness of reptiles and the Cairns-Cardwell Lowlands have the second most diverse rainforest assemblage (Table 2.6). This differs from the results of Covacevich and Couper (1994), who found that the highest diversity of reptile was in rainforest (cf. my study where the highest diversity is in sclerophyll forests) and that the highest rainforest diversity was in the Bellenden Ker Range / southern Lamb Range (cf. Atherton Uplands in my study); however, direct comparisons are difficult due to the different combinations of areas in the different studies. The total reptile species richness of lowland subregions is generally greater than in upland subregions with mean species richness of 56.9 and 40.2 species respectively, although this difference is not quite statistically significant at the 5% level (AOV, df = 1, F = 3.9,p = 0.0573). Higher lowland diversity is mostly the result of high diversity in a heterogeneous mixture of sclerophyll habitats. The diversity of rainforest reptiles in upland and lowland subregions is not significantly different, with mean species richness of 27.3 and 29.3 species respectively (AOV, df=1, F=0.2369, p=0.6317).

Frogs

The primary gradients affecting frog assemblages in the Wet Tropics seem to be a latitudinal change in composition coupled with distinct differences between wetter and drier habitats. Diversity is highest in the Cairns-Cardwell Lowlands (38 species) and Atherton Uplands (37 species) with a general trend of decreasing diversity to the north and to the south. The diversity of rainforest frog assemblages is highest in the Atherton Uplands (23 species), Cairns-Cardwell Lowlands (22 species) and the Carbine Uplands (21 species). There is no significant difference in the mean species richness of frogs (total or rainforest frogs) between upland and lowland subregions.

Environmental correlates of spatial patterns of species richness

The number of rainfall regimes within a subregion accounts for approximately 61% of the variance in the species richness of rainforest vertebrates (Table 2.7). None of the other environmental variables explain a significant amount of the variance beyond that already explained by the number of rainfall regimes. Similarly the species richness of birds and reptiles in rainforest is best explained by the number of rainfall regimes with 41% and 45% of the variance being explained respectively (Table 2.7). The combination of rainforest shape, rainforest area and rainfall diversity explain 81% of the variance in the species richness of rainforest mammals while rainforest area, latitude and altitudinal diversity explain 82% of the variance in patterns of frog species richness. Since most measures of habitat heterogeneity increase with area the analyses were repeated, for those groups where area was significant (mammals and frogs), with area excluded from the analysis. Similar amounts of the variance in patterns of species richness could be explained by the combination of several indices of habitat heterogeneity as with area (Table 2.7). With the exclusion of area, vegetation diversity became significant for both mammals and frogs. Annual rainfall became significant in the regression of frog species richness and latitude became non-significant when area was not included in the analysis. When the indices of environmental heterogeniety (vegetation, altitude, rainfall) are not included in the analyses, rainforest area becomes highly significant in the explanation of patterns of species richness in all groups (see Table 3.2 in Chapter 3).

Table 2.7: Relationships between species richness and the environmental characteristics of each subregion.

Multiple regression results using rainforest species richness as the dependent variable and a set of ten environmental variables as the initial set of independent variables (area, shape, rainfall diversity, latitude, latitudinal range, altitudinal diversity, mean minimum winter temperature, annual rainfall, dry season rainfall, number of rainforest structural vegetation types). Values in the upper part of the table are the probability that the factor is significant in the regression. Regression model uses backward removal of variables. Only variables which significantly contributed ($P<0.1$) to at least one of the multiple regression models are included in the table. The lower part of the table details the final regression model (df - degrees of freedom) ($n = 21$ for all analyses; Elliot Uplands excluded due to an incomplete set of environmental data). "-" indicates that the variable did not make a significant contribution to the model and therefore removed from the analysis. Negative correlations are indicated by (-) in front of the probability value for the significance of that factor. Regressions where area was excluded to examine the effects of habitat heterogeneity are indicated by 'ex Area'. $p = 0.0000$ indicates that $p<0.0001$.

Variable	Vertebrates	Mammals	Mammals (ex Area)	Birds	Reptiles	Frogs	Frogs (ex Area)
Rainfall Diversity	0.0000	0.0173	0.0001	0.0018	0.0009	-	0.0054
Altitudinal Diversity	-	-	-	-	-	0.0051	0.0570
Vegetation Diversity	-	-	0.0582	-	-	-	0.0011
Rainforest Area	-	0.0144	excluded	-	-	0.0000	excluded
Shape	-	(-) 0.0001	(-) 0.0001	-	-	-	-
Annual Rainfall	-	-	-	-	-	-	0.0662
Latitude	-	-	-	-	-	(-) 0.0036	-
Number of Species	235	28	28	112	65	30	30
Overall F	29.26	23.46	19.53	13.19	15.54	26.71	19.51
df	1,19	3,17	3,17	1,19	1,19	3,17	4,16
Overall P	0.0000	0.0000	0.0000	0.0018	0.0009	0.0000	0.0000
Overall R^2	0.6063	0.8055	0.7751	0.4098	0.4499	0.8250	0.8298

Discussion

There are several strong patterns evident in these results which are congruent between taxa. The sclerophyll forests within the Wet Tropics contain more species than the rainforest in all taxonomic groups; however, most of the species endemic to the region are rainforest species. The high diversity of the sclerophyll habitat is probably due to it being a mixture of many habitats. It was not analysed in detail since the emphasis of this study is on rainforest. Species richness is highest in the Atherton Uplands in all taxonomic groups and there is a general tendency in all taxa for diversity to decrease to the north and south of the Atherton Uplands.

The diversity of terrestrial vertebrates is similar in upland and lowland rainforest except in mammals where there is a significantly higher diversity in upland subregions. However, regional endemics are primarily upland species in all taxa examined and, although species richness may be similar, there are large differences in species composition between upland and lowland subregions in most taxonomic groups. Altitudinal gradients need to be examined in detail as all taxonomic assemblages exhibit large altitudinal changes in structure and there is a general paucity of information at mid-altitudes (300-600m). The processes behind altitudinal patterns are likely to be complex with the effects of habitat gradients, physiological tolerances and historical habitat fluctuations all contributing to the observed patterns and all interwoven with topography.

Habitat diversity, at the rather coarse landscape scale, consistently explains large amounts of the variance in the species richness patterns of rainforest vertebrates with all classes combined and within each class separately. The relative effects of the spatial heterogeneity in patterns of altitude, rainfall and vegetation are difficult to untangle since all three parameters are undoubtedly inter-related to some degree. The relative importance of each of these measures of habitat diversity varies between taxonomic groups, although the number of different rainfall regimes, which is probably an index of the number of broad habitat types, has the most consistent influence. The multiple regression results summarized in Table 2.7 clearly show that habitat diversity, as expressed by the various combinations of rainfall diversity, altitudinal diversity or vegetation diversity, explains large amounts of variance in spatial patterns of species richness. The similar r^2 values obtained from habitat diversity on the removal of area suggests that the effect of habitat area on species richness patterns at this spatial scale is primarily though the associated increase in habitat diversity with area, rather than an effect of area *per se*. A positive relationship between area and habitat heterogeneity has been observed many times in other studies (Southwood 1996); however, at this spatial scale, the indices of habitat diversity used here (spatial diversity of rainfall, altitude and vegetation) are indexing the coarse number of habitat types, not the finer scale habitat diversity usually related to niche partitioning. At this spatial scale (landscape habitat diversity), the relationship is more likely to to be indicating landscape scale processes such as movements between habitats and the spread of taxa within a region (see Chapter 1). That is, the presence of more habitat types within each subregion increases the number of generalist or nomadic / transient species which are likely to be recorded within the rainforest of that subregion due to movement within the subregion and long term diversification in habitat preferences (Shmida & Wilson 1985; Schluter & Ricklefs 1993; Southwood 1996; Gaston 1996b).

Rainforest shape explained significant amounts of the variance in patterns of species richness for mammals only (Table 2.7). This is particularly interesting since the shape is independent of area and habitat diversity. This relationship will be discussed in detail in chapters 3 and 4. The effect of latitude on frog species richness is probably a spurious relationship due to latitudinal changes in rainforest area, rainfall patterns and habitat diversity (Williams & Hero in review, see attached papers in appendix 8).

The subregions defined by Winter *et al.* (1984), and used in this study, represent a biogeographic division of the Wet Tropics based on the biogeomorphology of the region. There are real differences in the fauna between most of the subregions, and the subregions provide a useful scheme for analysis of patterns of vertebrate biodiversity in the Wet Tropics. Using the subregional scheme, rather than scanty point data, has enabled the species lists to be more complete and the analyses more robust. Even at this scale (subregions) it was extremely difficult to compile a complete species list of all vertebrates in each subregion.

Since the completion of this study a detailed definition of the biogeographic regions of Australia has been completed by Thackway and Cresswell (1995), on the basis of climatic and vegetation data. The boundaries they propose provide a better biological delineation of the Wet Tropics and thereby a better framework for a biological analysis of the Wet Tropics than the scheme used in this study. Future analyses should use the region boundaries defined by Thackway and Cresswell (1995) except that the Mount Elliot Uplands, which represent a small island of wet tropical rainforest approximately 50km south of the region defined in their report, should be included in any analysis of the Wet Tropics fauna. However, since the primary interest of my study is rainforest biodiversity, the differences in the definition of the region boundary are not of major importance. All of the major blocks of rainforest are contained within both of the regional definitions. The boundaries used in this study include more of the drier forests along the western boundary of the region than the scheme proposed by Thackway and Cresswell (1995). To allow for these differences, species recorded in this study which are primarily distributed in the more western and drier Einasleigh Uplands (Thackway and Cresswell 1995), with only the edge of their range intruding into the Wet Tropics, have been indicated in the appendices and tables as “Edge species”.

Predicted occurrences have also been used, as described in the methods, to attempt to remove some of the sampling bias between subregions. These predictions were extremely conservative and alleviate, but do not entirely remove, these sampling biases. Some subsets of the data contain a large proportion of predicted occurrences (e.g. birds in the Cooktown Lowlands (CL) – mostly aquatic species); however, all quantitative analyses consider only those subsets of the data where a much smaller number of predicted occurrences are used, although all records and predictions are included in the appendices for completeness. In most groups about 10% of the data are predicted rather than recorded presences. This methodology has allowed a much more detailed description of diversity patterns than has been possible previously and it allows the generation of specific models and hypotheses on the determinants of patterns of vertebrate biodiversity. The use of predicted occurences, by well qualified experts, is necessary to remove some of the bias in the patterns caused by the lack of a record of common and often widespread species in a particular subregion.

The distributional information presented in this chapter is based on presence/absence data. Replicated, standardised sampling to provide estimates of relative abundances throughout the region would greatly enhance the pattern analysis. Sampling bias between subregions could be minimised by standardisation. Abundance data would greatly improve the pattern resolution, as would more detailed point data on species occurrences. All species have variable abundances through the region, so presence/absence data can be misleading when comparing the assemblage composition of different subregions. An example of this is the small observed differences in diversity between Atherton Uplands and the Kirrama Uplands: experience in these localities shows that although species richness is very similar, there are large differences in the abundances of many species between these two adjacent areas (unpublished data). However, the species composition data presented here are the sum of many years of observations by numerous people, making the species lists for each subregion much more complete than could be achieved in any survey.

Collation of information has highlighted several geographical gaps in the distribution data. There is a large degree of variation in the amount of sampling which has been undertaken in different areas of the Wet Tropics. There has been much more research done in rainforest than in other habitats. Some areas have been extensively surveyed, including Atherton Uplands, Townsville Lowlands, Cairns Lowlands, Windsor Uplands, Carbine Uplands, Lamb Uplands, Kirrama Uplands and Spec Uplands. Other areas have received very little attention, including the Finnegan Uplands, Thornton Uplands, Malbon-Thompson Uplands and Lee Uplands.

McDonald (1992) points out that there has been little frog research in mid-altitudes, and this probably applies to all taxa. I have found several species of vertebrates at 400-450m in the southern Atherton Tablelands which are supposedly restricted to above 600m (e.g. Atherton Scrubwren, Fernwren) (unpublished data). This is probably a reflection of the general lack of sampling at mid-altitudes.

There is a need for systematic surveys to be carried out in poorly surveyed areas and over the complete altitudinal gradient rather than simply comparing upland and lowland as I have done here. High altitude areas are of particular significance because they are important centres of endemism and because information on them is scarce due to the difficulties in surveying these areas.

The Finnegan Uplands, Thornton Uplands, Malbon-Thompson Uplands and the Lee Uplands are the areas most in need of sampling[2], as previously indicated by Nix (1991) also. These areas are important in examining biogeographic patterns within the Wet Tropics. The Lee Uplands are separated from the largest and most diverse rainforest within the region (AU, KU, BK, LU) by the Herbert River gorge. Comparison of assemblage structure across this gap may be of great interest in interpreting biogeographic patterns (as is the Black Mountain Corridor barrier); however, this is difficult because of the lack of information about the fauna of the Lee Uplands. The Malbon-Thompson range is important in examining determinants of biodiversity since it is in the centre of the region and very close to the areas of highest diversity in the Atherton Uplands, but it is separated by a coastal low altitude plain. The effects of this separation are difficult to judge without more detailed information on the fauna of the Malbon-Thompson Uplands.

Individual species which are important to conservation and management (VIS) are identified in Appendices 1-4, with the largest concentrations of important species

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[2] Since the completion of this study, I have conducted additional surveys of vertebrates at the Lee Uplands and the Malbon-Thompson Uplands. The results of these surveys support the hypothesis that the low observed species richness in these areas was due to inadequate sampling. An additional 77 species of vertebrates were recorded at the Lee Uplands and 16 at the Malbon-Thompson Uplands.

occurring in the Atherton and associated uplands (AU, KU, BK, LU) and Carbine/Windsor Uplands (CU, WU) (Table 2.6). However, most areas within the region contain significant numbers of species important to management and conservation. The data collated and summarised in this chapter provide baseline information on the distribution and diversity of the terrestrial vertebrate fauna of the Wet Tropics which should be a useful resource for the conservation and management of the region. Additionally, the data contained in this chapter form the basis of detailed analyses of comparative assemblage composition and the ecological correlates of patterns in diversity (Chapters 3 & 4).

Chapter 3: Regional patterns of vertebrate endemism in the Wet Tropics[3]

Introduction

Endemic species have a high conservation priority and one of the primary reasons for the protection of the rainforests of the Australian Wet Tropics under World Heritage legislation is the high levels of regional endemism in both the flora and the fauna. Approximately 25% of the terrestrial vertebrates (Chapter 2) and 37% of the plants (Keto and Scott 1986) are regional endemics. Understanding the processes that affect patterns of endemism is of great importance both in the management and conservation of these rainforests, and in the study of the structure and evolution of faunal assemblages in general. Anderson (1994) suggests that there is a general tendency for endemism to be higher in larger areas, in environmentally heterogeneous areas and in low-vagility taxa, and that historical factors will have an important influence on areographic patterns in endemism. History is recognised as an integral part of understanding current assemblage structure and species diversity (Ricklefs and Schluter 1993a; Kupfer 1995). Comparisons between the vertebrate assemblages of the Wet Tropics and those in New Guinea or southern Australia have often cited historical processes as major influences on assemblage patterns (Brereton and Kikkawa 1963; Schodde and Calaby 1972; Winter 1988; Crome 1990; Nix 1991). Habitat shape is another factor which has often been implicated in patterns of endemism and assemblage structure; however, its demonstrated effects have been variable (Kupfer 1995). In the context of this study, habitat or rainforest shape refers to the geographic shape of the rainforest present within each sub-region of the Wet Tropics (see Chapter 2).

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[3] This chapter has been published in:
Williams, S.E. & Pearson, R.G. 1997. Historical rainforest contractions, localised extinctions and patterns of vertebrate endemism in the rainforests of Australia's Wet Tropics. *Proceedings of the Royal Society London B*. **264**: 709-716.

In this study, an endemic species is defined as one which is found only in the Wet Tropics biogeographic region of north-eastern Australia (Figure 2.1); that is, a species demonstrating "geographic endemism" (Anderson 1994). Endemism is defined as the proportion of species in a geographic or taxonomic group which are endemic to the Wet Tropics region. The analyses presented here relate only to rainforest species, which comprise the majority of Wet Tropics endemics (Williams *et al.* 1996).

Here I examine the possible determinants of spatial patterns of vertebrate species richness and regional endemism by examining distributional data for the terrestrial vertebrates of the Wet Tropics biogeographic region within each of 22 discrete sub-regions. I examine the hypothesis that spatial patterns of vertebrate endemism are largely the result of localised extinctions in those sub-regions most affected by historical contractions of rainforest area, and that the relative effect of these contractions is reflected by the combination of current rainforest area and shape.

Methods

The data collated and presented in Chapter 2 and Appendices 1-4 are used in the analyses in this chapter. However, only 22 of the subregions are included in the analyses. Offshore islands were excluded in this and subsequent chapters due to the large number of confounding effects and the paucity of records of their fauna.

Information describing the environmental characteristics of each subregion was compiled, including total rainforest area, rainforest area by structural vegetation types and altitudinal bands, rainforest shape, vegetation diversity, altitudinal diversity, latitude, latitudinal range, annual rainfall, spatial rainfall diversity, rainfall consistency and temperature (Chapter 2). When variables were strongly collinear those variables with the lowest r^2 value were removed from the analyses. Multiple regression modelling (backward removal), with species richness as the dependent variable and the environmental factors as the independent variables, showed that although many of the variables explained small amounts of the variance for various taxonomic groups, only rainforest area and shape consistently explained large amounts of the variance in patterns of endemism and endemic species richness. Therefore, subsequent analyses, presented in this chapter, consider these two primary variables only.

Multiple regression models of the effects of rainforest area and shape

Multiple regression was used to examine the relative contributions of rainforest area and shape in explaining patterns in vertebrate species richness. Separate analyses were conducted for total species richness and the species richness of regional endemics for all vertebrates combined and for each of the major taxonomic groups. Multiple regression models use species richness as the dependent variable and log rainforest area and log shape index as the independent variables (log transformation was used to normalise data). Bats and water birds were excluded from the analyses due to insufficient data on bats and the fact that water birds are dependent on a specific resource (water bodies) which is largely independent of rainforest. Partial residual analysis was used to examine the relationship between species richness and shape independent of area, and species richness and area independent of shape. Analysis of covariance was used to determine if there were significant difference in slopes and intercepts between regressions.

Nestedness

Nestedness is a measure of the degree to which the assemblages in sub-regions with a low species richness are simply a subset of the more diverse sub-regions. The implication is that archipelago systems with a high degree of nestedness are the result of non-random extinctions in order of the specific extinction proneness of each species and usually related to the habitat area of each 'island'. The concept of nested sub-sets was first quantified by Patterson and Atmar (1986). However, their nestedness index was affected by the size of the species/island matrix and emphasized presences more than absences (Atmar and Patterson 1993). A more sophisticated index of nestedness (matrix temperature - T) which is independent of matrix size, was subsequently developed from thermodynamic theories of order and disorder (Atmar and Patterson 1993). The degree to which the matrix temperature departs from randomness can be tested statistically using monte-carlo simulations. This index of nestedness, 'matrix temperature', is used here to decribe the degree of nestedness of the endemic rainforest vertebrates in the Wet Tropics. Matrix temperature and the probability of significant nesting were calculated using the software developed by Atmar and Patterson (1995).

Results

The area of rainforest, rainforest shape index, species richness of endemic vertebrates (total and by class) and proportion of endemism within rainforest for each of the sub-regions are listed in Table 3.1.

Species richness in rainforest (all species)

Species richness of all terrestrial rainforest vertebrates is positively correlated with the area of rainforest in each sub-region (Table 3.2). However, multiple regression analysis shows that shape does not significantly contribute to the pattern of overall species richness of rainforest vertebrates in any of the sub-groups examined, except for mammals, after controlling for the effects of area. Separation of the mammal assemblage into arboreal and ground dwelling groups shows that only the species richness of arboreal rainforest mammals is related to shape.

Species richness in rainforest (regional endemics only)

In contrast to the patterns of total species richness in rainforest, the species richness of endemic rainforest vertebrates in the Wet Tropics (Figure 3.1) is highly correlated with area *and* shape of the rainforest in each sub-region (Table 3.2). There is a decrease in the species richness of endemic vertebrates with increase in the shape index. Shape explains 66% of the residual variation in the species richness of endemic vertebrates after removing the effect of area. This pattern is congruent in all classes, with shape explaining 34 - 74 % of the residual variation in the groups examined. However, in all groups except birds, more of the variance in species richness is explained by area than by shape.

These relationships, with area and shape, remain highly significant if the analysis is restricted to upland sub-regions (all endemics - $P = 0.0003$, $r^2 = 0.7739$, $n = 14$). Additionally, the patterns are not greatly affected by the removal of the nine sub-regions which have significant anthropogenic clearing of vegetation ($P = 0.0009$, $r^2 = 0.7523$, n

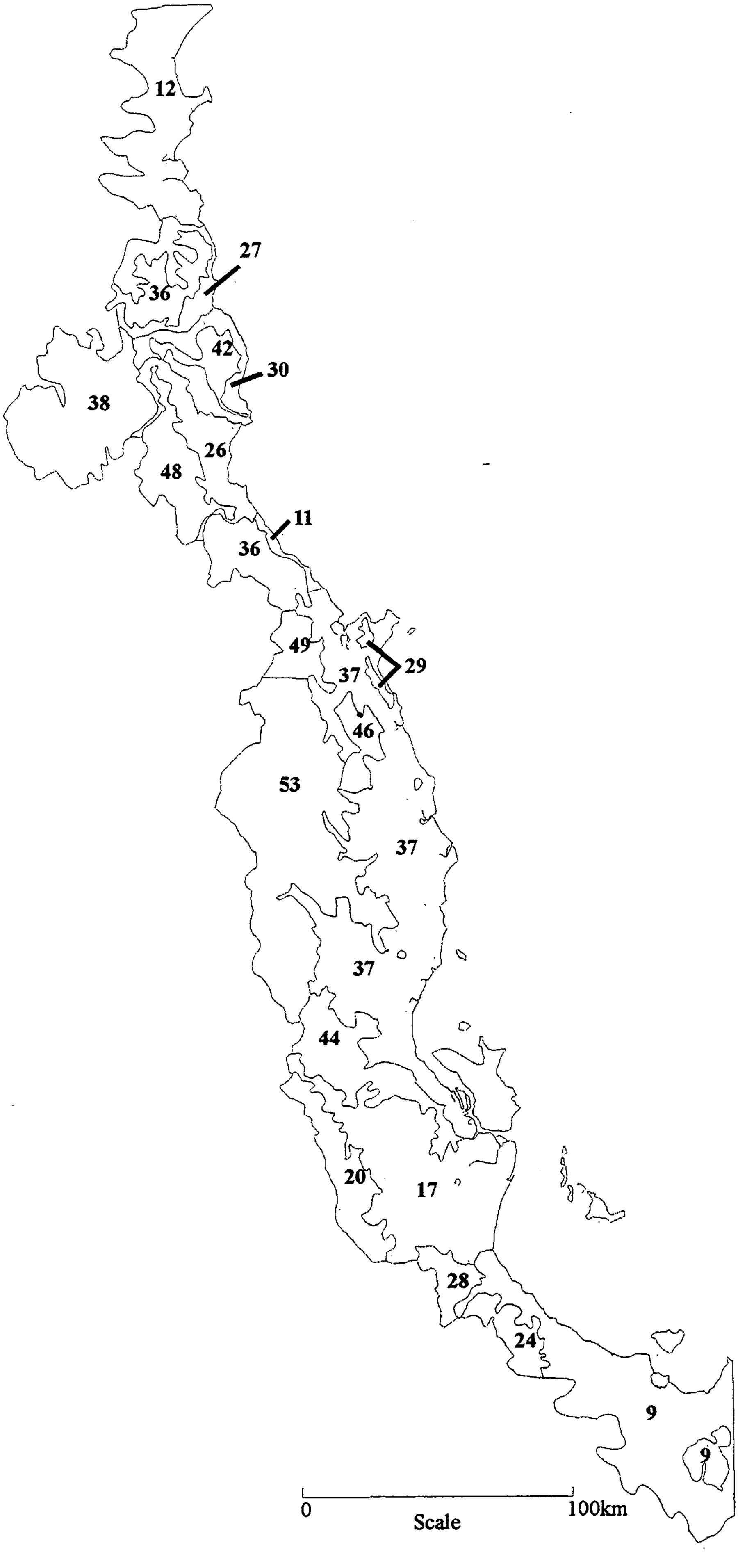
= 13). Therefore, the results are not an artifact of anthropogenically-induced high shape indices in the lowlands or in those regions where there has been significant clearing and fragmentation, but are related to the natural distribution of rainforest.

Table 3.1: Vertebrate species richness and endemism of the rainforest within each subregion.

The area of rainforest, shape index (SI), level of endemism and species richness for all vertebrates and each vertebrate class separately within the rainforest in each sub-region within the Wet Tropics biogeographic region, listed in order of increasing regional endemism.

Subregion	Rainforest Area (ha)	Shape (SI)	Vertebrates	Endemic Vertebrates	Endemism (%)	Mammals	Endemic Mammals	Birds	Endemic Birds	Reptiles	Endemic Reptiles	Frogs	Endemic Frogs
McAlister Foothills (MF)	1060	6.2	130	11	8	10	2	87	3	24	4	9	2
Townsville Lowlands (TV)	3879	9.8	118	8	8	10	0	72	1	28	5	8	2
Cooktown Lowlands (CL)	4400	8.8	126	8	10	11	2	76	2	31	3	8	1
Elliot Uplands (EU)	3500	5.8	84	9	11	8	0	56	4	18	4	2	1
Ingham Lowlands (IL)	17780	21.1	128	15	13	14	2	80	3	20	4	14	6
Lee Uplands (LE)	36580	7.0	115	19	17	16	3	83	7	8	4	8	5
Mossman Lowlands (ML)	35380	9.0	149	26	17	16	3	85	5	32	12	16	6
Halifax Uplands (HU)	12140	7.5	134	24	18	13	0	90	11	23	9	8	4
Spec Uplands (SU)	16780	5.1	150	27	19	15	1	98	12	27	9	10	5
Thornton Lowlands (TL)	31570	10.5	149	30	20	17	3	82	6	32	12	18	9
Cairns - Cardwell Lowlands (CC)	157030	20.1	181	35	20	16	2	101	7	43	15	21	11
Black Mountain Corridor (BM)	34360	7.8	170	36	21	19	3	103	11	29	13	19	9
Bloomfield Lowlands (BL)	14390	11.5	131	23	21	14	2	73	6	29	8	15	7
Kirrama Uplands (KU)	59093	5.5	178	45	25	25	7	94	13	41	16	18	9
Windsor Uplands (WU)	25620	3.2	148	36	26	21	4	81	13	29	11	17	8
Malbon Thompson Uplands (MT)	6192	4.0	108	28	26	15	2	69	10	14	9	10	7
Finnegan Uplands (FU)	28090	5.2	136	35	26	15	2	75	11	31	14	15	8
Atherton Uplands (AU)	170489	8.2	205	51	26	26	8	109	13	47	17	23	13
Lamb Uplands (LU)	20824	3.7	183	48	27	25	8	104	13	35	16	19	11
Bellenden-Ker/ Bartle Frere Range (BK)	29260	2.4	160	46	29	22	7	95	13	27	15	16	11
Carbine Uplands (CU)	39430	2.8	164	47	29	22	6	90	13	31	15	21	13
Thornton Uplands (TU)	23770	2.6	116	42	36	17	4	59	13	21	14	19	11

Figure 3.1: Species richness of endemic vertebrates in each subregion of the Wet Tropics. Refer Figure 2.1 for subregion names and codes.



Patterns of endemism

The degree of endemism within the rainforest in each sub-region (proportion of endemic species in the total rainforest assemblage present in that sub-region, as opposed to the *number* of endemic species) shows a positive correlation with area and a negative correlation with shape (Figures 3.2A and 3.2B). That is, the proportion of endemic species is higher in rainforest blocks with a smaller shape index (closer to circular) and a larger area. Shape explains more of the variance in endemism than area although the difference is slight, whereas area explains more of the variance in the species richness of endemics (Table 3.2): this means that in blocks of rainforest which are more circular the rainforest assemblage contains a higher proportion of endemics and a lower proportion of rainforest generalists (ie. Species not restricted to rainforest). Conversely, generalist species are more prevalent in blocks with a more fragmented or convoluted shape.

Does the effect of shape decrease in larger areas of rainforest ?

Shape has traditionally been used in landscape ecology as an important indicator of edge effects (Noss 1983; Temple 1986; Laurance 1991a; 1991b; 1994). This paradigm predicts that as area increases the effect of shape should decrease due to the decrease in the proportion of edge to core habitat area. To examine whether the effect of shape decreases with area, the subregions were divided into those with larger (> 20 000ha) and smaller (< 20 000ha) areas of rainforest (Figure 3.2B). This division was based on a tendency for the species-area curve for the total number of endemic vertebrates in each sub-region to plateau at about 20 000 ha. The slopes of the negative correlation between endemism (residual variation in endemism after removing the effects of area) and shape (Figure 3.2B) are not significantly different in small or large areas of rainforest (ANCOVA, df=1, F=0.00, P=0.985 - compares separate regression models for small and large rainforest areas: the dependent variable is the residual variation after regressing log rainforest area against endemism; and the independent variable is log SI). There is also no significant difference in the relationship between shape and the species richness of endemics in sub-regions with either small or large areas of rainforest (ANCOVA df=1, F=0.18, p=0.673). The important result here is that shape, independent of area, has a very significant effect on the species richness of endemic vertebrates and the level of vertebrate endemism in both small and large areas of rainforest.

Table 3.2: Relationships between species richness, endemism, rainforest area and rainforest shape.

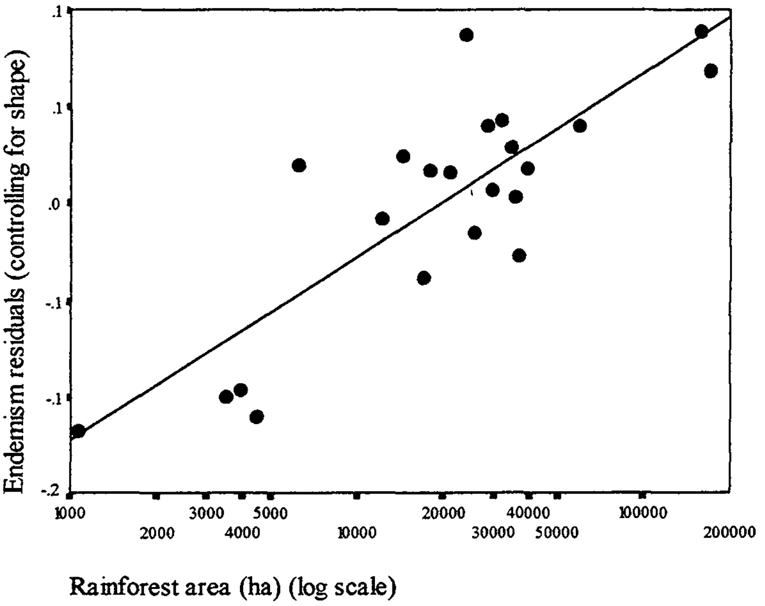
Multiple regression analyses use total species richness of rainforest terrestrial vertebrates, endemic species richness and endemism (dependent variables) and area and shape (independent variables - log transformed) within each sub-regional zone of the Australian Wet Tropics (N=22) for each taxonomic group and the groups combined.

	Total Species Richness						
	All Vertebrates (235 spp.)	Mammals (28 spp.)	Arboreal Mammals (17 spp.)	Ground Mammals (15 spp.)	Birds (112 spp.)	Reptiles (65 spp.)	Frogs (30 spp.)
AREA p	0.0002	0.0000	0.0000	0.0000	0.0099	0.0111	0.0000
partial r	0.7246	0.8329	0.7862	0.8291	0.5492	0.5422	0.7983
SHAPE p	0.7917	0.0012	0.0016	0.1170	0.8296	0.4833	0.3213
partial r	0.0616	- 0.6577	-0.6444	-0.3526	0.0500	0.1619	- 0.2276
Overall $F_{2,19}$	10.5101	26.9765	20.6600	21.5387	4.2009	4.3979	16.8596
Overall P	0.0008	0.0000	0.0000	0.0000	0.0308	0.0269	0.0001
Overall R^2	0.5252	0.7396	0.6850	0.6939	0.3066	0.3164	0.6396

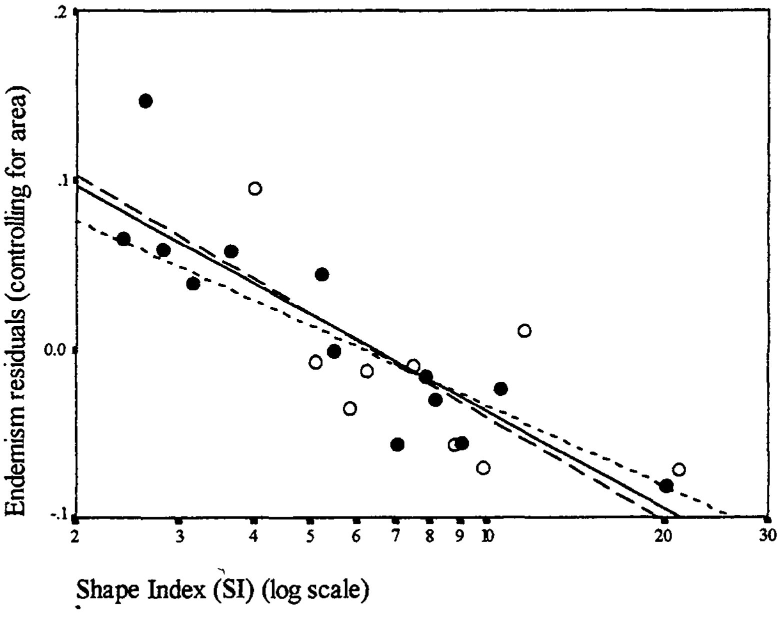
	Endemic Species Richness					
	Total Endemic Vertebrates (65 species)	Endemism (%)	Mammals (10 species)	Birds (13 spp.)	Reptiles (23 spp.)	Frogs (19 spp.)
AREA p	0.0000	0.0000	0.0011	0.0000	0.0000	0.0000
partial r	0.8973	0.8147	0.6629	0.8246	0.8392	0.8629
SHAPE p	0.0000	0.0000	0.0051	0.0000	0.0023	0.0046
partial r	- 0.8147	-0.8266	- 0.5873	- 0.8606	- 0.6285	- 0.5931
Overall $F_{2,19}$	54.0835	41.7638	11.5668	43.9405	27.1363	31.1836
Overall P	0.0000	0.0000	0.0005	0.0000	0.0000	0.0000
Overall R^2	0.8506	0.8147	0.5491	0.8222	0.7407	0.7665

Figure 3.2: The relationships between geographic endemism (proportion of endemic species in the total rainforest assemblage of each sub-region) and (A) rainforest area and (B) shape.

Analyses use a multiple regression model with endemism as the dependent variable and log rainforest area and log shape index as the independent variables (Table 3.2). The relationship between endemism and shape (B) is shown for all sub-regions (solid regression line), sub-regions with large areas (>20000 ha) of rainforest (solid circles, dashed regression line) and for sub-regions with small areas (<20000 ha) of rainforest (open circles, dotted regression line). Regressions for large and small areas are not significantly different (ANCOVA, df=1, F=0.00, p=0.985). Plots are the residual variation in endemism for each independent variable (area and shape) controlling for the other independent variable.



A. Endemism / Area (all endemics)



B. Endemism / Shape (all endemics)

Nestedness

The distribution of endemic vertebrates is highly nested. The index of nestedness, matrix temperature (T) was 15.1°. The probability that this degree of nesting is random ($T<15.1$) was calculated to be 3.8×10^{-64} which is over 20 standard deviations below the mean temperature (using 50 monte-carlo simulations) of a random matrix with the same number of species, sub-regions and species presences in the matrix (matrix fill). Therefore, the endemic vertebrates in each subregion are simply a subset of the assemblage in the most diverse subregion (Atherton Uplands). Some of the variance in the nestedness matrix is undoubtedly the result of the Thornton Uplands being a secondary centre of endemism and the northern subregions (FU, BL, TL) are probably subsets of the Thornton Uplands; however, they are all significantly nested within the Atherton subregion.

Discussion

The significant influence of rainforest area on species richness is not surprising and has been demonstrated in numerous studies (Southwood 1996); however, the strong effect of shape on vertebrate endemism is very interesting. Shape does not influence the species richness of all rainforest vertebrates, but is closely tied to the assemblage composition, specifically to the proportion of the assemblage which is endemic. Areas which have a convoluted and fragmented shape have a greater proportion of more generalist species. Rainforest area remains the main factor in the pattern of species richness, while shape is the best predictor of the level of endemism. It is important to note that in all cases it is the *combination* of rainforest area and shape which explains most of the variation in the spatial patterns of endemic species richness and proportion of endemism.

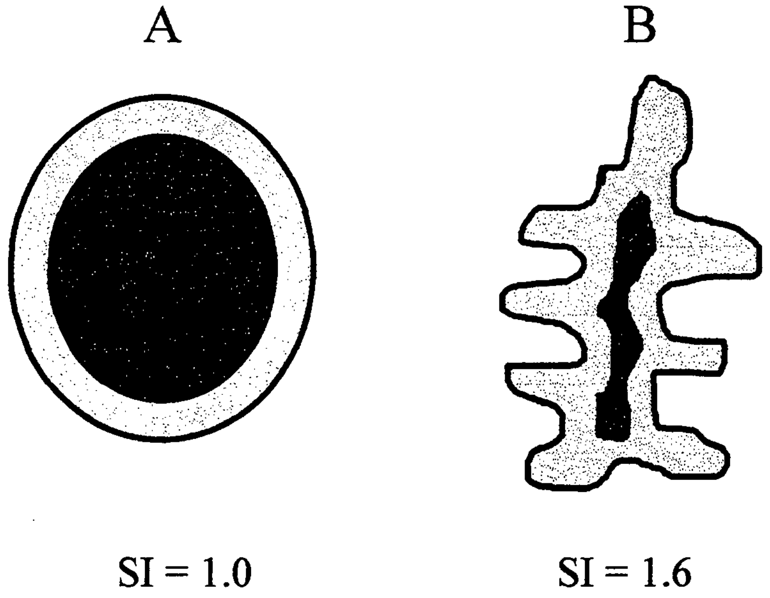
Having established that shape is related to patterns of endemism, it is important to consider what processes may be involved in producing the relationship. Habitat shape has been shown to be related to a number of processes which affect assemblage structure: dispersal between patches (Game 1980; Schonewald-Cox and Bayless 1986; Stamps *et al.* 1987); internal dispersal / recolonisation (Pickett and Thompson 1978);

extinction (Game 1980; Schonewald-Cox and Bayless 1986); habitat heterogeneity (Noss 1983); and a variety of edge effects (Noss 1983). Edge effects are caused by the interaction of two adjacent habitats and the effects penetrate into each habitat reducing the suitability of the habitat for the organisms which specialise in that habitat (Murcia 1995). The factors which contribute to an edge effect include: increased predation from external predators (Noss 1983; Andren and Angelstam 1988; Laurance *et al.* 1993); changed microclimate (Laurance 1991b; Matlack 1993); competition with species from other habitats (Noss 1983); and reduction in core area (Temple 1986; House and Moritz 1991; Laurance and Yensen 1991; Malcolm 1994). These factors are primarily landscape processes. Under current paradigms of landscape ecology, my results could be interpreted as a core area or edge effect pattern where most endemic species are core rainforest species, diversity is strongly related to habitat area, and the area of this core habitat is related to both area and shape. However, this hypothesis predicts that shape should decrease in importance with area because the proportion of edge habitat will decrease (Kupfer 1995). The fact that shape remains a significant factor, even when restricting the analyses to large areas, suggests that the importance of shape in influencing regional patterns of endemism in the Wet Tropics rainforest is not due to an edge effect.

The low diversity of regional endemics in sub-tropical mammal assemblages compared to the tropical rainforests in Australia has been previously attributed to extinctions during Pleistocene contractions in the extent of rainforest (Winter 1988). Similarly, the general paucity of bird and mammal species which are rainforest habitat-specialists in Australia's Wet Tropics has been attributed to the contraction of the tropical rainforest to small refugia (Brereton and Kikkawa 1963; Crome 1990). Therefore, the combination of rainforest shape and area may be acting as an index of the relative effect of historical rainforest contractions within each sub-region of the Wet Tropics.

Figure 3.3 shows that the extent to which a habitat patch is reduced during a contraction will be dependent on the area and the shape of the rainforest block: assuming similar initial area in shapes A and B, a contraction will have a much greater effect on the area of shape B; shape A will maintain a much larger core or refugial area and be less prone to fragmentation than shape B. Many of the rainforest sub-regions within the Wet Tropics are similar in shape to B because the climatic conditions are largely determined by altitude, meaning that the rainforest often lies along the upper slopes of a mountain range which is deeply dissected by valleys. The rainforest vertebrate fauna is considered to have once been widespread in northern Australia (Winter 1988), so therefore the current spatial pattern of endemic species richness could be the result of sub-regional extinctions during periods of contraction. The number of extinctions within a specific sub-region would be determined by the interaction of the degree of contraction, indexed by current area and shape, and the relative extinction-proneness of each species. Additional support for this interpretation is provided by the fact that, except for a small number of species with highly restricted distributions, the species present in all of the sub-regions are almost entirely a nested subset of the two main centres of endemism within the region (the Thornton Uplands for the sub-regions north of the Daintree River and the Atherton Uplands for the rest of the region). The highly significant nestedness exhibited here is indicative of a regional fauna which has been spatially structured by selective extinction (Patterson and Atmar 1986; Wright and Reeves 1992; Atmar and Patterson 1993).

Figure 3.3: Schematic diagram to illustrate the effect of shape on refugial area in two equal areas of different shape.
Dark area approximates the remaining rainforest after a contraction of the same magnitude from all edges. Shape Index (SI) is indicated for each shape.



Molecular studies have shown that refugial vicariance has had a significant influence on speciation in the Wet Tropics, although current evidence indicates that speciation did not occur in Pleistocene refugia and is mostly much older (Joseph and Moritz 1993; 1994; Moritz *et al.* 1993; Joseph *et al.* 1995). This supports the hypothesis that the effect of the Pleistocene refugia has been a sifting of species, via local extinctions, dependent on the size and fragmentation of refugia. Ongoing studies (C. Moritz, M. Cunningham and C. Schneider, pers. comm.) show that in at least one species of rainforest endemic frog, the southern populations (Spec Uplands) are genetically very similar to those from the Kirrama range to the north. In contrast, the Kirrama population is very different from those on the Atherton Uplands, despite the fact that the geographic separation is much less than that between Kirrama and the Spec Uplands. This would be consistent with the hypothesis that this species went locally extinct in the Spec Uplands and has subsequently recolonised from the more northern Kirrama population.

I suggest that current rainforest area and shape reflect the relative susceptibility of each area to historical contractions, with the implication that historical fluctuations in rainforest area have been an important process, via sub-regional extinctions of rainforest specialists (species sifting), in determining current patterns of distributions, species richness and endemism in the vertebrates of Australian tropical rainforests. Although Pleistocene refugia are an integral part of this hypothesis, it should not be confused with the refugial hypothesis which was proposed by Haffer (1969) to explain high species diversity in the tropics. Haffer (1969) suggested that the high species richness in the Amazon was the result of allopatric speciation in Pleistocene refugia. Here, I am suggesting that the Pleistocene refugia in the Australian Wet Tropics acted primarily as a species filter, rather than the species pump implied by Haffer's hypothesis.

The tendency to examine total species richness only is a problem in many studies, and an examination of the species richness within meaningful ecological sub-sets (functional groups) of the assemblage may be more informative. The importance of considering sub-sets within the assemblage is highlighted by the results of this study where the shape index is not correlated with total species richness, but is negatively correlated with endemic species richness and positively correlated with non-endemic species richness.

The importance of shape to endemic species diversity has serious implications for long-term management and conservation, and the much-debated design principles for nature reserves. With regard to the argument over the selection of a single large or several small reserves (SLOSS, Simberloff and Abele 1982) for the long-term preservation of endemic species, my results would favour the selection of large, round reserves rather than a number of small reserves. There would be a higher risk of extinction of rainforest specialists in the smaller reserves, especially those with a more fragmented shape, especially if the rainforest contracted due to global warming. I disagree with the conclusions of Blouin and Connor (1985) who suggested that "shape is not of major concern in the design of nature reserves", and stress that it is the shape of the habitat, not of the reserve, which is important. The hypothesis presented here suggests that the extant rainforest vertebrates in the Australian Wet Tropics are relatively resilient since they are the survivors of quite severe historical fluctuations in rainforest area. Assuming that the protection provided by World Heritage listing remains in place, the prospects for the conservation of the unique vertebrate biodiversity of the Australian Wet Tropics are relatively positive when compared to most other regions of the world.

Chapter 4: Regional Patterns of Mammal Biodiversity[4]

Introduction

Chapters 2 and 3 have discussed the patterns of species richness of all rainforest vertebrates, including mammals. This chapter examines the spatial patterns of species richness and assemblage structure in the rainforest mammals of the Wet Tropics biogeographic region in more detail, and relates these patterns to particular species and guilds within the assemblage. The effects of altitude and history have been previously cited as the most important determinants of spatial patterns of mammalian assemblage structure (Winter 1988) and these determinants are re-examined here with a more complete distributional database and using quantitative multivariate techniques. Determining the species or ecological groups responsible for patterns of assemblage structure can be combined with knowledge on the autecology of the species or guilds involved to provide more informed and specific hypotheses on the determinants of the observed patterns. Mammals were identified in Chapter 3 as possibly being more strongly affected by historical rainforest contractions than the other vertebrate groups: the possible reasons for this difference will be examined in this chapter. Patterns on the local scale are dealt with in Chapter 5.

I examine patterns of distribution and diversity of rainforest mammals over 22 subregions of the Wet Tropics, using pattern analysis and multiple regression to indicate major correlates with diversity. Patterns of mammalian diversity are shown to be related to the areographic shape of the rainforest blocks, altitude, spatial heterogeneity of structural vegetation types and rainfall, consistency of rainfall throughout the year and rainforest area. Regression analyses indicate that area and shape are the most important variables, and it is hypothesised that these two variables index the relative effects of historical rainforest contractions that resulted in localised extinctions of the more susceptible rainforest mammals.

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[4] This chapter has been published in:
Williams S.E. 1997. Patterns of mammalian species richness in the Australian tropical rainforests: are extinctions during historical contractions of the rainforest the primary determinant of current patterns in biodiversity ? *Wildlife Research, in press.*

Methods

The 22 subregions and faunal data described in Chapter 2 and Appendices 1-4 were used as the basis for the regional scale analyses of mammal assemblages conducted in this chapter. Information on bats was patchy and was insufficient to include in the analyses, so bats are excluded from further consideration. All environmental variables used in the analyses are described in chapters 2 and 3.

Analytical methods

Assemblage similarity of each of the subregions was examined using a combination of ordination (Detrended Correspondence Analysis - DCA) and classification analysis (Two-Way Indicator Species Analysis - TWINSPAN) on the species list for each subregion because of the suitability of these methods for presence/absence data. Multiple regression (backward removal) was used to select environmental variables which explained the most variance in the patterns of species richness in each subregion. Multi-Response Permutation Procedures (MRPP) (Zimmerman *et al.* 1985) are analogous to a multivariate analysis-of-variance and were used to test for significant differences in assemblage composition. Area and shape (SI) were $\log_{10}$ transformed in all analyses to normalize their distributions.

The spatial patterns of mammal biodiversity are examined using two complementary approaches. The first uses pattern analysis to group subregions based on the similarity of the mammal assemblages (*Assemblage analysis*). The environmental characteristics of those subregions with similar assemblages can be compared and contrasted with the mean species richness of the assemblage to indicate which environmental parameter may be important in determining patterns of mammal diversity. The second analysis uses the species richness of each subregion as the dependent variable and environmental variables as independent variables in multiple regression analyses (*Subregion analysis*).

Guild analyses were conducted using the guilds described by Braithwaite *et al.* (1985) using multivariate classification techniques to define guilds for tropical Australian mammals. A description of the guilds used are contained in Appendix 9.

Results

Overall mammal diversity (all habitats)

Diversity is highest in the central uplands which are centred on the Atherton Tablelands where there are 26 species of non-volant mammals (Table 3.1). Species richness tends to decrease to the north and south, and with decreasing altitude. The overall species composition of upland areas is also significantly different from lowland areas (MRPP statistic = -2.53, p = 0.02). There are eight species recorded exclusively from lowland subregions and 12 species which are found exclusively in the uplands (Chapter 2).

There is a strong correlation between the size of each subregion and the species richness of mammals (Table 4.1). Other factors which correlate with the total mammal diversity within a subregion are the diversity of rainfall regimes, annual rainfall and the latitudinal range of the subregion (Table 4.1). These patterns are examined in detail for the rainforest assemblages.

Table 4.1: Correlations between environmental variables and mammal species richness.
(* = significant at <0.05 level, ** < 0.01, *** <0.001, (-) indicates negative relationship, N/A - not applicable).

Variable	Total Species Richness	Rainforest Species Richness	Endemic Species Richness
Total Area	*	N/A	
Rainforest Area	N/A	***	**
Shape Index (SI)	N/A	(-)**	(-)**
Rainfall regime diversity	**	**	*
Annual Rainfall Index	(-)*		
Dry season rainfall		**	*
Rainforest Vegetation Types		*	*
Latitudinal range	*		
Area between 0-40m		(-)*	
Area between 40-200m		(-)*	
Area between 200-600m	*	*	*
Area between 600-1000m	*	**	*
Area above 1000m		***	***

Mammal diversity in rainforest

Assemblage analysis

Restricting the pattern analyses (DCA, TWINSPAN) to rainforest species (Figure 4.1, Table 4.1) changes the general patterns described above. The analysis of rainforest assemblages suggests a far northern group (Group 1 (Figures 4.2a & 4.2b) - FU,BL,TU,TL) characterised by *Dendrolagus bennetianus* and *Pseudocheirus cinereus*, and a central upland group (Group 3 - LE,LU,BK,AU,KU) characterised by *Hemibelideus lemuroides, Pseudocheirus herbertensis, Antechinus godmani* and *Sminthopsis leucopus*. Group 2 (WU and CU), although more closely related to the far northern group (Figure 4.2a), is actually intermediate between the far northern and central upland groups (Figure 4.2b). There are two groups of subregions with a relatively depauperate rainforest mammal fauna, a group dominated by non-rainforest habitat (Group 5 - CL,EU,TV) characterised by the absence of most rainforest obligates, and a mixed (mostly lowland) group with a reasonably strong rainforest influence (Group 4 - ML,BM,IL,MF,CC,MT,SU,HU) characterised by the presence of the more generalist rainforest species. The two analytical methods differ in the affinity of the Lee Uplands (LE) with DCA suggesting this subregion has a Group 4 mammal assemblage while TWINSPAN places it in Group 3 (cf. Figures 4.2a&b). The two most diverse rainforest mammal assemblages occur in groups 2 & 3. The subregions in these groups are characterised by large areas of rainforest, high annual rainfall, more rain during the dry season and a greater diversity of rainfall regimes (Table 4.2).

Subregion analysis

Mammal species richness within rainforest in each subregion is correlated with ten of the factors examined (Table 4.1). Species richness decreases with increases in the shape index (SI) (that is, diversity is lower in those blocks of rainforest which have a more convoluted or fragmented shape) and increases with area at higher altitudes (especially above 1000m), diversity of rainfall regimes, rainfall consistency in the dry season and the diversity of rainforest vegetation types.

Table 4.2: Characteristics of each group of subregions with a similar rainforest mammal assemblage.

Assemblages defined by TWINSPAN classification of mammal assemblages (Figure 4.2b). Each parameter is tested by 1-way AOV to determine if the parameter is significantly different between groups of subregions with different mammal assemblages (P value from either parametric 1-way AOV (continuous variables - mean values given in table) or non-parametric Kruskal-Wallis 1-way AOV (rainfall variables are ranked on a 1-7 scale - median values given in table).

	Mammal Assemblage					
Variable	1	2	3	4	5	P
Rainforest Species Richness	15.8	21.5	22.8	14.8	9.7	0.0000
Endemic Species Richness	2.8	6.0	6.4	2.3	0.7	0.0000
Rainforest Area (ha x10000)	2.4	3.3	6.3	3.5	0.4	NS
Shape Index (SI)	7.5	3.0	5.3	10.1	8.2	NS
Area above 1000m (ha)	297	24310	7154	3	0	0.0007
Rainforest Vegetation Types	7.8	7.5	6.2	5.1	4.3	0.01
Vegetation Diversity Index	0.6	0.7	0.8	0.7	0.2	0.02
Latitude at centre of Subregion	15.9	16.3	17.8	17.7	18.0	0.07
Annual Rainfall Index	5.5	3.5	3	3.5	2	0.08
Rainfall regime diversity	1.5	4	3	3	1	0.07
Dry season rainfall	3.5	3.5	3	2	1	0.06

Multiple regression suggests that the most important factors explaining the variation in the species richness of rainforest mammal assemblages are the area of rainforest, and the shape of the rainforest block (SI). Seventy-four percent of the variation in rainforest mammal species richness can be explained by combining these two factors ($p<0.0001$). The relationships between mammal species richness and each of these two variables (rainforest area and shape), independent of the other, are shown by the plots of the partial residuals (Figures 4.3 a & b). The Lamb Uplands is the most significant outlier in this relationship (> 2 standard deviations) with 25 species of rainforest mammals, six more than predicted by the regression. Total residuals still show a linear trend with the diversity of rainforest mammals ($r = 0.46$, $p=0.031$) suggesting that there is one or more important variables which have not been included in the multiple regression model.

Figure 4.1: Species richness of rainforest mammals in each subregion. See Figure 2.1 for subregion names and codes.

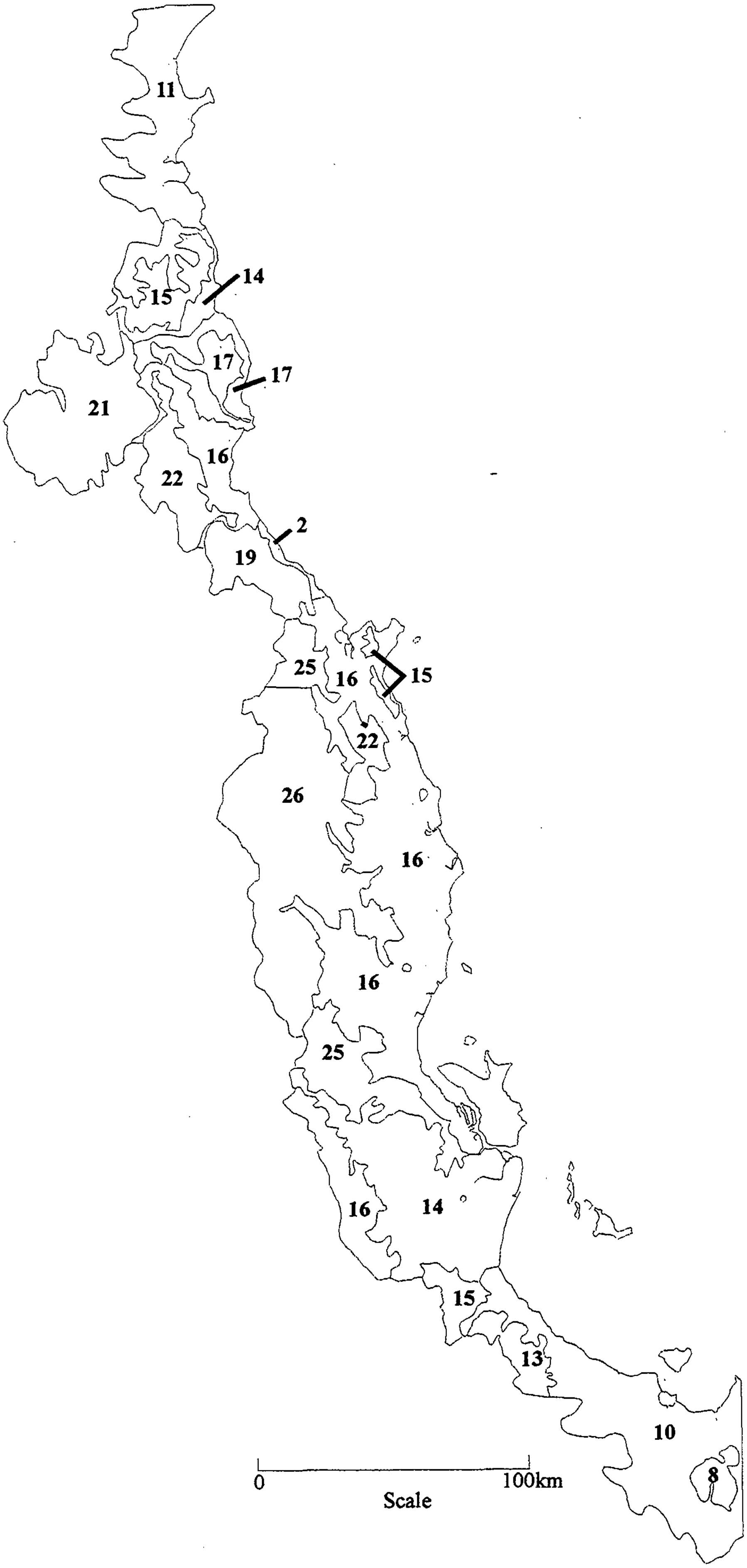


Figure 4.2a: TWINSPAN classification of subregions by rainforest mammal assemblages (see Figure 2.1 for key to subregion codes).

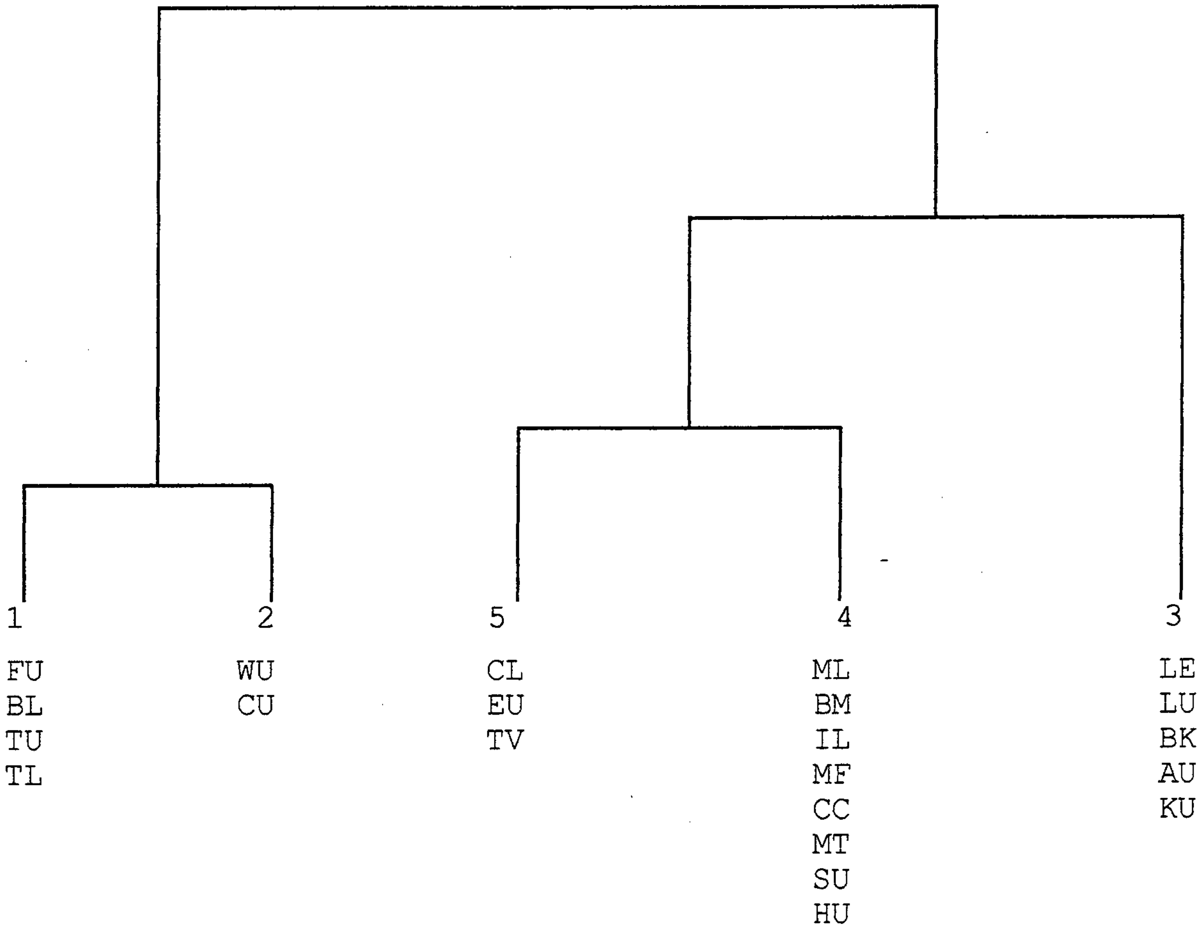


Figure 4.2b: DCA ordination of subregions by rainforest mammal assemblages. Axes 1 & 2. (refer to Figure 2.1 for key to subregion codes). Assemblage groups 1-5 are those suggested by TWINSPAN (Figure 4.2a), except that LE was placed with group 3 in the TWINSPAN analysis rather than in group 4 as shown here.

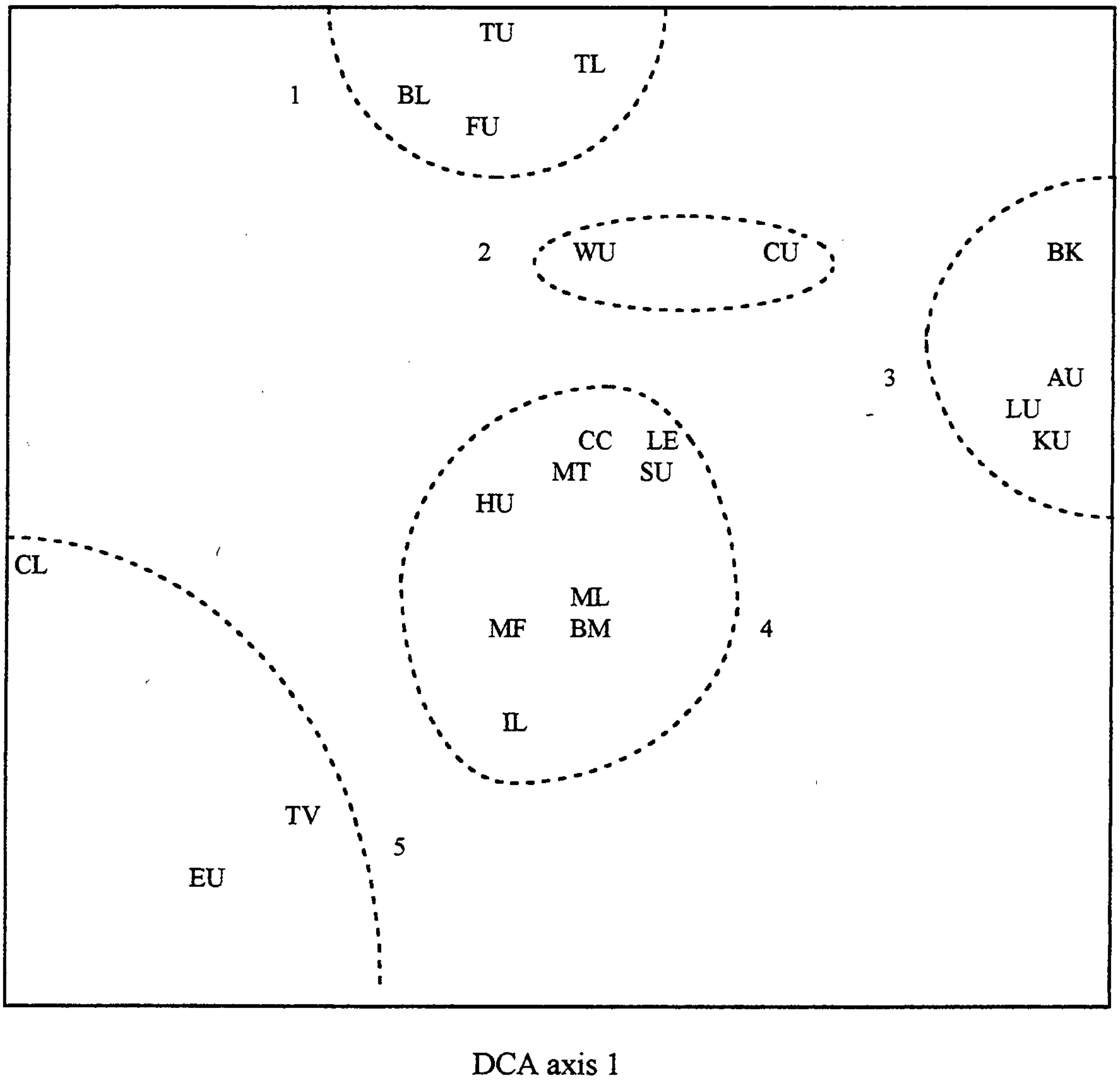


Figure 4.3a: Relationship between the species richness of rainforest mammals and rainforest area, independent of rainforest shape
(partial residual plot, refer to Table 3.2 - partial r = 0.8329, p = 0.0000).

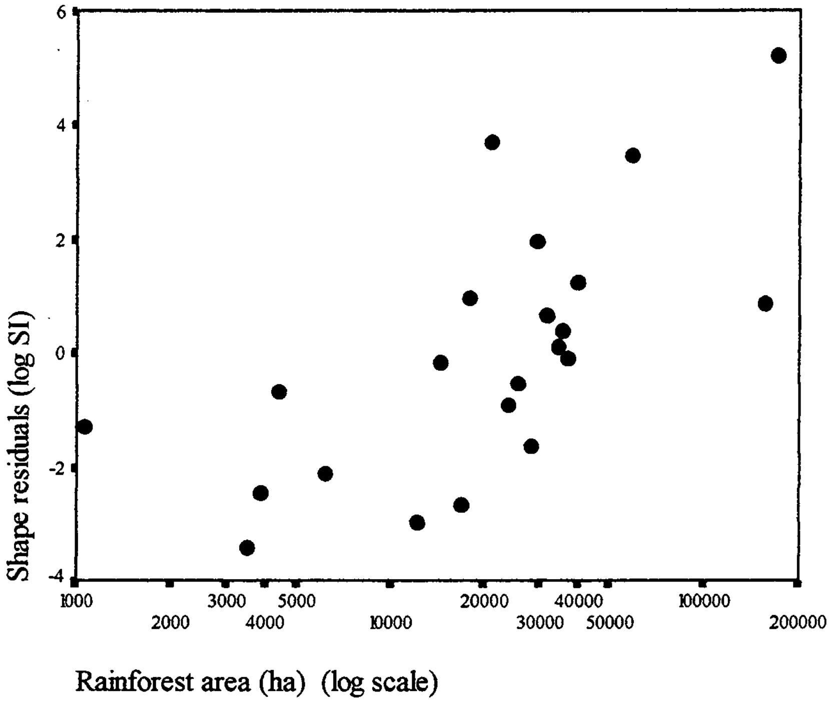
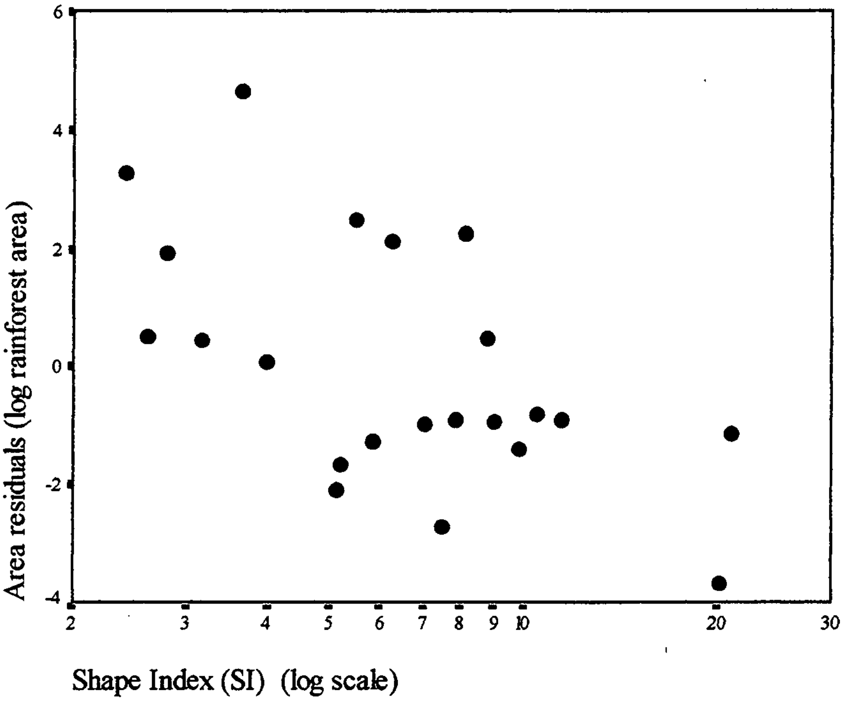


Figure 4.3b: Relationship between rainforest mammal species richness and rainforest shape, independent of rainforest area
(partial residual plot, refer to Table 3.2 - partial r = -0.6577, p = 0.0012).



Since most measures of habitat heterogeneity will almost always increase with area, the use of area as a variable in a multiple regression could be expected to swamp the explanatory power of any single habitat variable. The exclusion of area from the multiple regression analysis tests this hypothesis. When area was excluded from the model, 78% of the variability in the patterns of species richness of rainforest mammals was explained by three variables: shape, spatial rainfall diversity and diversity of rainforest vegetation types ($F = 19.53$, $p<0.0001$, $r^2 = 0.78$). Therefore, the combination of shape and spatial heterogeneity of rainfall and vegetation explains 4% more of the variation in species richness than area and shape alone.

Species richness of endemic rainforest mammals

The subregions with the highest number of endemic mammal species are the Atherton, Lamb, Kirrama, Bellenden-Ker/Bartle Frere, Carbine and Windsor Uplands (Table 4.1). There were significantly more endemic species in upland subregions (mean = 3.9 species) than lowland subregions (mean = 1.6 species) ($df=1$,$F=4.55$,$p=0.04$).

There are positive correlations between the number of endemic species and the area of rainforest, the shape of the rainforest block, diversity of rainfall regimes, the amount of rainfall during the dry season, the diversity of rainforest vegetation type and area at higher altitude (especially above 1000m) (Table 4.1). There is a strong negative correlation between the diversity of endemic mammals and the shape index (SI). Multiple regression analysis suggests that the most important variables are area and shape, with 55% of the variance being explained by these variables. Outlier analysis of the residuals suggests that the Lamb Uplands (LU) has significantly more species of endemic mammals than is explained by the regression (eight species compared to a predicted species richness of 4.5 species). Total residuals still show a linear trend with the diversity of endemic mammals ($r = 0.60$, $p = 0.002$) indicating that there is probably another important variable(s) which has not been included in the multiple regression model. Endemism has been considered in more detail in Chapter 3.

Guild structure

I closely examined assemblage structure in order to determine which component of the assemblage is responsible for changes in the patterns of diversity. Do areas of higher diversity have a greater number of niches or functional guilds, and/or do they have more species within each guild? Are the number of guilds and number of species per guild different in the major assemblage types (Groups 1-5) described in the pattern analyses presented above (Table 4.2; Figures 4.2 a & b)?

Braithwaite *et al.* (1985) used numerical techniques to define 11 mammal guilds in the Australian tropics on the basis of body size, diet, daily activity patterns, feeding microhabitats and shelter requirements. I used this classification to examine the guild structure of the rainforest assemblage. Comparison of the number of guilds in each of the five assemblages indicates that only those subregions with very little rainforest (Group 5) have a significantly different number of guilds of rainforest mammals from the other guilds (Figure 4.4a). There was no significant difference in the number of guilds present in Groups 1-4. However, there are significant differences in the mean number of species per guild in the different assemblages (Figure 4.4b). The subregions in the central uplands (Group 3) and the Windsor/Carbine Uplands (Group 2) had a significantly higher within-guild diversity than the other assemblages.

Figure 4.5 shows the relationships between the species richness and the number of guilds (Figure 4.5a) and species per guild (Figure 4.5b), using individual subregions. A larger proportion of the variability in species richness is explained by the mean number of species per guild (88%) (Figure 4.5b) compared to that explained by the number of guilds (70%) (Figure 4.5a). This is similar to the results discussed above that were obtained by comparing mean species richness of the assemblage groups (Figures 4.4a & b). Therefore, analyses of the mammal guild structure using both assemblage level and subregion level approaches indicate that both the number of guilds and the mean number of species per guild are important in explaining patterns in mammalian species richness. However, it is the number of species per guild which has more influence on the overall patterns of species richness.

Figure 4.4a: Mean number of mammal guilds in each of the five assemblages.
Assemblages were defined by the similarity analyses (Figures 4.2 a & b). Error bars are 95% confidence intervals.

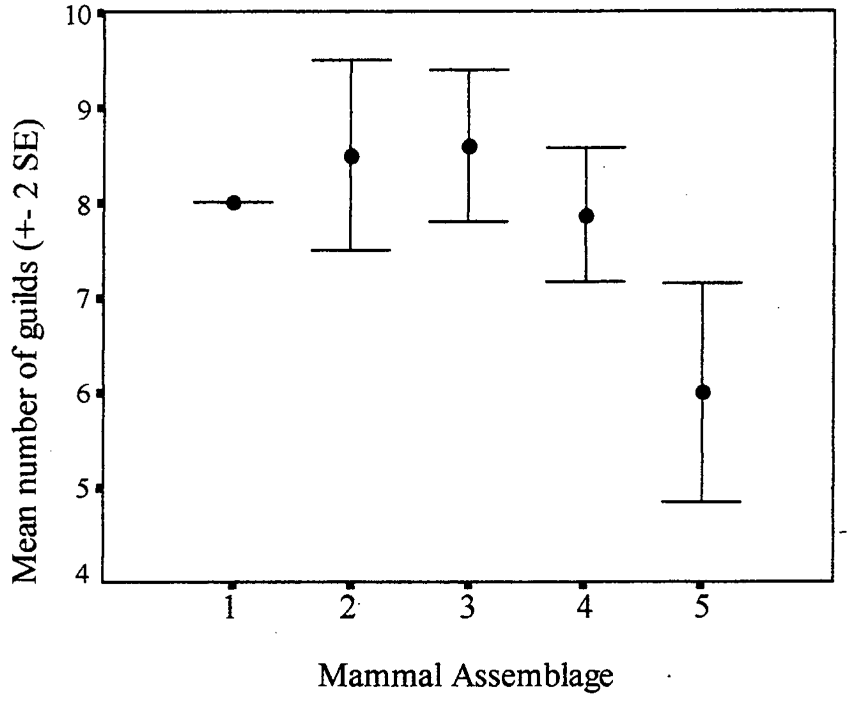


Figure 4.4b: Mean number of species per guild in each of the five mammal assemblages.
Assembalges were defined by the similarity analyses (Figures 4.2 a & b). Error bars are 95% confidence intervals.

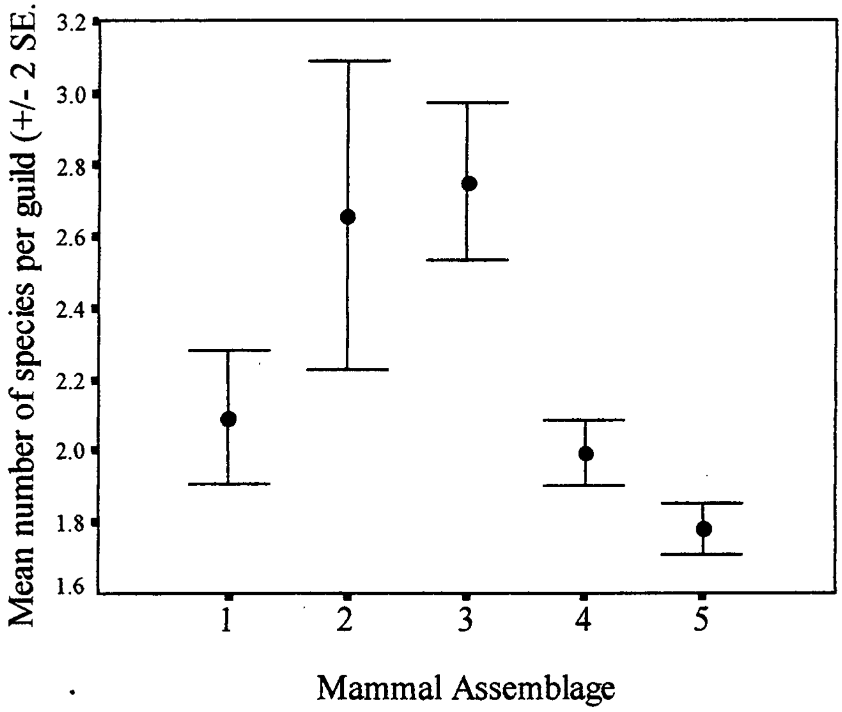


Figure 4.5a: Relationship between the species richness of mammals and the number of guilds in each subregion.

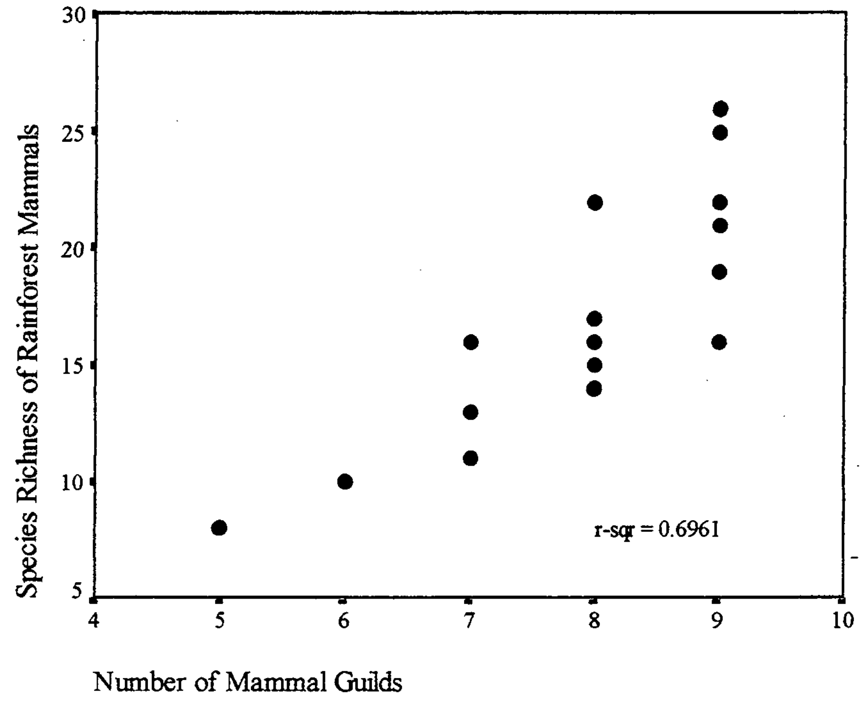
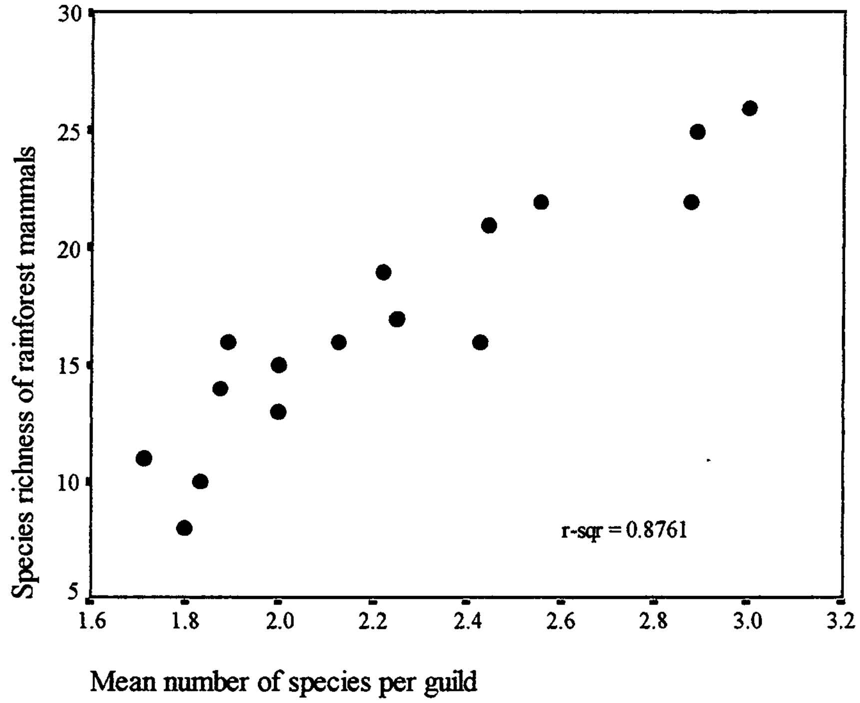


Figure 4.5b: Relationship between the species richness of mammals and the mean number of species per guild in each subregion.



Which guilds have the most influence on these patterns ?

Regression analyses indicate that 96% of the variation in total species richness can be explained by variation in the species richness within three guilds. Species richness in the large, arboreal folivore/omnivore guild (Guild 7 in Braithwaite *et al.* 1985) is the most important, followed by the small, scansorial insectivores (Guild 3) and the small, scansorial folivore/granivore guild (Guild 8) with 73%, 18% and 5% of the variation in total species richness being explained, respectively, by variation in species richness within these three guilds. All of the species in these guilds are strongly or completely arboreal.

Nestedness of spatial distribution patterns

The spatial distribution patterns of rainforest mammals within the 22 subregions of the Wet Tropics exhibited a structure which consisted of highly nested subsets (see Chapter 3 for explanation of nestedness). The index of nestedness, matrix temperature (T), was 15.5° for rainforest mammals. The probability that this degree of nesting was random ($T<15.5°$) was calculated to be 2.8×10^{-35} which is over 13 standard deviations below the mean temperature (using 50 monte-carlo simulations) of a random matrix with the same number of species, sub-regions and species presences in the matrix (matrix fill). Rainforest specialists showed an even higher degree of nesting ($T = 12.1°$, $p\,(T<12.1°) = 2.9\times10^{-18}$), although endemic species showed a lower degree of nesting ($T=22.5°$, $p\,(T<22.5) = 6.2\times10^{-4}$).

Discussion

Habitat heterogeneity is obviously important in promoting mammal species richness within the Wet Tropics, both in the broad number of habitats within a subregion (rainforest, wet sclerophyll etc) and in the finer-scale structural vegetation types within rainforest. The combination of habitat types within an area has a large effect on both the species richness and on the type of assemblage present. In almost all cases species richness increases with the area of the subregion; however, since each subregion is a mixture of habitat types and considering that it is only appropriate to consider species/area relationships within a habitat type, the remainder of this discussion will be limited to patterns of species richness within the rainforest only.

Rainforest mammals

The assemblages defined in the pattern analyses based on the species composition of the rainforest mammals in each subregion were very similar to the patterns described by Winter *et al.* (1984), except that they described the distribution patterns of endemic species only. The pattern consists of two distinct subregions (northern - group 1 and central uplands -group 3), with the Windsor/ Carbine Uplands (Group 2) forming an overlap zone (Figure 4.2b). The lowlands and southern uplands form a depauperate subset of these assemblages. Comparison of the mean environmental attributes between each of these groups of subregions (Table 4.3) shows that altitude, the diversity of structural types of rainforest, rainfall patterns and latitude are correlated with the species composition and species richness in each assemblage.

Regression analysis using each subregion as a separate data point reveals very similar correlations (area of rainforest, rainfall diversity and continuity in the dry season and the diversity of rainforest structural types) with one important addition. The species richness of rainforest mammals and the number of endemic species are also highly correlated with the shape of the rainforest block (Table 4.2). Chapter 3 described the strong relationship between the species richness of endemic vertebrates and levels of endemism with rainforest shape in the Wet Tropics, but showed that mammals are the only group where the species richness of all rainforest species is also related to rainforest shape, unlike the other terrestrial vertebrate groups for which the number of endemics was related to shape but total species richness was not (Table 3.2). The hypothesis presented in Chapter 3 to explain the importance of shape is that the combination of current area and shape is an index of the relative effect that an historical contraction would have had on each block of rainforest. This suggests that historical processes (dispersal, extinction, vicariance) during contraction and expansion of rainforest have been important influences on vertebrate patterns of diversity. The remainder of this discussion will examine this question in more detail for mammals and suggest an hypothesis which may explain why patterns of mammalian diversity differ from those of the other vertebrate groups (Chapter 3).

The analyses of guilds and assemblage structure in this chapter have shown that the guilds which were the most significant in determining patterns in mammalian species richness in the Wet Tropics include the same species that Laurance (1991a; 1994) showed to be the most prone to extinction due to an inability to cross the between-patch matrix in a fragmented area of rainforest. Mammals, in general, are considered to be more extinction prone than the other vertebrate groups due to their larger body size, larger area requirements and higher energy requirements.

These results could be interpreted as support for the hypothesis that habitat diversity is the major determinant of mammal species richness. However, this does not explain the importance of shape. In the analysis which excluded area, shape was the single most important variable. In landscape ecology the importance of shape is usually interpreted as an index of edge effects. This is not the case on a regional scale in the Wet Tropics, as demonstrated in Chapter 3, since theories of landscape ecology would predict that, as habitat area increases, the importance of shape should decrease as the proportion of edge-affected habitat becomes insignificant. In fact, I have shown that in the Wet Tropics that shape was of slightly greater significance in the larger subregions (Chapter 3). Additionally, rainforest area does not explain the absence of species in subregions where there are large areas of suitable habitat. These patterns do not fit with a core-area/edge-effects hypothesis since all of the core rainforest mammals are present right to the natural edge of the rainforest in the subregions where they occur, albeit at lower densities (Chapter 5). If core species were present in these subregions (large area but high shape index due to a highly convoluted or naturally fragmented rainforest area) at a lower density than similar-sized areas with a rounder shape, and the importance of shape decreased in the larger rainforest blocks, then a simple “area=habitat diversity combined with edge effects” explanation might apply.

Winter (1988) suggested that extinctions during rainforest contractions may be the reason for the low numbers of rainforest specialists in the rainforests of south-eastern Australia. The hypothesis I suggest here is that localised extinction may also be the major process behind patterns in mammalian species richness in rainforest within the Wet Tropics. I suggest that in those subregions where the rainforest is smaller and has a more convoluted or fragmented shape (high Shape Index), there would have been many local extinctions of the more extinction-prone mammals (Guilds 7,8 and 3) during historical contractions of the rainforest. Extinctions would depend on the degree of habitat specialisation and the minimum viable area for the survival of a population of each species. As the rainforest expanded again there would no doubt have been some areas where recolonisation occurred, dependent on the width and harshness of habitats separating areas of rainforest, and on dispersal ability. It is this ability to cross unsuitable habitat which Laurance (1991a) found to be the best predictor of extinction proneness in rainforest mammals. In a study of the boreal mammals of the Great Basin (USA), Brown (1971) concluded that post-pleistocene extinction has been the most important process determining current patterns of species richness: a result very similar to this study.

The results of this study suggest that the species-area relationship is due to a habitat diversity / area relationship and is not an effect of area *per se*. Therefore, the most likely process involved in extinctions during rainforest contractions would be the reduction in the diversity of rainforest habitats during area bottlenecks. That is, there was a succession of events (contractions and expansions) which sifted out those species which were most extinction prone because of their specialised habitat requirements, often coupled with reduced recolonisation due to poor dispersal ability across non-rainforest habitats.

The significant nesting of subregional mammal assemblages (all rainforest species, rainforest specialists and endemic species), implies that regional patterns of mammal assemblage structure have been significantly influenced by differential extinctions and/or immigrations (Lomolino 1996). The evidence discussed above gives considerable support to differential extinctions being the primary process in determining the mammal assemblage present in each subregion of the Wet Tropics. This is not to say that immigration has not been significant; indeed, the greater similarity of mammal assemblages in subregions which are geographically close (Figure 4.2a) suggests the influence of immigration. However, this does not conflict with the hypothesis that extinction has been the most important process: it would be expected that species which survived a rainforest contraction event in any given subregion would be most likely to recolonise nearby subregions with the expansion of rainforest, resulting in the similarity of assemblages in adjacent subregions.

It is surprising that the nestedness of rainforest mammals (T=15.5) and rainforest specialists (T=12.1) is higher than that of endemic species (T=22.5). Intuitively, I would have expected the endemic species, being the most restricted, to exhibit the highest level of nesting. However, at this fine scale (10 species) it seems that the patterns are less general and more idiosyncratic. Four of the ten endemic mammals are spatially segregated sister species (*Pseudochirulus cinereus/herbertensis and Dendrolagus lumholtzi/bennetianus*) with one of each pair present in the two centres of endemism (Northern Uplands and Southern Uplands - see Figure 4.2a). *Hemibelideus lemuroides* has quite separate and genetically different populations also, with a much higher proportion of white individuals in the northern populations (Winter *et al.* 1984). This suggests that vicariant speciation may have had a very significant effect on the distribution patterns of endemic mammals. Another endemic species *Antechinus godmani* appears to be restricted to the central uplands. Clearly the endemic mammals do not really represent a nested subset of the most diverse sub-region, the Atherton Uplands, despite the significant degree of nesting. Rather, the endemic mammals are nested subregionally both within the northern subregions centred on the Thornton Uplands and within the central uplands centred on the Atherton Tableland. One of the assumptions of the theory of nested subsets (Patterson & Atmar 1986; Atmar & Patterson 1993; Lomolino 1996) is that species were originally distributed throughout the region; this assumption is probably significantly violated in the case of endemic mammals. The effect of the two centres of endemism causes a breakdown in the overall pattern of regional nestedness and the higher levels of disorder (higher T) in the nestedness matrix. Therefore, speciation in these two long-isolated areas has had a greater effect on the patterns of species richness of endemic mammals than it has on the overall pattern of rainforest mammals where differential extinction has probably been the primary process.

Examination of biogeographic patterns in genetic similarity (phylogeographic structuring) is the only method available to determine whether the presence of a species is the result of recolonisation or *in situ* survival. It would be particularly interesting to determine the phylogeographic relationships between populations on the Lamb Range (LU) and the surrounding subregions to try to determine if the seemingly high diversity is a result of recolonisation from the Atherton Uplands or whether these species have survived *in situ.* The higher than expected diversity in the Lamb Range may be due to it being part of the Atherton Tableland and, if so, the separation in the analysis is unwarranted, although it is probable that the Lamb Range was historically isolated from the Atherton rainforest during the more severe contractions.

It is possibe that altitude has an effect on mammal species richness independent of its effect on historical refugia. For example, higher temperatures at lower altitudes may be imposing a physiological limit on the distribution of some of the mammals (Ridpath 1985; Lagos *et al.* 1995).

The results in Table 3.2 suggest that historical rainforest contractions have had an effect on the endemic birds, reptiles and frogs similar to that on all rainforest mammals (not just the endemics). The implication is that all of the rainforest mammals have been strongly influenced by historical contractions (localised extinctions) whereas only the more specialised sub-sets of the other vertebrate groups have been similarly affected. I would predict that the rainforest-specialists subset of these taxonomic groups (birds, frogs, reptiles) would exhibit the highest degree of extinction proneness in their reaction to fragmentation. Another prediction stemming from this hypothesis is that the species richness of groups with a greater ability to survive contractions *in situ* (less specialised or smaller area requirements) would not exhibit this shape-area relationship.

These patterns are not the result of anthropogenic clearing over the last 200 years. This was tested by removing from the analysis those subregions which have significant areas of cleared rainforest. All of the patterns discussed here were robust with similar levels of statistical significance when only pristine areas were included in the analysis.

My hypothesis suggests subregional extinctions during historical contractions to be the primary determinant of geographic patterns of mammalian species richness within the Australian Wet Tropics. Although refugia are central to my hypothesis of differential localised extinctions, the processes being inferred are quite different from the refugial hypothesis for high diversity in the tropics (Haffer 1969). Haffer (1969) suggested that high diversity in the Amazon was the result of fragmentation into refugia followed by allopatric speciation. This study was not an attempt to explain high levels of diversity in the Tropics *per se*.

Summary of hypothesis

I suggest that the geographic patterns in the species richness of rainforest mammals within the Australian Wet Tropics biogeographic region are largely the result of historical extinctions in the predominantly arboreal mammal guilds. These extinctions have resulted from rainforest contractions due to climatic fluctuations, leading to historical bottlenecks in rainforest area and, therefore, habitat heterogeneity. The relative degree of sifting which has occurred in each block of rainforest is correlated with the current area and shape of the rainforest block, which together index the relative reduction in rainforest area, and thereby heterogeneity, due to a contraction. Extinction of particular species has occurred with the loss of a necessary microhabitat in the remaining refugia or by reduction to a size where a viable population was not possible, and where subsequent recolonisation was prevented by a poor ability to disperse across unsuitable habitats.

Unfortunately, experimental testing of this hypothesis is not possible, and supporting evidence is largely inferential and complicated. The selection of the above hypothesis as the best explanation of the observed patterns is based on the following points:

1. Important correlated environmental factors are: rainforest area; rainforest shape; habitat diversity; altitude and rainfall.
2. Low diversity areas represent nested subsets of the higher diversity areas.
3. High diversity subregions are mostly the result of more species within guilds.
4. Most of the variance in spatial patterns of species richness can be attributed to three specific guilds (78% to just one guild).
5. It is these same guilds which are the most extinction-prone.
6. There are several arguments against the importance of shape being an edge effect.
7. The combination of shape and area would be strongly correlated with refugial area during a contraction.
8. The data show a strong effect of habitat diversity, which is related to area. Historical bottlenecks in area, and therefore habitat diversity, present a likely process for localised extinction either due to minimum viable population size or loss of a necessary microhabitat.
9. It is widely accepted in the literature that the rainforest in northern Queensland underwent a series of historical contractions and expansions during the Pleistocene (Nix & Switzer 1991; Hopkins *et al.* 1993; 1996).
10. The hypothesis is supported by evidence from phylogeographic patterns of several vertebrate species (Moritz *et al.* 1993; Joseph and Moritz 1993; Joseph and Moritz 1994; Moritz 1995; M. Cunningham unpublished data), including evidence for past localised extinctions and recolonisations.

Chapter 5: Spatial patterns in mammal assemblage structure at the local / landscape scale

Introduction

Local species diversity is a product of the dynamic balance between local ecological interactions and the available species pool. Previous chapters have examined the patterns of mammalian diversity at the regional scale; however, analyses at the regional scale can only infer processes responsible for the sub-regional or landscape species pool. Schluter and Ricklefs (1993) point out that there are at least seven types of process which contribute to patterns of diversity, three of which operate at the spatial scale of landscapes or smaller (local), namely:

1. local ecological interactions;
2. the within-habitat dynamics of individuals and populations (movements and spatial variability); and
3. the interaction between habitats.

This chapter examines patterns of mammal assemblage structure at these smaller spatial scales in order to explore the influences of local scale patterns and processes.

Most empirical studies of the determinants of faunal diversity have been at the local scale, probably due to the logistic constraints associated with larger spatial scales and the pervasiveness of competition and niche theory in explanations of the determinants of species richness within a community. Local diversity must be set within the framework of the surrounding region as the available species pool for any locality is limited by the regional species pool. Within the limitations set by the regional species pool, local diversity is determined by the "habitat capacity" (Southwood 1996) and the influence of adjoining habitats via mass effects, rescue effects, and source-sink dynamics (Shmida & Wilson 1985; Schluter & Ricklefs 1993). "Habitat capacity", which is usually related to habitat area, is determined by the combination of habitat heterogeneity and productivity (Southwood 1996). There is general agreement in the literature that habitat heterogeneity is positively linked to diversity; however, there is no general rule for the relationship between productivity and diversity. Recent evidence suggests that there is a humped relationship, with diversity being highest at intermediate levels of productivity (Owen 1988; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993) and that in some cases it may be diversity which controls productivity, rather than the reverse (Tilman 1996; Tilman *et al.* 1996).

Habitat heterogeneity has an almost infinite number of dimensions, although all dimensions affect either the "architectural complexity" or the spatial heterogeneity of the habitat (Southwood 1996). Vertical complexity and spatial heterogeneity both increase the number of available niches and, usually, the diversity of the resident fauna (Southwood 1996). The work of MacArthur on birds (MacArthur & MacArthur 1961; MacArthur 1964) sparked off a spate of studies examining the effects of vegetation structure on bird assemblages (e.g. Karr & Roth 1971; Tomoff 1974; Roth 1976; Rotenberry & Wiens 1980; James & Wamer 1982; Arnold 1988). Similarly, there has been considerable research on the relationships between habitat structure and mammal assemblage structure (M'Closkey 1976; Barnett *et al.* 1978; Braithwaite & Gullan 1978; Dueser & Shugart 1978; Gullan & Robinson 1980; Fox 1981; Hockings 1981; Fox 1982; August 1983; Friend & Taylor 1985; Schwarzkopf & Rylands 1989; Fox 1990; Williams 1990; Shenbrot *et al.* 1994; Dunstan & Fox 1996; Williams & Marsh 1998). Despite this extensive research, generalities are often elusive and some researchers have cast doubt on the validity of applying findings from local scale studies to larger spatial scales (Ricklefs 1987; Ricklefs & Schluter 1993a; Marquet 1994). It is important to address the ecological interactions occurring at the local scale and the interface between processes at local and broader scales, and to consider both the variability in assemblage structure and the spatial scale of this variability.

The aim of this study was to describe the patterns of mammal assemblage structure, and diversity in particular, over a range of spatial scales and to investigate how these patterns related to habitat structure. I wished to determine the effects of vertical complexity and spatial heterogeneity of vegetation on the assemblage structure of forest mammals over several spatial scales, and then to relate these patterns to the mesoscale and regional patterns of mammalian assemblage structure discussed in the previous chapters. Specifically, I posed several questions regarding the ecological interactions at the local scale:

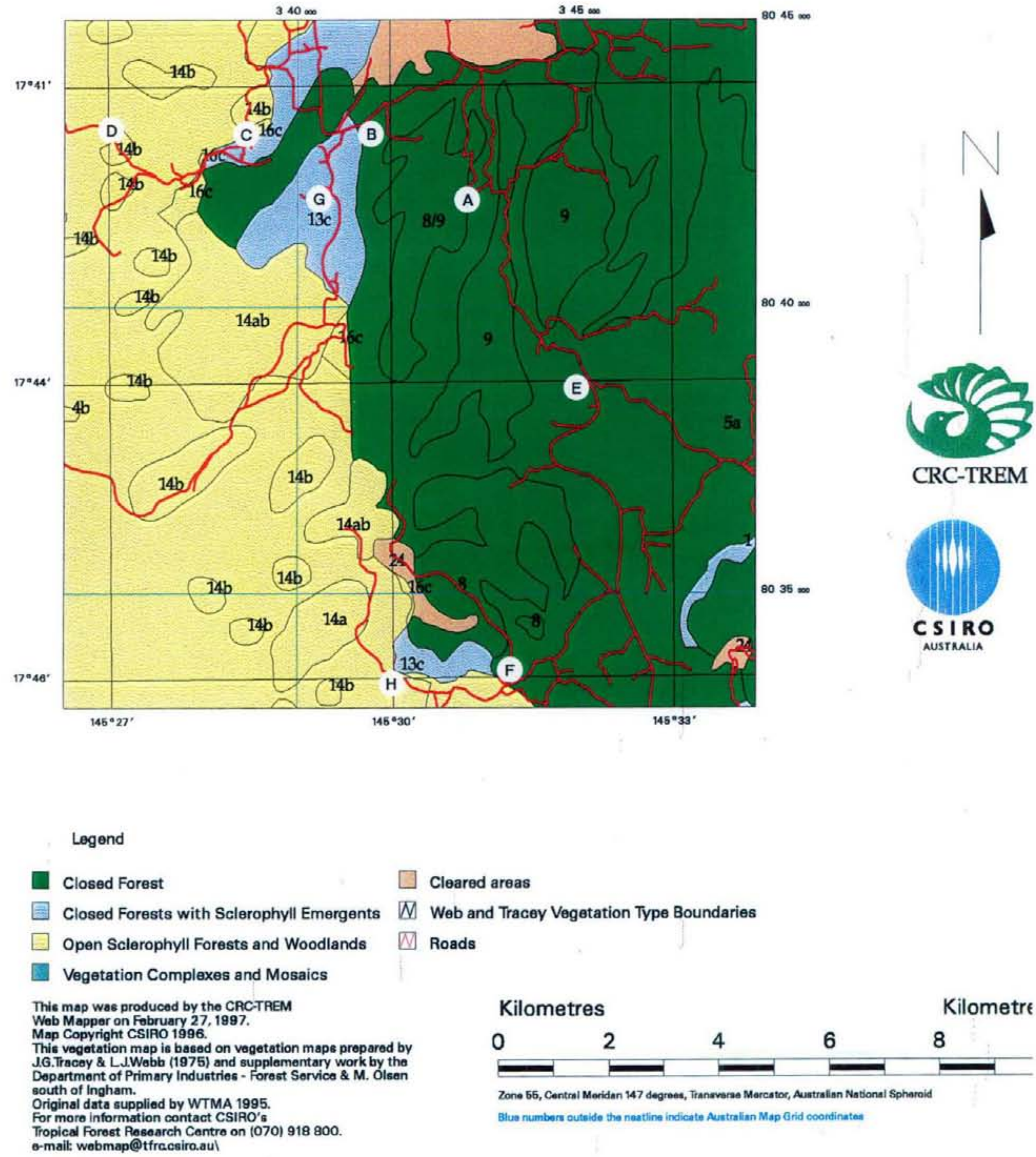
1. Can the spatial patterns in the structure of the mammal assemblage (composition, abundances, diversity, biomass, numbers of individuals, guild structure) be explained by vegetation structure?
2. Does habitat complexity or spatial heterogeneity have a significant influence on mammal diversity?
3. Are relationships consistent across spatial scales and taxonomic/ecological subsets of the mammal assemblage?
4. Does habitat structure affect arboreal and ground-dwelling species in a similar way?
5. Do the local patterns match the regional patterns discussed in previous chapters?

Sampling along the gradient from the rainforest to open forest provided detailed information on the habitat preferences of each species and changes in assemblage structure. Sampling beyond the limits of the rainforest assemblage is particularly informative in determining the relationships between the assemblage structure and habitat structure because it is much easier to detect patterns where changes are occurring. The sampling design was nested within and between habitats (see methods), so it was possible to address patterns of ecological interactions, spatial variability within each habitat and the influence of movement between adjoining habitats, all of which are necessary for a comprehensive study of patterns of local diversity (Schluter & Ricklefs 1993).

Local studies of mammal diversity were undertaken on the southern Atherton Tableland (Figure 2.1) as it has the highest species richness of both rainforest and non-rainforest mammals in the Wet Tropics biogeographic region and possibly in Australia (Winter *et al.* 1984; Williams *et al.* 1996). Additionally, this locality has an ideal environmental gradient along which to study the effects of habitat structure on the mammal assemblage. From east to west there is a gradient from a very complex vegetation structure (notophyll vine forest) to a simpler vegetation structure (open eucalypt woodland) within a distance of only 5 km (Figure 5.1). The boundary between the closed forest and the open forest is very abrupt with a complete transition from closed to open forest occurring within 50 m in most areas. Since all of the sites are no more than 10 km from each other, confounding influences associated with climate or biogeographic history are minimised. Given the dispersal ability of the species present, all species could be present over the study area within the limits of their individual habitat tolerances. Thus, all of the sites have the same biogeographic history and species pool, so differences in assemblage structure should reflect processes at the local and landscape scales only.

Spotlighting and live trapping were used to determine the non-volant mammal assemblage present over a range of nested spatial scales from 500m^2 (a single trapping grid) to 25 km^2 (the whole study area). Thirty-five species of mammals were observed, representing all but three of the species that could occur within the study area (Williams *et al.* 1996). The results show that the structure of the mammal assemblages was very closely related to vegetation structure both across habitats and within habitats. Local species richness of small mammals was mostly a product of spatial variability in assemblage structure within a habitat, which is related to the spatial variability in vegetation structure. However, spatial variability in the vegetation structure of a specific vertical stratum only affects the species richness of those species that utilise that stratum. Total species richness of mammals across the study area is not related to vegetation structure; however, there are more ground dwelling species in the areas of high spatial heterogeneity of ground vegetation, more scansorial species and arboreal folivores in the complex vegetation and more arboreal nectarivores in the open forest.

Figure 5.1: Vegetation map of study area, with locations of each site (A - H).
Numbers represent vegetation types (Tracey & Webb 1975).



This map was produced by the CRC-TREM
Web Mapper on February 27, 1997.
Map Copyright CSIRO 1996.
This vegetation map is based on vegetation maps prepared by J.G.Tracey & L.J.Webb (1975) and supplementary work by the Department of Primary Industries - Forest Service & M. Olsen south of Ingham.
Original data supplied by WTMA 1995.
For more information contact CSIRO's
Tropical Forest Research Centre on (070) 918 800.
e-mail: webmap@tfrc.csiro.au\

Zone 55, Central Meridan 147 degrees, Transverse Mercator, Australian National Spheroid

Blue numbers outside the neatline indicate Australian Map Grid coordinates

Methods

Study Area

The study area was on the southern Atherton Tableland, approximately 20 km south of Ravenshoe along the Tully Falls road (Lat. 17° 50' south, 145° 32' east) at an altitude of 740 to 1000m (Figures 2.1 & 5.1). The rainfall in the study area is about 2500 mm per year with a pronounced wet season between January and April (Laurance 1996). The Atherton Tableland contains the largest area of upland rainforest within the Wet Tropics (Bell *et al.* 1987; Williams *et al.* 1996) despite the significant amount of clearing which has occurred over the last 150 years. Winter *et al.* (1987) estimate that about 21% of the rainforest on the Atherton Uplands has been cleared. This area is believed to have contained the most significant area of refugial rainforest during the Pleistocene climatic fluctuations (Webb & Tracey 1981; Nix & Switzer 1991), although evidence from charcoal deposits within rainforest soils suggests that the refugia were fragmented and discontinuous (Hopkins *et al.* 1993; 1996). The study area was situated within continuous forest which had not been subject to clearing, although the whole area had been selectively logged. Vegetation classifications and rainforest structural types (Tracey & Webb 1975) for all sites are listed in Table 5.1 and the distribution of the vegetation types is shown in Figure 5.1.

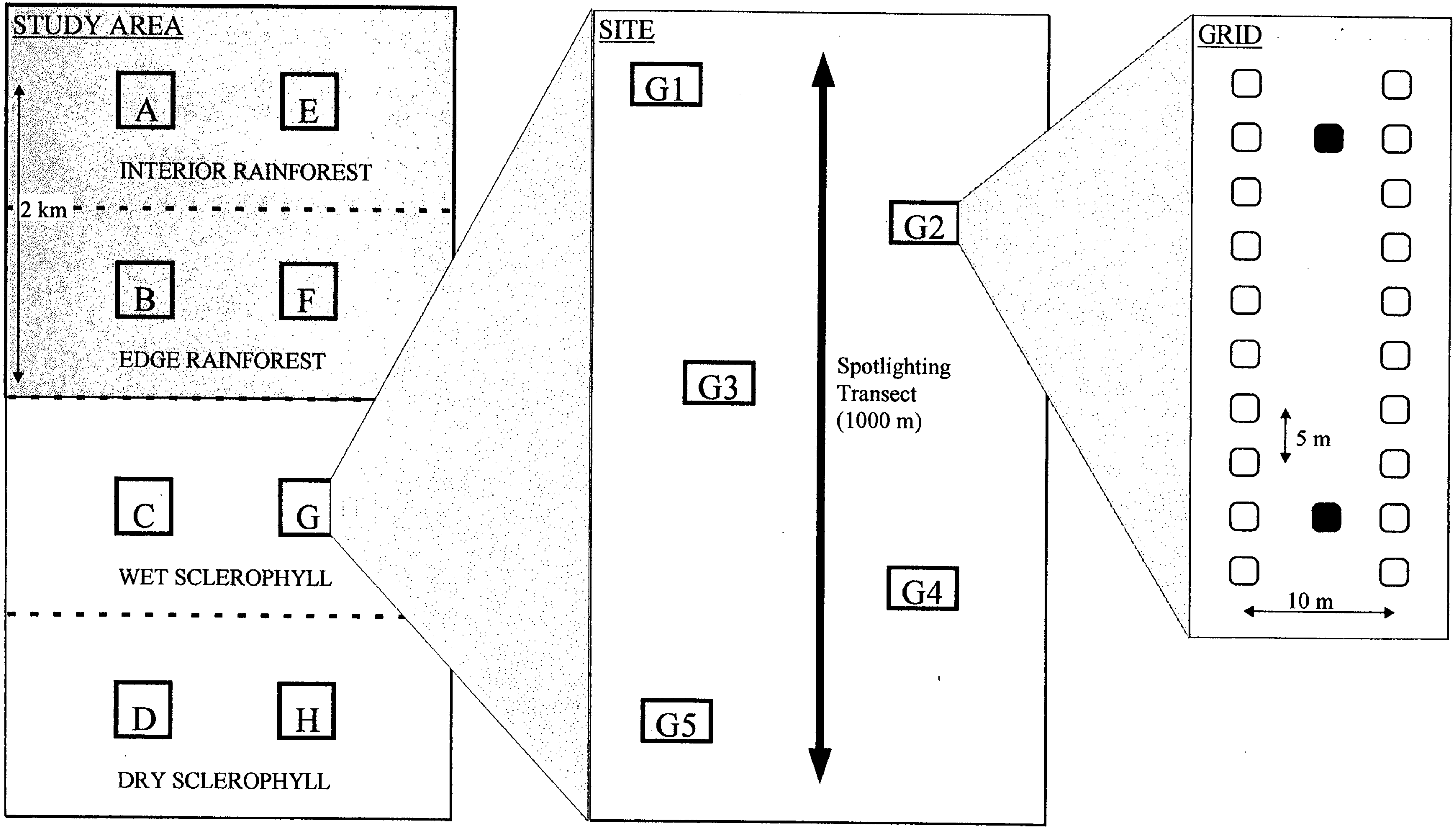
Site selection criteria

Four broad habitat types were selected to represent the main changes along the vegetation gradient, namely: interior rainforest (IRF - notophyll vine forest at least two kilometres from the ecotone: sites A & E); edge rainforest (ERF - notophyll vine forest often with *Acacia, Eucalyptus* and *Agathis* emergents and no further than 500m from the rainforest/open forest edge: sites B & F) ; wet sclerophyll (WS - tall open forest often with an understorey of rainforest shrubs: sites C & G); and, dry sclerophyll (DS - medium open forest and woodland: sites D & H) (Figures 5.1 & 5.2). This sampling design also allowed a coarse examination of edge effects, by comparing interior and edge rainforest sites. Two sites were selected within each of the four habitat types. They were at least five kilometres apart to ensure independence, that is a greater distance than the normal movements of most of the mammal species in the area, with the possible exception of the larger macropods. An exception was the two wet sclerophyll sites (sites C & G) which were only about two kilometres apart: however, they were separated by a range of rainforest covered hills which ensures biological separation and independence (Figure 5.1). The spatial scale for a site was approximately one kilometre (Figure 5.2). The driest sites (D & H) were far enough out along the gradient to have no species of rainforest specialists, that is beyond the edge of the 'rainforest' assemblage. Although these last two sites are referred to here as 'dry sclerophyll', they are really representative of the drier end of the spectrum of wet sclerophyll forest.

Table 5.1: Habitat type and vegetation classification of each site.
Habitat abbreviations are: IRF - interior rainforest; ERF - edge rainforest; WS - wet sclerophyll; DS - dry sclerophyll. AMG - Australian Map Grid reference for approximate centre of site. Vegetation classifications including numbered structural rainforest types in parentheses follow Tracey and Webb (1975), refer Figure 5.1 for vegetation map of study area.

Site	Habitat type	AMG	Vegetation classification	Altitude (m)
A	IRF	433423	Notophyll vine forest (8 & 9)	920
B	ERF	407427	Notophyll vine forest with *Acacia*, *Eucalyptus* and *Agathis* emergents (5a and 13c)	1000
C	WS	383424	Tall open forest often with an understorey of rainforest shrubs (13c & 14 mix)	960
D	DS	373423	Medium open forest (14 & 16 mix)	945
E	IRF	451381	Complex notophyll vine forest (5a)	850
F	ERF	437333	Notophyll vine forest with *Acacia*, *Eucalyptus* and *Agathis* emergents (5a & 13c)	740
G	WS	407421	Tall open forest with mixed *E. grandis*, *Allocasuarina* & bloodwoods (13c & 14 mix)	980
H	DS	431332	Medium open forest with bloodwoods & *Allocasuarina* (16)	730

Figure 5.2: Schematic diagram of the sampling design for local scale studies of mammal assemblage structure.
The study area box shows the placement of sites within habitat types (shaded area is closed forest). The expanded site box shows an approximate layout of the five trapping grids and the spotlighting transect within each site. The expanded grid box shows the layout of traps within a grid (open squares represent Elliot traps and solid squares are wire cage traps). The diagrams are schematic and not to scale.


STUDY AREA
A
E
INTERIOR RAINFOREST
2 km
B
F
EDGE RAINFOREST
C
G
WET SCLEROPHYLL
D
H
DRY SCLEROPHYLL
SITE
G1
G2
G3
Spotlighting
Transect
(1000 m)
G4
G5
GRID
5 m
10 m

Sampling methods

Trapping

Previous studies (Williams 1990; Laurance 1994; Williams & Marsh in review) have shown that the vertical stratification of foliage density has a significant effect on the structure of small mammal assemblages in the rainforests of the Wet Tropics. Therefore, in order to sample as much of the gradient in vegetation structure as possible, the placement of trapping grids was subjectively chosen to include as much variability in the vegetation structure as possible within each site. Five grids were established at each site with at least a 100m gap between adjacent grids (Figure 5.2). Each grid consisted of 20 small mammal traps (Elliott type A) and two wire cage traps (Mascot Wire, 30 x 30 x 60 cm, folding, treadle type). The traps were set out in two parallel lines 10 m apart with 10 Elliot traps (5 m apart) along each line (Figure 5.2). The two cage traps were placed between the lines at the second trap in from each end. Traps were baited with a mixture of rolled oats and vanilla essence. Traps were checked and rebaited each morning for four nights at each site on each trip. All animals caught were identified, tagged with individually numbered monel metal ears tags, sexed, weighed and released at the trap site.

All sites were sampled in April 1992, August 1992, November 1992, March 1993 and June 1993. Two sites were sampled simultaneously for four nights and then the traps were moved to another two sites and so on until all eight sites had been sampled. This usually took between 18 - 20 days to complete. Therefore the total trapping effort was 5 trips x 8 sites x 5 grids x 22 traps x 4 nights = 17600 trap nights.

Spotlighting

A single spotlighting transect one kilometre long was established at each site (Figure 5.2). All transects were along tracks or roads as it is very difficult to see into the canopy without a break in the understorey vegetation. Numbered reflectors were attached to trees every 50 m so that the position of any animal along the transect could be recorded.

Spotlighting was standardised to reduce biases in a technique which is intrinsically highly variable. I used a single 30 w hand-held spotlight and binoculars to identify animals on all transects. Sampling effort was standardised by search time rather than total time, as total time is heavily biased by the abundance of animals (Williams 1995). A stopwatch was used to record search time. The stopwatch was paused as soon as an animal was observed and was restarted after the animal had been identified and the data recorded. Four minutes of search time was spent in each 100m section of the transect giving a total search time of 40 minutes per kilometre. This usually equated to about one hour of total spotlighting time. Standardising the search time, and hence the sampling effort, in each 100m segment within the transect has the advantage that patterns in relative abundance can be examined both between and within transects.

Each transect was sampled on three different nights per field trip. Spotlighting was conducted between 1900h and midnight with two or three sites sampled per night. Sampling order was rotated to avoid biases due to time of night. The number of times each transect was sampled is summarised in Table 5.2. Spotlighting censuses were conducted during August 1992, November 1992, March 1993, June 1993, March 1994, April 1994 and November 1994. Spotlighting was conducted only when the weather conditions were conducive to obtaining comparable results not unduly biased by extreme weather conditions, that is not in heavy rain, mist or wind. For each observation of an animal the time, species, position along the transect, estimated distance from the transect, estimated height and the method of detection (call, sight, heard movement) were recorded.

Miscellaneous

Other observations of mammals within the study area were recorded to supplement the total species list and the species list for each site.

Table 5.2: Summary of spotlighting sampling effort.

Site	No. Trips Sampled	Total number of transects	Total search effort (min)
A	7	21	801
B	5	15	604
C	4	12	463
D	4	12	416
E	7	21	796
F	7	21	832
G	4	12	449
H	4	12	451
Total		126	4812

Spatial and temporal scales of data combination

The sampling design was deliberately nested both spatially and temporally to allow the examination of assemblage patterns over a range of temporal and spatial scales. A sample refers to the assemblage found at a point during one field trip. Therefore, for the trapping program, the sample species richness refers to the number of species trapped at a grid over the four nights of trapping, while for spotlighting the sample species richness refers to the number of species observed over three repeats of a transect during one field trip. Relative abundances are technique-specific and are measured as the number of individuals of each species trapped at a grid over the four nights or as the mean number of individuals of each species observed on the three repeats of a spotlighting transect on each trip. It was not possible to identify individual animals by spotlighting so the mean over the three repeats was used as an estimate rather than the number of individuals as used in the trapping. Spatial variability within a spotlighting transect can be examined by dividing the one kilometre transect into five 200m segments, within the analytical constraints of pseudo-replication due to non-independence of adjoining segments.

Spatial and temporal variability of assemblage structure was assessed by combining samples within a site or by combining over time (combining samples from different field trips), or both. Broad-scale patterns across the rainforest-sclerophyll gradient were examined by pooling the data from the two sites within each of the four habitat types.

Description of assemblage structure

There are many ways to characterise the structure of a biotic assemblage. Because of the large effect of sampling effort on most assemblage descriptors (especially species richness), unless otherwise stated, all analyses of assemblage variables use the same number of samples at each of the eight sites. The following variables have been used in this study: species composition, which refers to the identity of the species which make up the assemblage; relative abundance of each species; species richness; species evenness (Pielou's J'); species diversity (Shannon-Weaver diversity index H'); mammal biomass index (see below); the number of individual animals; the mean number of species per guild; and the number of guilds. Guild definitions follow Braithwaite *et al.* (1985) and have previously been explained in Chapter 4. The guild classification of each species is included in Appendix 6. The term "assemblage structure" refers to the combination of the species composition and the relative abundance of each species; all other assemblage variables are derived from the combination of these two measurements. The biomass index was calculated from the trapping data as the total mass of all individuals captured at that grid during one sample. A biomass index was not possible for spotlighting data because animals were not captured.

Vegetation / habitat sampling methodology

Habitat structure was described at each of the 40 trapping grids of the eight sites (A-H). Description of the habitat at each grid included: altitude, aspect, slope, distance to water, distance to drainage line, a description of any present or past disturbance, and broad vegetation description including dominant species (sclerophyll forest only). Vegetation structure was described quantitatively at five points 10 m apart along a line through the long axis of each trapping grid. At each point the vegetation density within a 5.0 m radius was estimated in five vertical strata (ground cover 0-1 m, low shrubs 1-2 m, shrubs 2-5 m, subcanopy, and canopy) on an eight point scale (0 = absent; 1 = present (~1%); 2 = less than 5% cover; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%; 6 = 75-

95%; 7 = 95-100%). These measurements of vegetation density were used to derive estimates of vegetation complexity and heterogeneity. Complexity relates to the vertical development of vegetation strata while heterogeneity or patchiness refers to the horizontal variability in structure (August 1983). Estimates of canopy height and a count of trees (above 3m in height) were made at each of these five points also. Additionally, the abundance of a number of habitat features and vegetation life forms were estimated for the whole grid on a four point ordinal scale (0 - absent; 1 - present; 2 - frequent; 3 - common; 4 - abundant) (see vegetation proforma in Appendix 7 for a complete list of habitat variables recorded). One grid (G5) was removed from all analyses relating mammal assemblage structure to vegetation structure because the vegetation on the grid was burnt before the vegetation measurements were taken.

Detailed description of the vegetation structure along 11 km of spotlighting transects was not possible. Therefore, since the trapping grids were situated along the spotlighting transects at each site, the estimates of vegetation structure at the five grids within each primary site were used as an index of the vegetation structure of the site as a whole.

Spatial scales

Three spatial scales were examined in this study (Figure 5.2):

1) *Point scale:* The scale of the trapping grid which can be thought of as a point sample. The area of a grid was 500 m^2; however, the area of influence of the grid was probably between 3500 m^2 and 16500 m^2 (assuming a 20 - 50 m influence on all sides). The 200 m spotlighting segments were analogous to the grid point sample with an area of influence somewhere in the order of 4000 m^2 (200 x 20m). There were five point samples using each method (5 grids and 5 spotlight segments) within each site.
2) The spatial scale of a site was approximately one kilometre (Figure 5.2). The influence of the five trapping grids within a site covers approximately 8 ha, while the 1 km spotlighting transect has an area of influence between 2 ha and 4 ha.

3) The sites were distributed across the primary habitat gradient over a distance of about four kilometres, with the two transects (each of four sites) about 5 km apart (Figure 5.2). All of the sites were situated within an area of about 25 km^2.

The areas of influence differ between species depending on their movements, the attractiveness of the bait (trapping) and their relative detectability (spotlighting) (Williams 1995). The areas of influences were used to give an approximation of the spatial scales examined.

Analytical methods

Multidimensional scaling (MDS) was used to describe the structure of the vegetation and the small mammal assemblage. Multidimensional scaling is a procedure which spatially represents the similarities of objects, like a map (Schiffman *et al.* 1981). It does this by using a measure of direct similarity (or dissimilarity) to rank the similarity of objects and computing the spatial arrangement of objects in multidimensional space which best represents the spatial similarity of each object to the other objects (Schiffman *et al.* 1981). MDS is commonly used in ecological studies because of its lack of assumptions about the distribution or type of data and because of its general robustness (Schiffman *et al.* 1981).

Interpretation of the relative contribution of each variable or species to the MDS axes was measured by the correlation between the variable and the MDS axis scores. The relationships between vegetation structure and the mammal assemblage structure can be examined by correlating the gradients defined by the MDS axes (vegetation and mammals) and measures of mammal assemblage structure.

The means of the MDS scores (either the mammal or the vegetation analysis) at each of the five trapping grids or five spotlighting segments provide a measure of the mean position of the site along the gradient described by the MDS axis, relative to the other sites. The standard deviation (s.d.) of the MDS scores was used as an index of the spatial variability within the site in either assemblage or vegetation structure, that is a measure of beta diversity (refer to Table 1.1). Beta diversity is a measure of the degree, or rate, of change in community composition either spatially, temporally or over an environmental or community gradient (Whittaker 1972; 1977). Many indices of beta diversity have been used, most of which compare species composition only (Magurran 1988; Wiens 1989a). Spatial variability in multidimensional space has advantages over the more traditional measures of beta diversity, such as Jaccard's coefficient, as it uses both species composition and relative abundances to index spatial variability in assemblage structure, rather than simple presence/absence data. This is particularly useful when comparing sites in a relatively homogeneous habitat such as rainforest, where the species present may not vary greatly but relative abundances do vary. The measure of the beta diversity of the habitat structure can then be compared with measures of the mammal assemblage structure, such as species richness, relative abundances, diversity, biomass and the number of individuals, and similarly the beta diversity of the mammal assemblage can be related to the habitat structure.

The distance measure used in the MDS analyses was euclidean distance, and variables were standardised between 0-1 (each value divided by the maximum value for that variable). Euclidean distance reduces the impact of numerically dominant species and the standardisation of all relative abundances to between 0-1 results in all species making an equal contribution to the analysis while maintaining the between site differences in relative abundance for each species. Both of these standardisations are desirable when the emphasis of the analysis is on patterns of species richness.

The mean and standard deviation of the first MDS axis scores of the vegetation analysis were used as measures of the vegetation complexity and the spatial variation in complexity (heterogeneity or patchiness), in a similar manner to August (1983) where the mean and standard deviation of the axis scores of principle components analysis was used. A second index of vegetation complexity was derived by adding the mean estimate of the density of vegetation in each of the vertical vegetation strata for each grid. The contribution of each stratum was weighted to allow for the different stratum widths. Mean scores of each layer were multiplied by the appropriate weighting and then summed for all strata, providing an index of the Total Vegetation Density (TVD) of each grid. Weightings were: 1.0 for the 0-1m and the 1-2m strata; 3.0 for the 2-5m layer; and, 5.0 for the subcanopy and canopy strata.

Bias analysis

There are many biases associated with sampling assemblage structure, including environmental conditions, season, observer, spatial scale, technique, sampling design, habitat, species and density (Wiens 1989a; Williams 1995[5]). All of these biases were addressed in this study: for example, spotlighting was not conducted during times of heavy rain, wind or mist; environmental variables were recorded so that analysis of any significant effects could be considered; seasonal biases were reduced by sampling over a period greater than a year; I conducted all samples personally to remove observer bias; and the spatially nested sampling design allowed an examination of any trends at several spatial scales to minimise and examine biases due to inappropriate sampling scale.

The two techniques employed in this part of the study (trapping and spotlighting) have considerable biases affecting which species are observed and estimates of their relative abundances (Williams 1995). However, these techniques are the best available for sampling the respective sub-set of the mammal assemblage. Analyses of species richness and relative abundances were limited to those species best observed by each method. Most of the species which could reasonably be expected to occur in the study area were recorded. Thirty-eight species of non-volant mammals are known to occur on the southern Atherton Tableland (Chapter 2), of which 35 (92%) were observed in the study area. The three species which were not recorded were *Rattus tunneyi, Dasyurus maculatus* and *Planigale maculata.* The Spotted-tailed Quoll (*Dasyurus maculatus*) was historically quite common in the area; however, it is now very rare and was not observed during this study, although it is still present in nearby areas (Scott Burnett pers. comm.). Pit traps are usually needed to record *Planigale maculata* and it seems unlikely that *Rattus tunneyi* was present in the study area since it is readily trapped and, given the intensity of trapping effort, I would have expected to capture this species if it

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[5] This paper was a direct result of this study but has not been incorporated in the main body of the thesis. A copy is provided in Appendix 8:
Williams S.E. 1995. Measuring and monitoring wildlife communities: the problem of bias. *in* Conservation through sustainable use of wildlife, ed. by G.C. Grigg, P.T. Hale and D. Lunney. Centre for Conservation Biology, The University of Queensland.

were present. A further seven species which have been recorded either in the northern Atherton Tableland or in the dry western woodland (*Dasyurus hallucatus, Mesembriomys gouldii, Uromys hadrourus, Petrogale mareeba, Petaurus norfolcensis, Phascolarctus cinereus, Macropus agilis*) could occur in the study area, although it is unlikely. Of the 35 species observed, 24 species were observed by spotlighting, 16 species by trapping and two species not recorded by either method were observed during the day (*Macropus parryi, Hypsiprymnodon moschatus*). Six species were included in the combined analysis only, because they were not considered to be adequately sampled by either sampling method. These were *Sminthopsis leucopus (1 capture), Sminthopsis murina (1 capture), Hypsiprymnodon moschatus (1 miscellaneous record), Macropus parryi (several miscellaneous records), Pogonomys mollipilosus (2 miscellaneous records),* and *Hydromys chrysogaster (1 capture).* Two species were adequately sampled by both methods (*Isoodon macrourus* and *Aepyprymnus rufescens*).

Both methods are biased in the calculation of relative abundances even within the sub-set best sampled by that method. All small mammals vary in their "trappability". The bait used was tested by CSIRO and found to be suitable for this suite of species (L. Moore pers. comm.). The trapping methods were designed to minimise bias due to the variability in the relative "trappability" of each species. Each grid (500 m^2) was effectively treated as a point sample, thereby smoothing out some of the very fine scale variation when individual trap sites are used as the basic unit of analysis. Saturating the grid with traps (5 m trap spacing) meant that there were always traps available for species which are rare or less trappable (the highest number of captures in a single night during the study was 11 animals in the 22 traps on a grid). Using the number of individuals over four nights of trapping reduces the extreme species bias on recapture estimates produced by the high degree of "trappability" of some species (e.g. *Melomys cervinipes* or *Rattus fuscipes*) and/or highly unequal abundances. It was assumed that the trapping technique was equal in its effectiveness across the habitat gradient.

Rigorous standardisation of spotlighting minimises density bias (Williams 1995); however, there are still biases due to the highly variable detectability of species (species bias) and differences in vegetation density between sites (habitat bias). A simple estimate of detectability is the distance from the transect within which a standard percentile of animals are sighted for a species. Alternatively, comparison of the percentile distance of the same species at different sites can index the relative detectability bias of the site, which may vary with differences in vegetation density. Relative abundances can be adjusted to account for site and/or species detectability by calculating the mean abundance per effective sampling area for that species and/or site (Williams 1995; Laurance & Laurance 1996). When enough observations of each species are possible, more sophisticated estimates of detectability can be obtained by using "distance analysis" (Buckland *et al.* 1993).

An alternative method of removing the bias due to differing detectabilities between species is to standardise abundances between 0 and 1. This has the disadvantage that it equalises the relative effect of each species on assemblage structure; however, this may be acceptable where the primary aim is to examine patterns of species composition and species richness. Bias due to differing vegetation density is a significant problem with spotlighting; however, this bias can be largely ignored in the following analyses for two reasons. Firstly, analysis of the mean distance from the transect for the most detectable species in both open and closed forests (*Petauroides volans* and *Hemibelideus lemuroides* respectively) showed that there was no significant difference in the within-habitat mean observation distance for these species between sites (1-way AOV: *P.volans* in open forest with four sites and 143 observations, $F_{3,139} = 0.768$, $p = 0.514$; *H. lemuroides* in closed forest with 4 sites and 444 observations, $F_{3,440} = 0.885$, $p = 0.449$). Secondly, almost all species in the spotlighting analyses were restricted to either open or closed forest, so between-habitat effects were minimal. Therefore, standardisation by the relative detectability of each species is only necessary when estimates of absolute abundance are required or the same species is present in more than one habitat and the detectability of that species varies between habitats.

Identification problems (Rattus fuscipes / Rattus leucopus)

R. fuscipes and *R.leucopus* are two sympatric species of *Rattus* within the study area which are very difficult to identify without examining their skulls. Lidicker & Laurance (1990) described the method used to differentiate the two species in Laurance's study of small mammals in the Millaa Millaa area (~60 km north of this study). The degree of similarity in these two species varies greatly throughout the region (J. Winter and L. Moore, pers. comm.) and they become more similar in the southern Atherton Tableland. After many attempts at a reliable identification procedure it was decided that field identification was not possible. Hair samples were taken from several hundred individuals in an attempt to identify the species. Barbara Triggs, an acknowledged expert on hair identification, could only identify one species (*Rattus fuscipes*) from the samples taken. Subsequently, an attempt was made to collect 10 individuals of each species for identification by skull features to make a reference collection of hairs. Based on skull features, all of the twenty individuals were found to be R*attus fuscipes.* Other researchers in the area have found that the proportion of *R.leucopus* was very low in the more southern parts of the Atherton Tableland, and that this species is generally found at lower altitudes in the study area (Winter 1997). The result of this difficulty is that records of these two species have been combined in the analyses; however, it seems probable that the majority of the individuals were *R. fuscipes.*

Combining trapping, spotlighting and miscellaneous observations

In order to examine patterns within the whole mammal assemblage, rather than a subset determined by a specific sampling technique, an index of relative abundance which combines the information from all techniques is desirable. This was achieved by using a quantitative ordinal scale of abundance, only at the site scale. Using the best technique for each species, the mean number of individuals per sample was calculated and multiplied by 10 and rounded off to the nearest integer. This gives an index of 10 for a species which, on average, is observed once per sample and a species which was seen 10 times on every sample would have an index of 100. A species which was only observed once was given an abundance index of 1. Species which were recorded by miscellaneous observations were ranked on the scale dependent on the number of observations at each site. Data were standardised between 0 and 1 (MDS analyses) as previously. This procedure makes relative abundances comparable, regardless of which sampling method was used, since the relative abundance of each species will equal one at the site of its maximum abundance and the relative abundance at all other sites will be scaled according to the maximum.

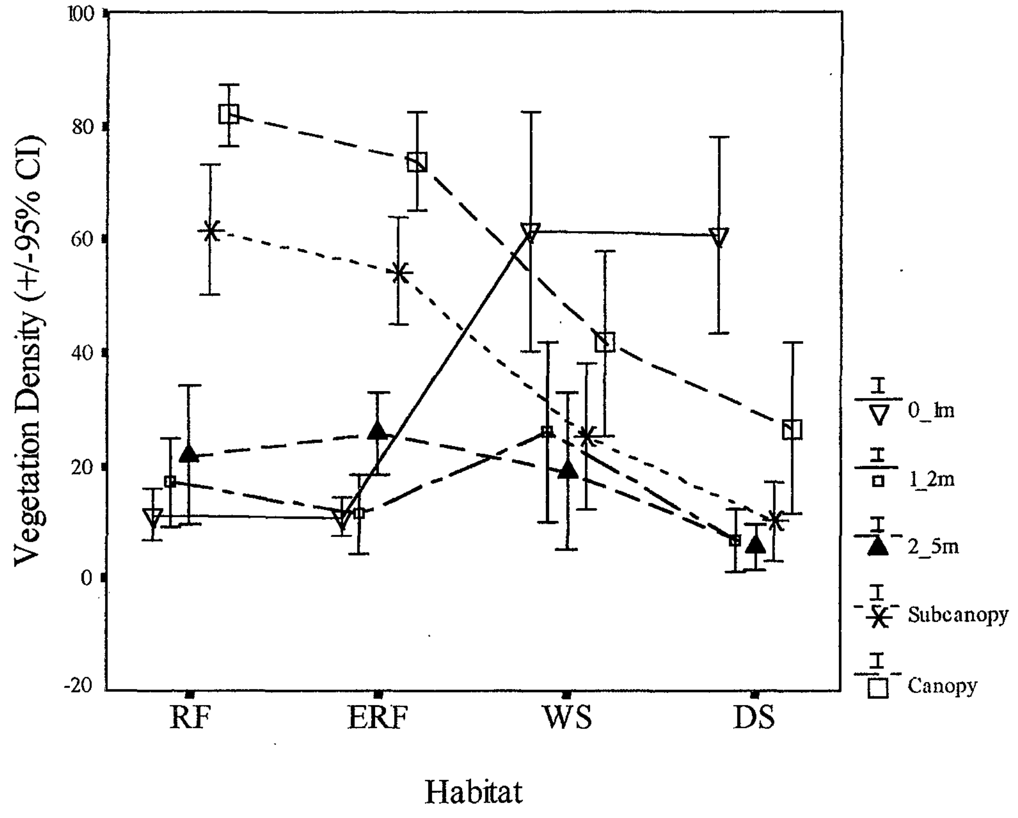
Results

Vegetation structure

Broad trends across the habitat gradient from rainforest to open forest

Vegetation structure changed dramatically across the gradient from rainforest to open forest, with canopy and subcanopy density significantly decreasing and ground cover significantly increasing (Figure 5.3). There was no significant trend in low shrub density and shrub density, although the density of low shrubs (1-2m) in the dry sclerophyll was higher than in the other three habitats.

Figure 5.3: Changes in vegetation density across the vegetation gradient. Habitats are interior rainforest (IRF), edge rainforest (ERF), wet sclerophyll (WS) and dry sclerophyll (DS). Values are the mean of 10 grids (five at each of two sites), except for wet sclerophyll where only nine grids are included (one grid removed due to fire), in each of the four habitat types. Error bars are 95% confidence intervals.

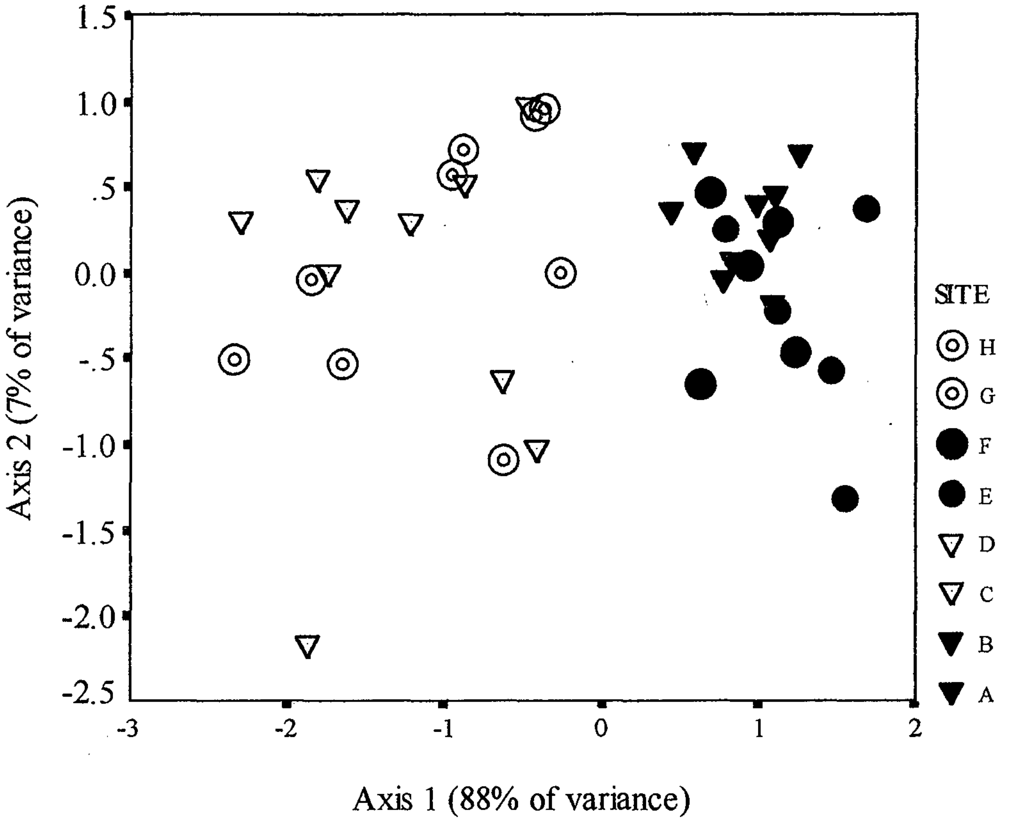


Point scale

Point scale refers to a single trapping grid (see Table 1.1 & Figure 5.2). Multidimensional scaling (MDS), using the mean density of vegetation in the five vertical strata, describes two main dimensions which explain 95% of the total variation in vegetation structure (Figure 5.4). Most of the variation in vegetation structure (88%) is explained by the first axis which is correlated with the density of ground cover, tall shrubs, subcanopy and canopy density (Table 5.3), and is therefore an index of vegetation complexity (similar to August 1983). A further 7% of the variance in vegetation structure is described by the second MDS axis which is correlated with the density of the shrub strata between 1 and 5 m (Table 5.3).

Figure 5.4: MDS plot of the vegetation at 39 trapping grids based on the density of vegetation in five vertical strata.

All variables were standardized between 0 and 1. Grid G5 removed from analysis due to fire. Open symbols - open forest grids; closed symbols - closed forest; circles - southern sites; triangles - northern sites; IRF - dark green; ERF - light green; WS - blue; DS - red.



The index of vegetation complexity derived from the total density of vegetation (TVD) and the index provided by the first MDS axis were highly correlated (Spearman's R_s = 0.90, p=0.002), as was the variability (s.d.) of TVD and the variability of the second MDS axis (Spearman's R_s = 0.95, p<0.0001). It seems that complexity was primarily a function of the increasing density of tall shrubs, subcanopy and canopy across the main vegetation gradient into rainforest and heterogeneity was indexed by both the variability within a site along this gradient (s.d. of MDS1 scores) and by the within-habitat variation of the density of the shrub layer (1-5m) (s.d. of the second MDS axis or s.d. of total vegetation density index).

Table 5.3: Correlations between vegetation structure and the MDS axes.
This shows the relationships between the variables (stratified vegetation density) used in the MDS analysis describing vegetation structure at 39 trapping grids and the first two MDS axes in Figure 5.4. (VEGMDS1 & VEGMDS2) (n = 39). p=0.000 indicates that p<0.001.

	VEGMDS1		VEGMDS2	
Variables	r	p	r	p
0-1 m	**-0.926**	**0.000**	-0.158	0.330
1-2 m	-0.083	0.609	**-0.850**	**0.000**
2-5 m	**0.488**	**0.001**	**-0.782**	**0.000**
Subcanopy	**0.887**	**0.000**	-0.164	0.312
Canopy	**0.847**	**0.000**	0.177	0.275

Local scale

The local scale incorporates the five grids within a site (see Table 1.1 & Figure 5.2). Complexity, as indexed by the mean of the first MDS axis scores of the five within-site samples (grids or segments), was lowest in the dry sclerophyll, increased in the wet sclerophyll and was highest in the rainforest (Table 5.4). However, there was no consistent trend in complexity between edge rainforest and core rainforest (Table 5.4). Three of the rainforest sites had very similar levels of complexity (A, B, F) while site E had a considerably more complex vegetation, as expected from its classification as complex notophyll vine forest (Figure 5.1). Vegetation patchiness or heterogeneity (s.d. of first MDS axis scores) was higher in the open forest sites than in the rainforest, although the level of heterogeneity was similar for the four sites within each habitat (Table 5.4). The second vegetation axis, although only describing seven percent of the variation in vegetation structure, separates the sites within open and closed forests on the basis of the density of the shrub layer (Table 5.3). Wet sclerophyll sites (C & G) had a relatively complex and patchy shrub layer compared to all other sites (Table 5.4).

Table 5.4: Vegetation complexity and spatial heterogeneity of each site.
Scores derived from the mean MDS axis scores (complexity) and the standard deviation of the MDS axis scores (patchiness) of each of the five grids within each site respectively. Habitat types are interior rainforest (IRF), edge rainforest (ERF), wet sclerophyll (WS) and dry sclerophyll (DS). TVD - total vegetation density. (Note: negative scores in second MDS axis correspond to increasing density of shrub layer 1-5 m, since the second vegetation MDS axis is negatively correlated with shrub density).

	Open Forest				Rainforest			
Site	D	H	C	G	B	A	F	E
Habitat	DS	DS	WS	WS	ERF	IRF	ERF	IRF
MDS 1 (mean)	-1.47	-1.29	-1.11	-0.73	0.89	0.92	0.93	1.33
MDS 1 (s.d.)	0.68	0.78	0.68	0.64	0.27	0.27	0.27	0.37
MDS 2 (mean)	0.39	0.34	-0.55	-0.38	0.17	0.38	-0.06	-0.29
MDS 2 (s.d.)	0.36	0.59	1.14	0.90	0.24	0.35	0.48	0.69
TVD (mean)	240.2	298.3	503.0	551.4	749.7	736.0	730.9	887.7
TVD (s.d.)	65.8	112.6	131.1	246.8	64.1	82.5	85.3	112.6

Gradient in Mammal Assemblage Structure

This section examines broad trends in assemblage variables across the habitat gradient from interior rainforest to dry sclerophyll. All samples were pooled within each of the four habitats (IRF, ERF, WS, DS).

Trapping results

The species richness of small mammals caught at a grid over a single sample (four nights trapping) was significantly higher in interior rainforest than in any of the other three habitat types (Figure 5.5a). However, the total species richness of each grid pooled over all five samples (trips) showed that the grids in edge rainforest had a significantly lower species richness than interior rainforest or the open forest habitats and that the species richness of interior rainforest grids was not different from that in either of the open forest habitats (Figure 5.5b). The pattern exhibited for the total species richness of each site (five grids combined at each site) shows an increase in species richness from rainforest to the dry sclerophyll (Figure 5.5c).

Spotlighting results

The number of species recorded on a single spotlighting transect appeared higher, on average, in closed forest than in open forest, but the difference was not significant (Figure 5.6a). Combining the three repeats of each transect per trip shows that the mean species richness per spotlighting sample (three repeats of each transect) was between about five and seven species per site and there was no significant difference across the four habitat types (Figure 5.6b). There was a slight decrease in the mean species richness per 200m segment from interior rainforest to dry sclerophyll forest but the decline is not significant due to the high variability in the open forest (Figure 5.6c). However, when samples were pooled over time (4 trips), there was a steady increase in species richness from rainforest to dry sclerophyll (Figure 5.6d).

Figure 5.5: Trends in the species richness of small mammals across the vegetation gradient from interior rainforest to dry sclerophyll (based on trapping)

a. mean species richness per sample within each habitat (2 sites x 5 grids x 5 times per habitat) (n=50); b. mean grid species richness (total species richness of each grid pooled over time - value is the mean of the 10 grids per habitat); and c. total species richness recorded at each site (5 grids x 5 times pooled per site). Error bars are 95% confidence intervals.

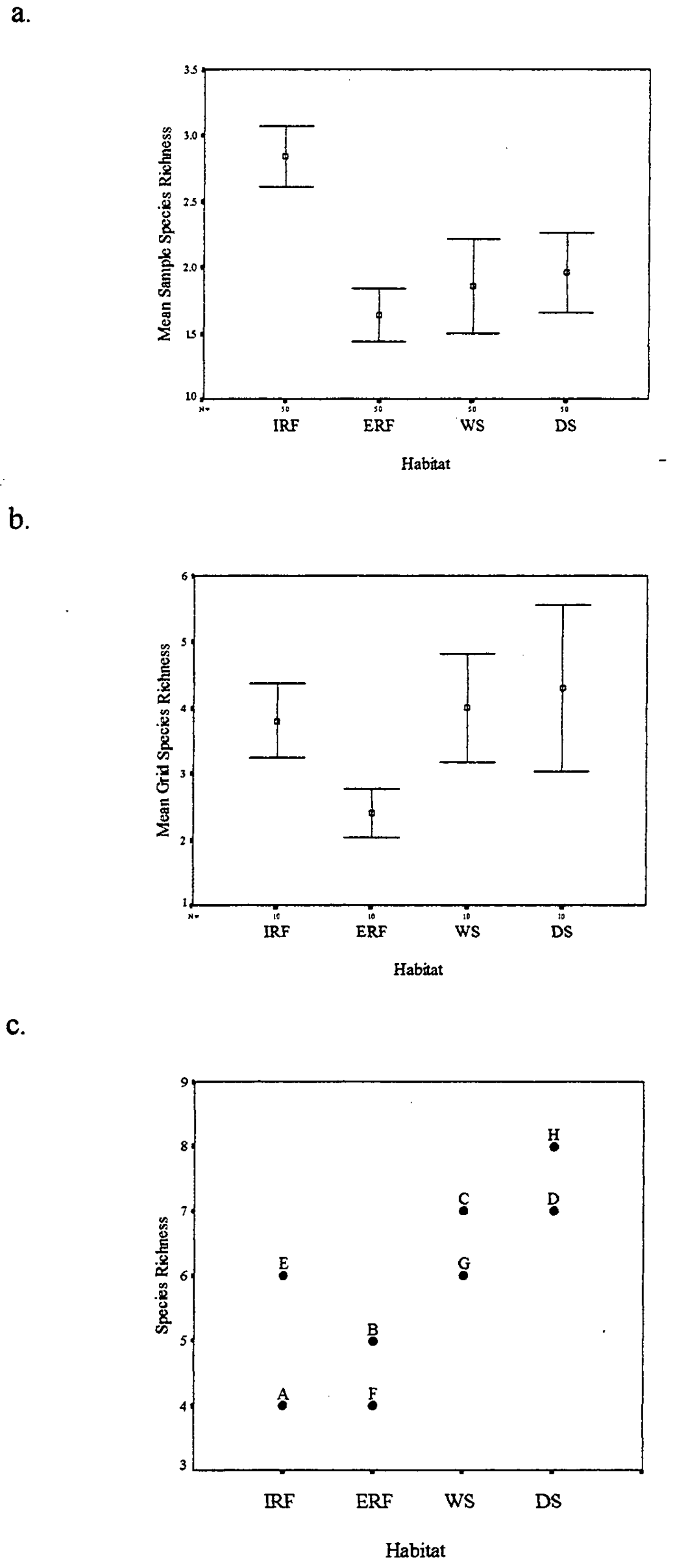
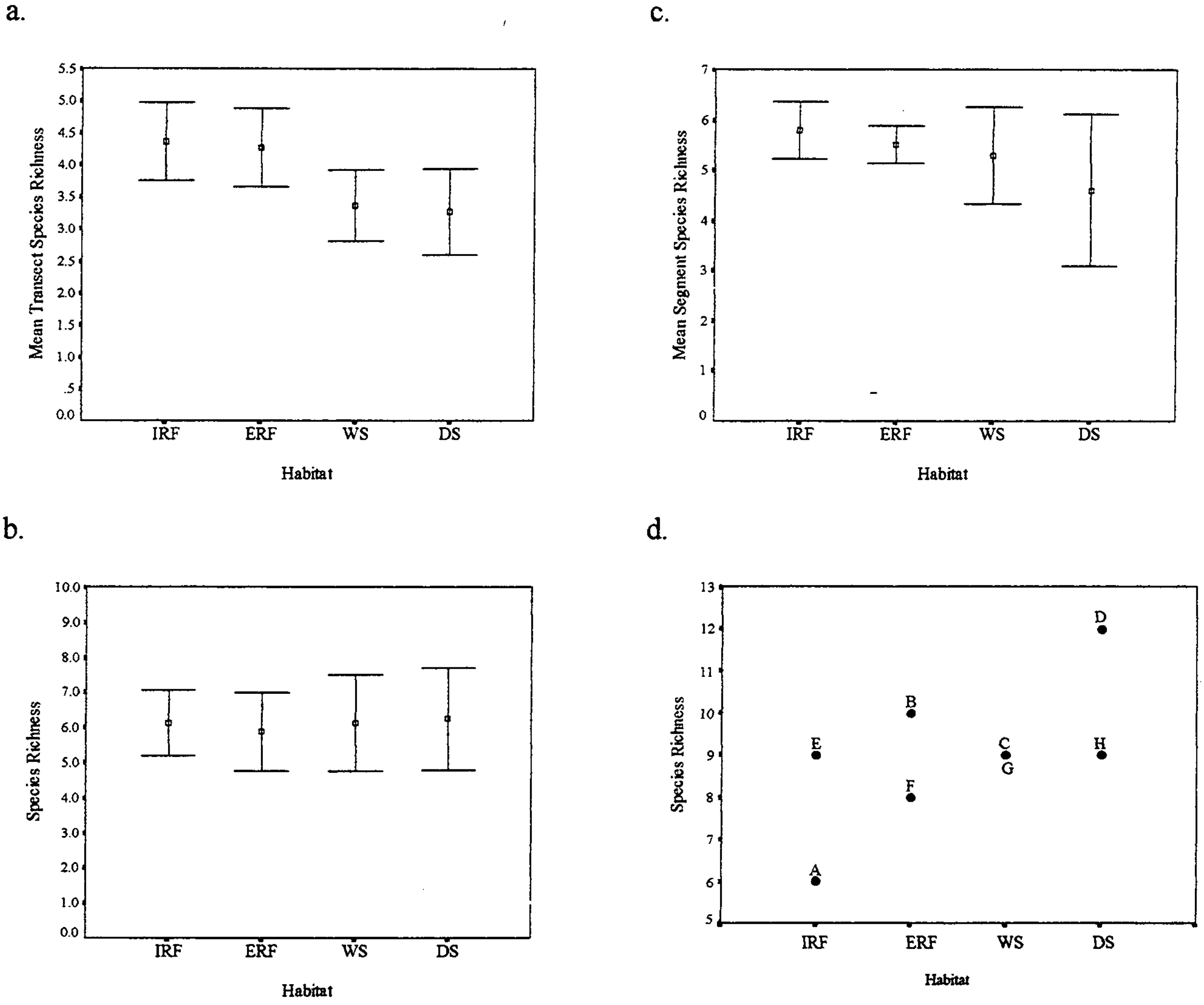


Figure 5.6: Trends in the species richness of mammals across the vegetation gradient (based on spotlighting)

a. mean species richness per transect within each habitat (2 sites x 11 repeats per habitat; n=22);
b. mean species richness per sample (2 sites x 4 trips; n=8);
c. mean species richness per segment (2 sites x 5 segments; n=10); and,
d. total species richness recorded at each site (8 samples pooled per site; n=8).
Error bars are 95% confidence intervals.

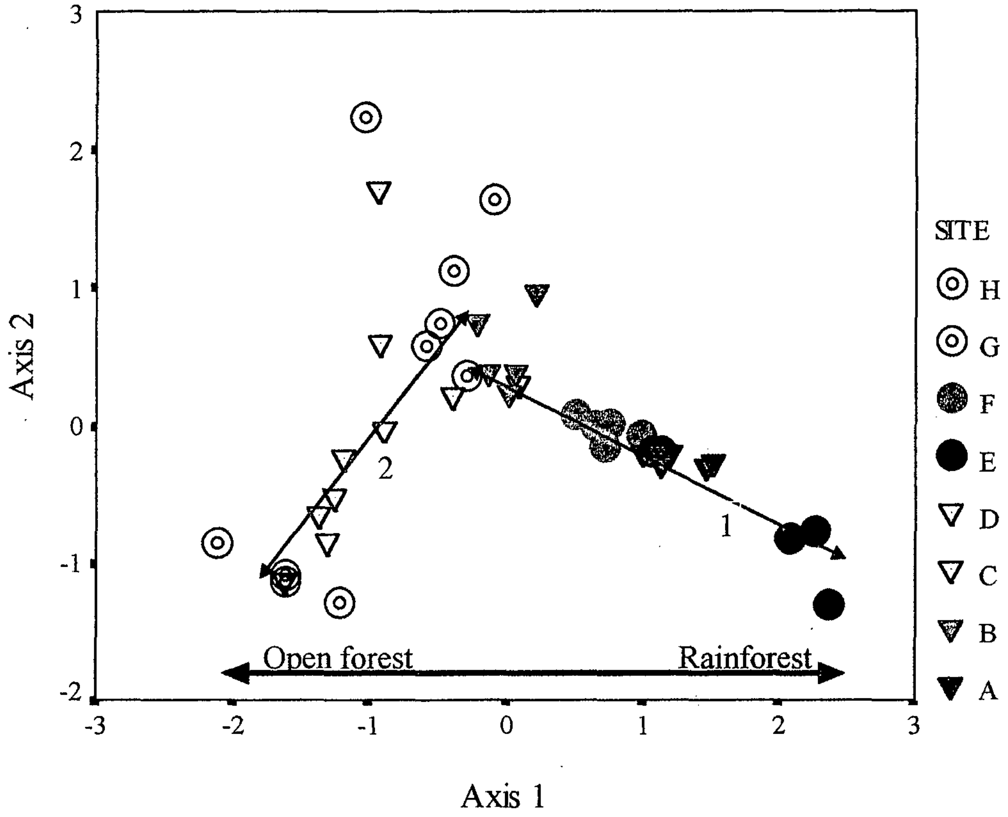


Small mammal assemblage structure - trapping data (samples pooled over time)

Point (grid) scale

The analyses in the previous section pool the data into four discrete habitat types; however, analysis of the small mammal assemblage structure at each of the forty trapping grids, using multidimensional scaling, shows that assemblage structure changes over relatively continuous gradients and not as four discrete assemblages in each of the four previously discussed habitats (Figure 5.7). The first MDS axis represents the gradient in assemblage structure across the main habitat gradient from rainforest to open forest and explains 69% of the variance in assemblage structure (Figure 5.7). The abundances of all eleven species of small mammals were correlated with this gradient (Table 5.5). This means that no species is equally abundant across the gradient; that is, all species are primarily associated with either open forest or closed forest. This causes some difficulty in the interpretation of the second MDS axis (which explains a further 16% of the variance) as the gradient of change along this axis is produced by completely different species in open and closed forest (Table 5.5 and see gradients 1 & 2 in Figure 5.7). To examine the correlations between the two within-habitat gradients, only the abundances of species recorded in each habitat were correlated with the MDS scores of the second axis for the twenty grids within each habitat (Table 5.5). The gradient of assemblage change within rainforest along the second MDS axis (see gradient 1 in Figure 5.7) was correlated with increases in the abundances of *Antechinus godmani, A. stuartii, Melomys cervinipes, Rattus fuscipes/leucopus* and *Uromys caudimaculatus* from edge rainforest to interior rainforest (Table 5.5). In the open forest, the second MDS axis was primarily associated with decreases in the abundance of *Aepyprymnus rufescens, Isoodon macrourus* and *Rattus sordidus,* and increases in the abundances of *Antechinus flavipes, Rattus lutreolus* and *Melomys cervinipes* going from dry to wet sclerophyll (Table 5.5). There was a much greater degree of assemblage dissimilarity within the open forest than in the rainforest, which shows that the differences between the drier sclerophyll forest and the wet sclerophyll were greater than those between interior and edge rainforest. These two gradients meet, and overlap to a degree, in the more complex of the wet sclerophyll grids (point where gradients 1 and 2 meet in Figure 5.7).

Figure 5.7: MDS plot of the small mammal assemblage structure at each grid based on the relative abundance of 11 species of small mammals.
Lines marked 1 and 2 highlight the within habitat gradients (refer to text). Open symbols - open forest grids; closed symbols - closed forest; circles - southern sites; triangles - northern sites; IRF - dark green; ERF - light green; WS - blue; DS - red.



Although the primary MDS gradient, illustrated in Figure 5.7, represents large changes in the structure of the small mammal assemblages, it was not correlated with any measure of point diversity; that is, the mean diversity at a grid was relatively constant across the main gradient from open to closed forest (Table 5.5). The number of individuals per grid did significantly increase with MDS 1, and the biomass index decreased (Table 5.5). The decrease in biomass was primarily caused by the high biomass index in the dry sclerophyll, which was due to frequent captures of the small macropod *Aepyprymnus rufescens*. The biomass trend is severely biased, since a similar sized macropod (*Thylogale stigmatica*) is present in the rainforest, but was rarely captured in traps.

In contrast to the between-habitat gradient, the within-habitat gradient in assemblage structure in rainforest (gradient 1 in Figure 5.7) is related to significant trends in the diversity of small mammals. The species richness, diversity, number of individuals and the biomass at a point (grid) all increase from edge rainforest to interior rainforest (Table 5.5) along the within-habitat gradient in assemblage structure represented by the second MDS axis (Figure 5.7). In the open forest, only biomass is significantly related to within-habitat changes in assemblage structure and is primarily caused by the influence of *Aepyprymnus rufescens*.

Local (site) scale

Local species richness (total species richness of the five grids combined at each site) is negatively correlated with the position of the site along the gradient in assemblage structure (mean MDS axis 1 scores, Figure 5.7); that is, species richness is higher in the open forest sites (Table 5.6). Local species richness is also correlated with the spatial variability along the first axis (s.d. MDS 1 in Table 5.6). However, local species richness is most strongly correlated with the within-habitat variability in assemblage structure, represented by the standard deviation of the second MDS axis scores. Multiple regression (backward removal), using species richness as the dependent variable, and the mean and s.d. of the sites' MDS scores for both axes as the four independent variables, removed all variables except within-habitat variability (s.d. MDS 2). None of the other variables explained a significant amount of the variance in the total species richness of a site beyond that already explained by the within-habitat spatial variability in the mammal assemblage structure. Essentially, this means that nearly 93% of the variability in the species richness of a site can be explained by the spatial variability of the assemblage structure within the site (beta diversity) (Figure 5.8a). The total species richness of the site is also correlated with the mean of the total species richness of each grid within a site (alpha diversity) (Figure 5.8b; $r = 0.773$, $p = 0.024$). However, only 60% of the variance in site species richness is explained using alpha diversity (mean grid species richness) only. Therefore, local species richness is more dependent on the spatial variability in assemblage structure than it is on the point diversity within the site, so sites with a spatially variable assemblage structure have a higher species richness than those with a more spatially homogeneous assemblage.

Table 5.5: Relationships between species abundance, diversity and assemblage structure.

Correlations between the MDS axes describing mammal assemblage structure at each trapping grid and (1) the relative abundance of each species of small mammal and (2) measures of assemblage diversity at each grid. Correlations with the second axis only use within-habitat scores, therefore correlations are between the second MDS axis scores and the abundance of the species (or assemblage measure) in the twenty grids in each habitat only (closed forest - gradient 1 in Figure 5.7; open forest - gradient 2 in Figure 5.7; n = 20). Species not recorded in that habitat are indicated by "-". p=0.000 indicates that p<0.001.

	MDS 1 (n=40)		MDS 2 only open forest grids (n=20)		MDS 2 only rainforest grids (n=20)	
	r	**p**	**r**	**p**	**r**	**p**
Open Forest Species						
Antechinus flavipes	**-0.376**	**0.017**	**0.492**	**0.028**	0.039	0.871
Aepyprymnus rufescens	**-0.537**	**0.000**	**-0.646**	**0.002**	-	-
Isoodon macrourus	**-0.675**	**0.000**	**-0.611**	**0.004**	-	-
Melomys burtoni	**-0.400**	**0.011**	**0.457**	**0.043**	-	-
Rattus lutreolus	**-0.436**	**0.005**	**0.512**	**0.021**	0.147	0.536
Rattus sordidus	**-0.506**	**0.001**	**-0.592**	**0.006**	-	-
Closed Forest Species						
Antechinus godmani	**0.378**	**0.016**	-	-	-0.418	0.067
Antechinus stuartii	**0.566**	**0.000**	-	-	**-0.678**	**0.001**
Melomys cervinipes	**0.943**	**0.000**	**0.508**	**0.022**	**-0.731**	**0.000**
Rattus fuscipes/leucopus	**0.913**	**0.000**	0.436	0.055	**-0.838**	**0.000**
Uromys caudimaculatus	**0.728**	**0.000**	-	-	**-0.753**	**0.000**
Assemblage Variables						
Species richness	-0.178	0.271	0.128	0.590	**-0.755**	**0.000**
Diversity (H')	-0.231	0.152	0.080	0.736	**-0.694**	**0.001**
Evenness	-0.062	0.702	0.130	0.584	-0.208	0.380
No. of individuals	**0.839**	**0.000**	0.287	0.221	**-0.879**	**0.000**
Biomass	**-0.413**	**0.008**	**-0.756**	**0.000**	**-0.886**	**0.000**

Figure 5.8: The relative influence of α and β diversity on total species richness. Relationship between the total species richness of each site and (a) spatial variability in assemblage structure of the grids within a site (β diversity) and (b) the mean grid species richness within each site (α diversity).

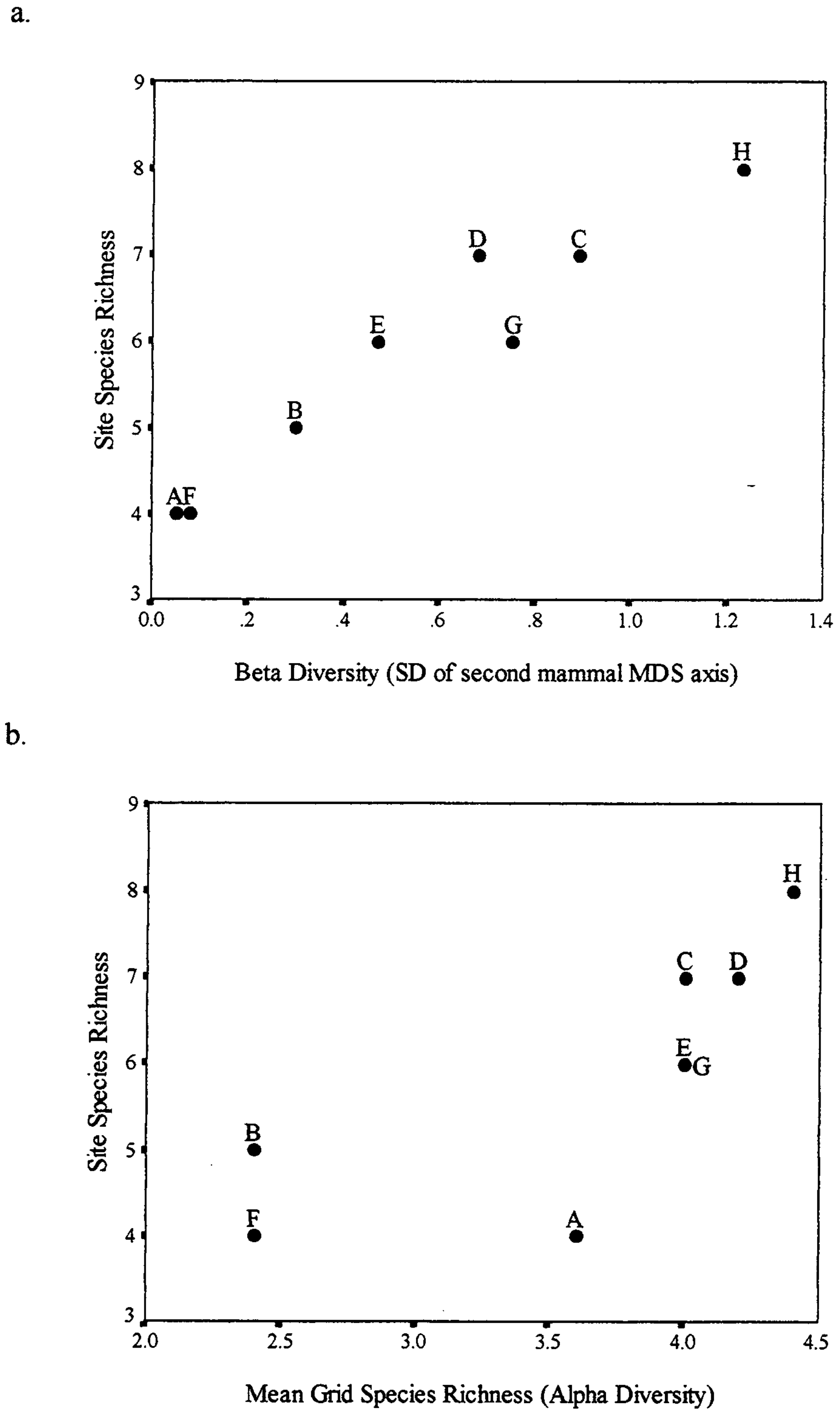


Table 5.6: Relationships between mammal diversity and assemblage structure. Correlations between position and variability along the gradient in mammal assemblage structure (mean and s.d. of MDS axis scores describing mammal assemblage structure at each grid, Figure 5.7) and measures of mammal diversity at each site (n=8). p=0.000 indicates that p<0.001.

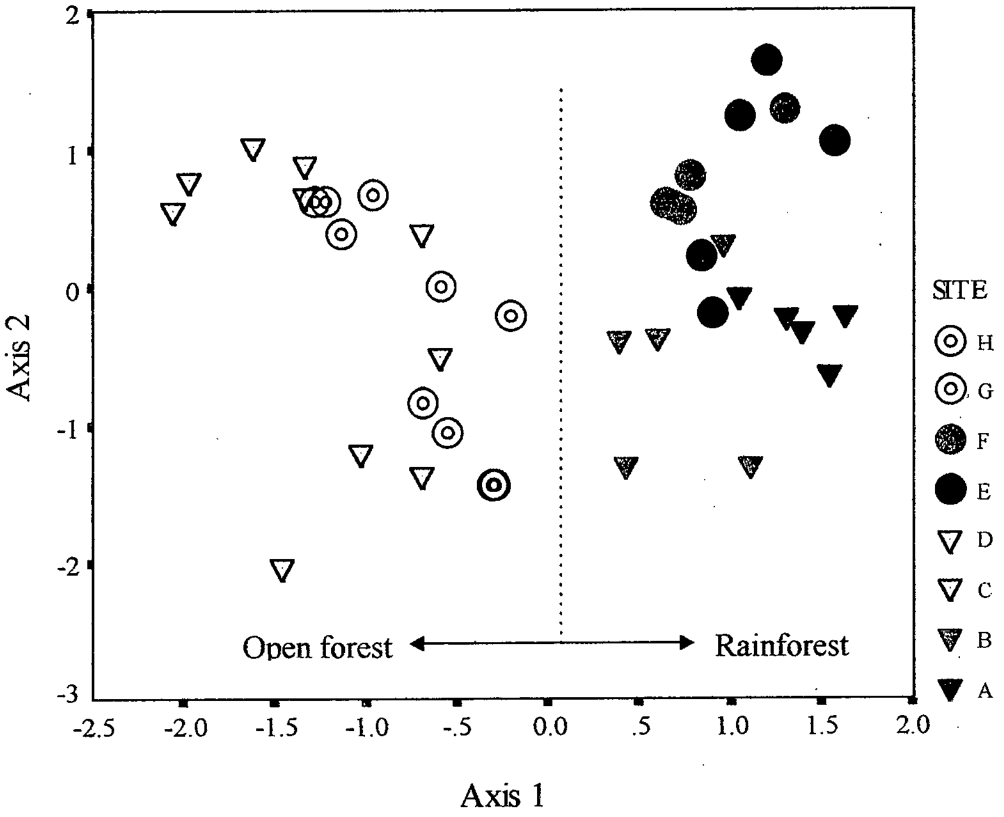
	Mean MDS1		s.d. MDS1		Mean MDS2		s.d. MDS 2	
	r	p	r	p	r	p	r	p
Sp. Richness	**-0.728**	**0.041**	**0.778**	**0.023**	-0.205	0.626	**0.963**	**0.000**
Diversity (H')	**-0.776**	**0.024**	0.596	0.119	0.053	0.901	**0.905**	**0.002**
Evenness	-0.660	0.075	0.383	0.349	0.186	0.659	**0.709**	**0.049**
No. Individuals	**0.906**	**0.002**	0.119	0.780	-0.537	0.170	-0.494	0.213
Biomass	-0.459	0.253	0.605	0.112	-0.705	0.051	0.614	0.105

Mammal assemblage structure - spotlighting data (samples pooled over time)

Point (200m segment) scale

Spotlighting results indicated very distinct differences between the mammal assemblages in open forest (Sites C, D, G, H) and rainforest (sites A, B, E, F) as illustrated by the MDS analysis of the mammal assemblage observed in each 200m segment of the eight spotlighting sites (Figure 5.9). Separating each 1 km transect into five segments allows an examination of the spatial variability in assemblage structure within a transect. This is an exercise in descriptive pattern analysis, as adjoining segments would violate the assumption of independence necessary in most statistical tests.

Figure 5.9: Mammal assemblage structure at the point scale (spotlighting data). MDS is used to describe the similarity of assemblage structure in each 200 m segment of the spotlighting transects at the eight primary sites, based on the relative abundance of 19 species. Open symbols - open forest grids; closed symbols - closed forest; circles - southern sites; triangles - northern sites; IRF - dark green; ERF - light green; WS - blue; DS - red.



The first MDS axis explains 52% of the variability in assemblage structure and primarily groups the segments into closed or open forest. Almost all species are correlated with this axis with most species being largely confined to one habitat (Table 5.7). The second MDS axis explained a further 19% of the variance in assemblage structure and describes the within-habitat differences in the mammal assemblage. In contrast to the trapping results, where there was a relatively low within-habitat variability in the rainforest, there was a similar degree of spatial variability in both habitats (Figure 5.9). In the open forest the second MDS axis was primarily related to higher abundances of *Petauroides volans, Thylogale stigmatica* and *Wallabia bicolor* in the wet sclerophyll and *Petaurus breviceps, Acrobates pygmaeus* and *Macropus giganteus* in the dry sclerophyll (Table 5.7). The within-habitat variation within rainforest was mostly related to higher abundances of *Perameles nasuta, Thylogale stigmatica,* and *Dendrolagus lumholtzii* in the southern, lower-altitude, more complex rainforest sites (E, F) and *Trichosurus vulpecula* and *Cercatetus caudatus* in the northern, higher-altitude, less complex rainforest sites (A, B). Neither MDS axis was correlated with species richness, diversity or evenness.

Table 5.7: Correlations between MDS axes from Figure 5.9 and the relative abundances of 19 species for each spotlighting segment

(MDS 1, n = 40; MDS 2, n= 20). Correlations for within-habitat variation (MDS 2) use only the twenty grids in each habitat and those species recorded in that habitat. p=0.000 indicates that p<0.001.

	MDS 1		MDS 2		MDS 2	
			open forest only		rainforest only	
Species	r	p	r	p	r	p
Acrobates pygmaeus	-0.213	0.188	**-0.641**	**0.002**	-	-
Aepyprymnus rufescens	**-0.429**	**0.006**	-0.113	0.636	-	-
Cercatetus caudatus	0.234	0.146	-	-	**0.534**	**0.015**
Dendrolagus lumholtzii	0.217	0.179	-	-	**-0.665**	**0.001**
Dactylopsila trivirgata	0.249	0.122	0.137	0.564	0.292	0.212
Hemibelideus lemuroides	**0.773**	**0.000**	-	-	0.109	0.648
Isoodon macrourus	**-0.560**	**0.000**	0.195	0.409	-	-
Macropus giganteus	-0.088	0.590	-0.401	0.079	-	-
Pseudochirops archeri	**0.561**	**0.000**	-	-	0.085	0.721
Petaurus breviceps	**-0.358**	**0.024**	**-0.711**	**0.000**	-0.160	0.501
Pseudochirulus herbertensis	**0.672**	**0.000**	-	-	0.107	0.653
Perameles nasuta	**0.587**	**0.000**	0.041	0.865	**0.776**	**0.000**
Pseudocheirus peregrinus	**-0.406**	**0.009**	0.120	0.616	-	-
Petauroides volans	**-0.751**	**0.000**	**0.805**	**0.000**	-	-
Trichosurus vulpecula	**0.453**	**0.003**	-0.033	0.890	**-0.530**	**0.016**
Thylogale stigmatica	**0.431**	**0.006**	**0.452**	**0.045**	**0.494**	**0.027**
Wallabia bicolor	**-0.676**	**0.000**	**0.457**	**0.043**	-	-
Petaurus australis	**-0.571**	**0.000**	-0.128	0.590	-	-

Local (site) scale

The species richness of mammals recorded by spotlighting was positively correlated with the spatial variability in assemblage structure within a site across both the main gradient (s.d. MDS 1) and the within-habitat gradient (s.d. MDS 2) (Table 5.8). Evenness is correlated with the second MDS axis (sites E, F and C, G have higher evenness than sites A, B and D, H in open and closed forest respectively). The combination of the species richness and evenness trends result in diversity (H') being correlated with both the mean and the variability of the second MDS axis. The total species richness of each site was not correlated with the mean species richness of the segments within the site (r = -0.038, p = 0.928). As with the trapping data, these results suggest that local species richness did not vary greatly across the main gradient, nor was it highly related to the levels of alpha diversity within the site; however, local species richness was strongly correlated with the spatial variability in assemblage structure within the site, i.e. beta diversity.

Table 5.8: Correlations between mammal diversity and assemblage structure. Mammal assemblage structure is indexed by the position and variability along the MDS axes using the relative abundances of the 19 species observed by spotlighting (mean and s.d. of MDS axis scores).

	Mean MDS 1		s.d. MDS 1		Mean MDS 2		s.d. MDS 2	
	r	p	r	p	r	p	r	p
Sp. Richness	-0.514	0.192	**0.743**	**0.035**	-0.356	0.387	**0.762**	**0.028**
Diversity (H')	-0.280	0.501	0.438	0.278	**-0.772**	**0.025**	**0.713**	**0.047**
Evenness	-0.046	0.914	0.128	0.763	**-0.849**	**0.008**	0.495	0.212

Relationship between mammal assemblage structure and vegetation structure

Point (grid) Scale

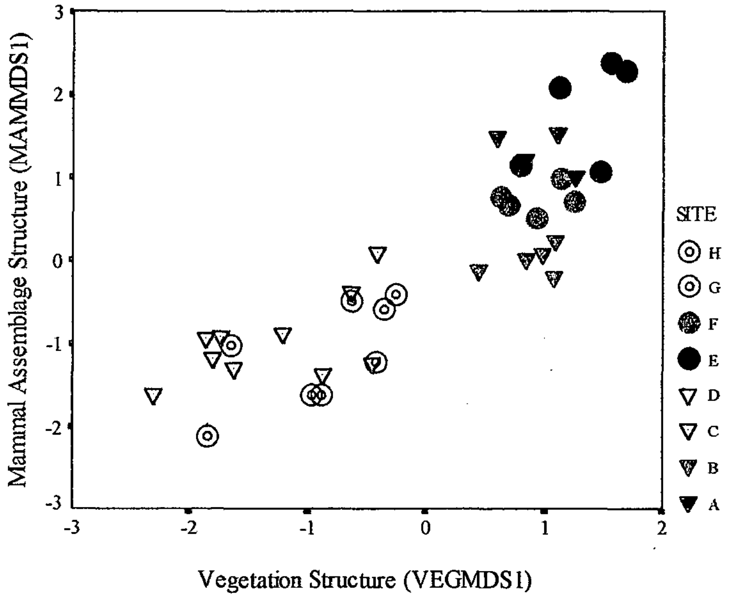
Trapping results

Figure 5.10a and Table 5.9 show that there was a very strong relationship between the structure of the vegetation and the mammal assemblage present at each trapping grid as shown by the correlation between the primary MDS axis describing the vegetation structure (from Figure 5.4) and the primary MDS axis describing the mammal assemblage structure at each grid (from Figure 5.5) ($r = 0.866$, $p = 0.000$, $n=39$). The second axis in vegetation structure is significantly correlated with the second axis in small mammal assemblage structure (Table 5.9, Figure 5.10b), indicating that the within-habitat variability in small mammal assemblage structure is related to the density of the shrub layers. Therefore, vegetation structure, using the density of vegetation in five vertical strata (both MDS axes), can explain 55% of the total variance in small mammal assemblage structure. This was calculated as follows: the first axis describing vegetation structure (MDS 1) explains 75% of the variation in mammal MDS1 (Table 5.9: $r=0.866$, so $r^2=0.75$), the primary MDS axis describing mammal assemblage structure explains 69% of the variability in mammal assemblage structure (from Figure 5.7), therefore 52% ($0.75 \times 0.69 = 0.52$) of the variance in the structure of the mammal assemblage was explained by the first vegetation MDS axis. Similarly, the second axis explains a further 3%, giving a total of 55%. This analysis cannot be undertaken for spotlighting data as vegetation was not measured in each segment of the spotlighting transects.

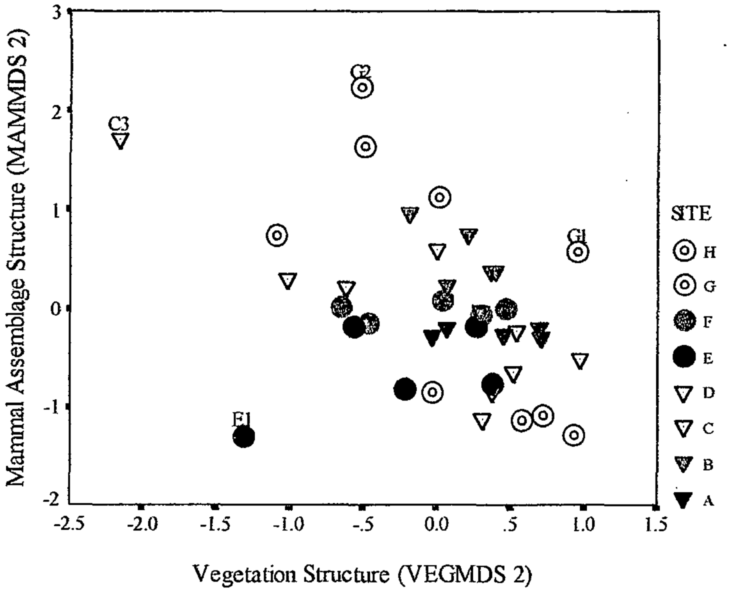
Multidimensional scaling, using the standard deviation of the vegetation density in each stratum over the five within-grid points, shows that most of the within-grid variability in vegetation structure was in the stratum between 0-5 m. The first MDS axis describes a gradient in the patchiness of the tall shrubs (2-5 m) and the second MDS axis describes a gradient in the patchiness of the ground cover and low shrubs (0-2 m). The total species richness of each grid was positively correlated with the within-grid variability in the ground cover/low shrubs (MDS axis 2, Table 5.9). Grid position along the primary gradient in mammal assemblage structure (Figure 5.7 - axis 1), biomass and the number of individuals were correlated with the variability in the tall shrub density (Table 5.9).

Figure 5.10: Relationship between the assemblage structure of small mammals at each grid and vegetation structure,
as expressed by the first and second MDS axes describing mammal and vegetation structure (mammal MDS axes from Figure 5.7 and vegetation MDS axes from Figure 5.4, see Table 5.10 for relevant statistics): a. relationship between first MDS axes; b. relationship between second MDS axes. Other combinations were not significant, see Table 5.10. Grid G5 excluded (see text). Open symbols - open forest grids; closed symbols - closed forest; circles - southern sites; triangles - northern sites; IRF - dark green; ERF - light green; WS - blue; DS - red.

a.



b.



Species richness and the biomass index were both negatively correlated with vegetation complexity, whereas the number of individuals increased with vegetation complexity (Table 5.9). Variation in mammal assemblage structure within each habitat (second MDS axis) was related to the density of the shrub layer (second vegetation MDS axis). Species diversity was positively correlated with shrub density and biomass was negatively correlated to shrub density (Table 5.9). However, it should be remembered that the second axes in the MDS analyses of both mammals and vegetation explained small amounts of the variance only, and the biological importance of this latter relationship is unclear. The species richness (and H') of a grid was positively correlated with the spatial variability in the density of the ground and low-shrub layer within the grid (Table 5.9).

Table 5.9: Correlations between small mammal assemblage structure and vegetation structure at each grid (n=39).

The MDS analysis of vegetation complexity at each grid used the mean density of vegetation in each of the five strata at five points within the grid. The MDS analysis of vegetation heterogeneity at each grid used the standard deviation of the vegetation density in each of the five strata over the five points within the grid. Strata which made the most significant contribution to each axis are listed in parentheses. p=0.000 indicates that p<0.001.

	Vegetation Complexity				Vegetation Heterogeneity			
	MDS 1 (Canopy, subcanopy)		MDS 2 (Shrubs)		MDS 1 (Tall shrubs)		MDS 2 (Ground & low shrubs)	
	r	p	r	p	r	p	r	p
Mammal MDS1	**0.866**	**0.000**	-0.171	0.305	**0.478**	**0.002**	0.107	0.517
Mammal MDS2	-0.089	0.594	**-0.415**	**0.010**	0.247	0.130	0.240	0.141
Species Richness	**-0.434**	**0.007**	**-0.280**	**0.088**	0.030	0.857	**0.382**	**0.016**
Diversity (H')	**-0.498**	**0.001**	**-0.320**	**0.050**	0.037	0.825	**0.361**	**0.024**
Evenness	-0.250	0.130	-0.260	0.115	0.112	0.499	0.212	0.195
No. of Individuals	**0.625**	**0.000**	-0.171	0.306	**0.334**	**0.038**	-0.038	0.818
Biomass	**-0.363**	**0.025**	**0.337**	**0.038**	**-0.409**	**0.010**	-0.046	0.782

Local (site) scale

Trapping results

The structure of the mammal assemblage at a site (as indexed by the mean of the first mammal MDS axis scores) was strongly correlated with both complexity and patchiness (Table 5.10). The mean position of the site along the within-habitat gradient (mean of the second mammal MDS axis scores) was not correlated with either complexity or patchiness. However, the within-habitat variability in assemblage structure (s.d. of the second MDS axis scores), which had a large influence on the total species richness of a site (Figure 5.8), was strongly correlated with vegetation patchiness (s.d. of the first vegetation MDS axis scores) (Table 5.10). The total species richness of a site was positively correlated with patchiness and negatively correlated with complexity, although much more of the variance was explained by vegetation patchiness than complexity (84% and 65% respectively). Similarly, diversity and evenness were correlated with both complexity and heterogeneity. The number of individuals increased with increasing complexity, although biomass was not related to either complexity or patchiness. The mean and s.d. of the second MDS axis for vegetation structure did not correlate with any measure of mammal assemblage structure at the site level and therefore were not included in Table 5.10.

Multiple regression analyses (backward removal) using species richness and beta diversity as the dependent variables and vegetation complexity and heterogeneity as the independent variables show that complexity does not explain a significant amount of the variance beyond that already explained by heterogeneity. These results suggest that the species richness of small mammals at the local scale (site) was limited by the species richness of the habitat where the site was situated and dependent on the spatial variability of the mammal assemblage structure within the site. In turn, the spatial variability of mammal assemblage structure within a site was strongly related to vegetation heterogeneity (Figure 5.11a & b).

Table 5.10: Correlations between vegetation complexity and patchiness and measures of small mammal assemblage structure and diversity (n=8).
Mammal MDS axes are those in Figure 5.7 and vegetation MDS axes are those in Figure 5.4.

	Vegetation Complexity (mean MDS1)		Vegetation Patchiness (s.d. MDS1)	
	r	p	r	p
Mammal mean MDS1	**0.931**	**0.001**	**-0.838**	**0.009**
Spatial Variability across gradient (s.d. MDS1 mamm)	-0.367	0.371	0.588	0.125
Mammal mean MDS2	-0.076	0.858	-0.034	0.936
Spatial variability within habitat (s.d. MDS2)	**-0.825**	**0.012**	**0.9359**	**0.001**
Species Richness	**-0.809**	**0.015**	**0.9156**	**0.001**
Diversity (H')	**-0.920**	**0.001**	**0.954**	**0.000**
Evenness	**-0.841**	**0.009**	**0.825**	**0.012**
Number of Individuals	**0.732**	**0.039**	-0.562	0.147
Biomass	-0.562	0.147	0.649	0.082

Spotlighting results

The assemblage structure of mammals, as indexed by the first axis of the mammal MDS analysis of spotlighting data, was related to both vegetation complexity and patchiness (Table 5.11). However, there were no significant correlations between the second mammal MDS axis, mammal spatial variability, species richness, diversity or evenness associated with either complexity or patchiness. The second axis, describing the within-habitat gradient in mammal assemblage structure, was strongly correlated with the within-habitat gradient in vegetation structure. Therefore, within each habitat (open or closed forest), the mammal assemblage structure was affected by the density of the shrub layer (see Figure 5.7 and Table 5.5 for the specific species affected by this vegetation gradient in shrub density). Mammal assemblage evenness and the second vegetation MDS axis were positively correlated, meaning that evenness was negatively correlated with the density of the shrub layer. Higher levels of evenness were observed at sites A, B, D and H where there was low shrub density.

Figure 5.11: Vegetation heterogeneity and mammal diversity (α and β).
The relationships between spatial heterogeneity of vegetation structure (patchiness) and, (a) local species richness of small mammals (α diversity) and (b) the β diversity or spatial variability in the structure of the small mammal assemblage (s.d. of mammal MDS 2 axis scores).

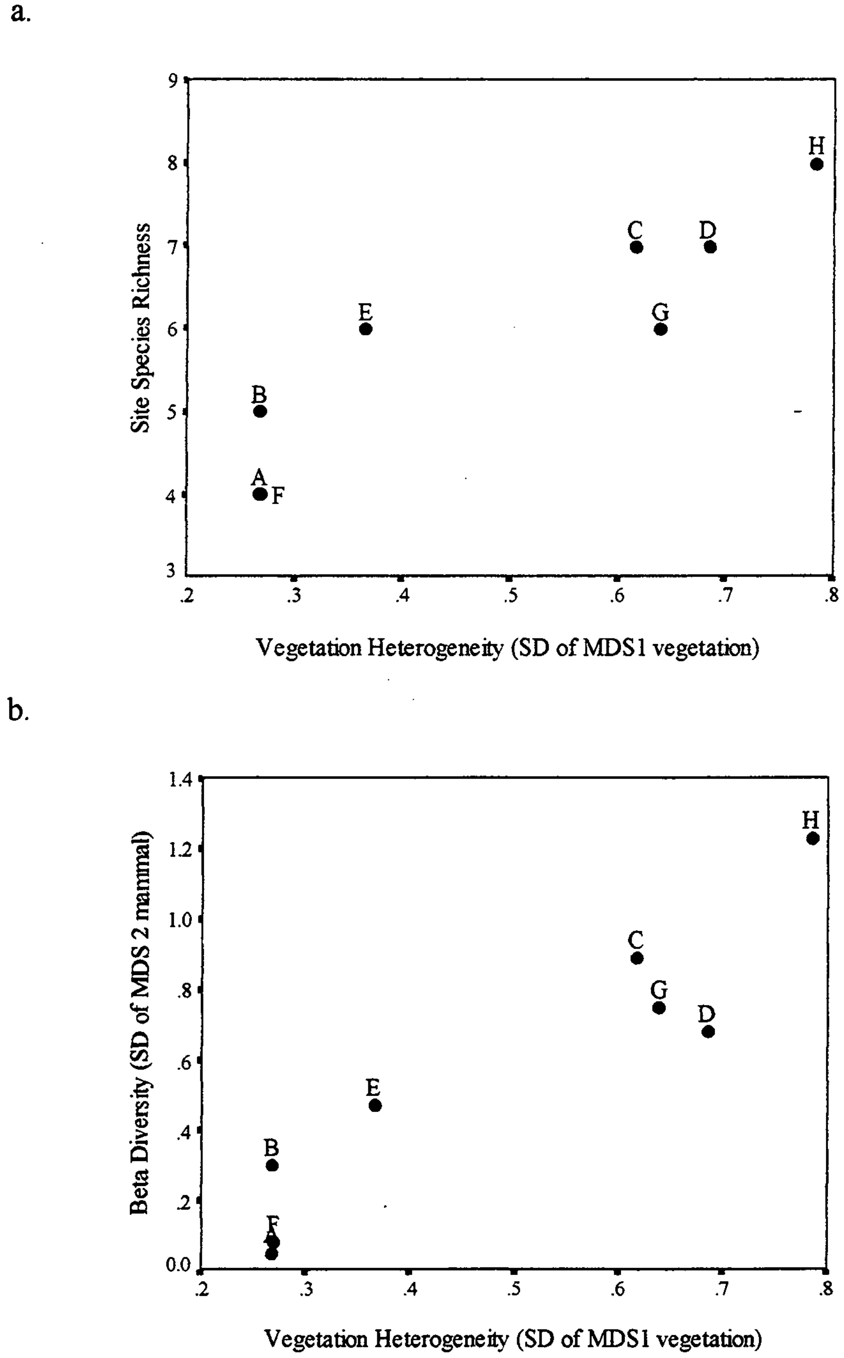


Table 5.11: Correlations between vegetation structure, and mammal assemblage structure and diversity.

Vegetation structure is represented by the first two axes of the MDS analysis of vegetation data and assemblage structure (represented by the first two axes of the MDS analysis of mammal assemblage structure using spotlighting data). (n=8)

	Vegetation (mean MDS1)		Vegetation (s.d. MDS1)		Vegetation (mean MDS2)		Vegetation (s.d. MDS 2)	
	r	p	r	p	r	p	r	p
Mammal (mean MDS1)	**0.889**	**0.003**	**-0.835**	**0.010**	0.087	0.838	-0.544	0.163
Mammal (s.d. MDS1)	-0.220	0.601	0.100	0.814	-0.221	0.600	-0.016	0.971
Mammal (mean MDS2)	0.400	0.326	-0.319	0.441	**-0.911**	**0.002**	0.625	0.098
Mammal (s.d. MDS2)	-0.056	0.895	0.110	0.796	0.234	0.578	-0.412	0.311
Species Richness	-0.522	0.185	0.489	0.219	0.087	0.839	-0.079	0.852
Diversity (H')	-0.525	0.181	0.412	0.311	0.674	0.067	-0.525	0.184
Evenness	-0.380	0.353	0.242	0.564	**0.888**	**0.003**	-0.687	0.060

Combined trapping and spotlighting results

Combining the data from spotlighting, trapping and miscellaneous observations gives a more complete picture of the total species assemblage at each site. However, since this analysis combines the results of different sampling methods using an ordinal scale of abundance, it was not possible to estimate the spatial variability in assemblage structure within a site. There is a clear difference between the assemblages in open and closed forest, as illustrated by the MDS plot of the eight sites (Figure 5.12). The primary axis represents a gradient from sclerophyll to interior rainforest and is essentially the same as the pattern shown in the separate trapping and spotlighting analyses. The abundance of 18 of the 28 species correlate with this axis (Table 5.12). The other ten species do not correlate with the axis either because (i) they were sampled in very low numbers (*Acrobates pygmaeus, Cercatetus caudatus, Dendrolagus lumholtzii, Pogonomys mollipilosus*), or (ii) at only one point on the gradient (*Antechinus stuartii, Macropus giganteus, Wallabia bicolor*), or (iii) because they were present right across the gradient (*Thylogale stigmatica, Trichosurus vulpecula*). In contrast to the separate analyses based on spotlighting and trapping, the combined MDS analysis does distinguish between edge and interior rainforest sites. The separation of edge from interior sites is mainly due to differences in abundance between interior rainforest and edge rainforest rather than a different species composition. Only one species (*Antechinus stuartii*) was recorded (at very low numbers) in the interior rainforest but not at an edge rainforest site: this species is known to be difficult to trap and to have a patchy distribution (Watt 1997). There was a difference in the assemblage structure of the southern (sites E, F) and northern (A, B) rainforest sites with *Perameles nasuta* being more common in the southern sites where the rainforest is more complex and *Trichosurus vulpecula* more common in the northern sites (second MDS axis, Table 5.12).

Figure 5.12: Mammal assemblage structure (combined data).
The similarity of mammal assemblages at each site as represented by multidimensional scaling using an ordinal index of relative abundance for 28 species based on the combined results of trapping, spotlighting and miscellaneous observations.

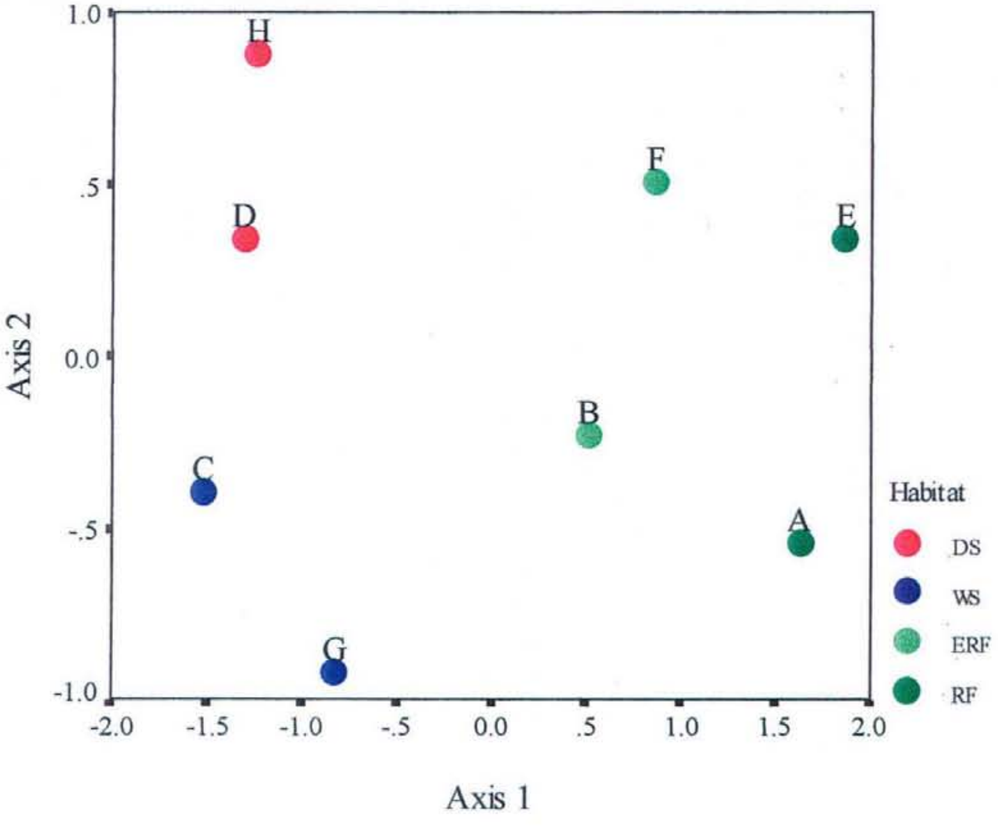


Figure 5.12 shows that there was much greater within-habitat variability (over the second MDS axis) in the structure of the overall mammal assemblage within the open forest sites than within the rainforest. In the open forest, there was a gradient from drier to wetter sclerophyll with some species being confined to the dry end of this gradient (*Rattus sordidus, Macropus giganteus, Acrobates pygmaeus*) and others to the wetter sclerophyll (*Wallabia bicolor, Rattus fuscipes/leucopus, Antechinus flavipes*) (Table 5.12).

Total species richness, diversity index, evenness, the number of mammal guilds (Braithwaite *et al.* 1985), the mean number of species per guild and the numbers of arboreal, scansorial and ground-dwelling species are shown in Table 5.13. The total species richness at a site was positively correlated to both the number of guilds ($n = 8$, $r = 0.730$, $p = 0.040$) and the mean number of species per guild ($n = 8$, $r = 0.752$, $p = 0.031$). However, the correlation between species richness and the number of guilds is trivial because the significant relationship was driven by the extreme leverage of one site (the low number of guilds at site A), whereas the relationship between species richness and the mean number of species per guild shows a more consistent trend. The number of scansorial species was positively related to vegetation complexity (Table 5.14) and negatively correlated with vegetation heterogeneity. In contrast, the number of ground-dwelling species was negatively correlated with complexity and positively correlated with heterogeneity. None of the other measures of diversity presented in Table 5.13 were correlated with either vegetation complexity or heterogeneity (Table 5.14).

Although there were no relationships between total species richness and the vegetation gradients, there were large differences in the numbers of species within specific guilds in rainforest and open forest. The guild classification of each species is shown in Appendix 6. The number of ground-dwelling species was significantly higher in the open forest while the number of scansorial species was higher in the closed forest (Table 5.14). There were seven species of arboreal folivores (Guild 7) in the rainforest (*Hemebelideus lemuroides, Pseudochirops archeri, Pseudocheirus herbertensis, Dendrolagus lumholtzi, Pogonomys mollipilosus, Melomys cervinipes* and *Trichosurus* *vulpecula johnstoni*) and only four in the open forest (*Pseudocheirus peregrinus, Petauroides volans, Melomys cervinipes* and *Trichosurus vulpecula vulpecula*). There were more species of scansorial insectivores (Guild 3) in the rainforest than in the open forest (four species in rainforest - *Antechinus godmani, A. stuartii, A. flavipes, Dactylopsila trivirgata*; and two species in open forest - *A. flavipes* and *D. trivirgata*). In contrast, arboreal nectarivores (Guild 1) were more common in the open forest than in the rainforest (open forest - *Acrobates pygmaeus, Petaurus breviceps, P. australis*; rainforest - *Cercatetus caudatus*); and grazing macropods (Guild 12, *Macropus giganteus, M. parryi, Wallabia bicolor*) and grass/sedge eating rodents (Guild 11, *Rattus lutreolus, R. sordidus*) were only found in the open forest. All of the gliders are predominantly open forest species (*Petauroides volans, Acrobates pygmaeus, Petaurus breviceps, P. australis*) with only *P. breviceps* being recorded in rainforest.

Table 5.12: Correlations between mammal assemblage structure, and mammal diversity and vegetation structure.

Correlations between MDS axes using the combined data (Figure 5.12) and the relative abundances of 28 species and the vegetation structure variables for each site (MDS 1, n = 8: MDS 2, n = 4). Correlations for within-habitat variation (MDS 2) use only the four sites in each habitat and those species recorded in that habitat. Only vegetation variables with correlation probability <0.1 are included here. Vegetation MDS axes are from Figure 5.4. "-" indicates that the species was not recorded in that habitat. "ns" - correlation probability >0.1. p=0.000 indicates that p<0.001. Quantitative estimates of abundances from spotlighting (S) ; or trapping (T).

		MDS 1		MDS 2 open forest only		MDS 2 rainforest only	
Species		r	p	r	p	r	p
Acrobates pygmaeus	S	ns	ns	ns	ns	-	-
Antechinus flavipes	T	-0.645	0.084	-0.988	0.012	ns	ns
Antechinus godmani	T	0.639	0.088	ns	ns	ns	ns
Antechinus stuartii	T	ns	ns	-	-	ns	ns
Aepyprymnus rufescens	TS	-0.768	0.030	ns	ns	-	-
Cercatetus caudatus	S	ns	ns	-	-	ns	ns
Dactylopsila trivirgata	S	ns	ns	ns	ns	ns	ns
Dendrolagus lumholtzii	S	ns	ns	-	-	ns	ns
Hemibelideus lemuroides	S	0.953	0.000	-	-	ns	ns
Isoodon macrourus	TS	-0.860	0.006	ns	ns	-	-
Melomys burtoni	T	-0.882	0.004	ns	ns	-	-
Melomys cervinipes	T	0.967	0.000	ns	ns	ns	ns
Macropus giganteus	S	ns	ns	ns	ns	-	-
Petaurus australis	S	-0.700	0.053	ns	ns	-	-
Petaurus breviceps	S	-0.637	0.089	ns	ns	ns	ns
Pogonomys mollipilosus	S	ns	ns	-	-	ns	ns
Pseudochirops archeri	S	0.873	0.005	-	-	ns	ns
Pseudochirulus herbertensis	S	0.881	0.004	-	-	ns	ns
Perameles nasuta	S	0.701	0.053	ns	ns	0.997	0.003
Pseudocheirus peregrinus	S	-0.788	0.020	ns	ns	-	-
Petauroides volans	S	-0.646	0.083	ns	ns	-	-
Rattus fuscipes/leucopus	T	0.907	0.002	-0.919	0.081	ns	ns
Rattus lutreolus	T	-0.736	0.037	ns	ns	-	-
Rattus sordidus	T	-0.644	0.085	0.977	0.023	-	-
Thylogale stigmatica	S	ns	ns	ns	ns	ns	ns
Trichosurus vulpecula	S	ns	ns	ns	ns	-0.961	0.039
Uromys caudimaculatus	T	0.824	0.012	-	-	ns	ns
Wallabia bicolor	S	ns	ns	-0.999	0.001	-	-
Vegetation variables							
Ground cover (0-1m)		-0.934	0.001	ns	ns	ns	ns
Ground cover patchiness		0.813	0.014	ns	ns	ns	ns
Subcanopy density		0.919	0.001	-0.991	0.009	ns	ns
Subcanopy patchiness		ns	ns	-0.986	0.014	ns	ns
Shrub density (2-5m)		ns	ns	-0.947	0.053	0.916	0.084
Shrub patchiness		ns	ns	-0.917	0.083	ns	ns
Vegetation MDS 1 axis		0.956	0.000	ns	ns	ns	ns
Vegetation MDS 1 s.d.		-0.878	0.004	ns	ns	ns	ns
Vegetation MDS 2 axis		ns	ns	0.904	0.096	ns	ns
Vegetation MDS 2 s.d.		ns	ns	ns	ns	ns	ns

Table 5.13: Measures of mammal diversity at each of the sites.
Data from the combination of all methods, including: the total recorded species richness, the species richness within different ecological groups, the number of guilds present, the mean number of species per guild, assemblage evenness (J') and diversity (H').

		Species richness							
Site	Habitat	Total species richness	Arboreal species richness	Ground species richness	Scansorial species richness	No. of guilds	Mean no. spp. per guild	Even (J')	Diversity (H')
A	IRF	11	5	3	3	5	1.80	0.85	1.95
F	ERF	14	6	3	5	7	2.00	0.69	1.82
G	WS	14	6	6	2	7	1.88	0.68	1.78
B	ERF	15	7	5	3	8	1.88	0.77	2.09
C	WS	15	5	8	2	8	1.88	0.71	1.93
E	IRF	15	7	3	5	7	2.14	0.72	1.94
H	DS	15	6	7	2	7	2.14	0.81	2.19
D	DS	17	7	8	2	7	2.43	0.89	2.53

Table 5.14: Correlations between vegetation complexity and heterogeneity and mammal assemblage structure.
Uses the data from the combination of trapping and spotlighting (n=8).

	Vegetation Complexity (mean MDS1)		Vegetation Heterogeneity (s.d. MDS1)	
	r	p	r	p
Species Richness - total	-0.488	0.220	0.516	0.190
Species Richness - arboreals	-0.017	0.969	0.102	0.809
Species Richness - scansorial	**0.838**	**0.009**	**-0.736**	**0.037**
Species Richness - ground	**-0.934**	**0.001**	**0.857**	**0.007**
Diversity (H')	-0.503	0.204	0.425	0.294
Evenness	-0.277	0.506	0.168	0.691
Number of guilds	-0.248	0.554	0.249	0.553
Number of species per guild	-0.419	0.302	0.464	0.247

Discussion

Small mammal trapping

Vegetation structure and mammal assemblage structure - point scale

The structure of small mammal assemblages at each grid was closely related to the vegetation structure at that grid (Figure 5.10). The primary and the secondary gradients in mammal assemblage structure and vegetation structure were significantly correlated, respectively. Therefore, variation in mammal assemblage structure can be linked to vegetation structure both between habitats and within habitats. This suggests that microhabitat selection was an important factor in the determination of the assemblage structure of small mammals. A significant relationship between vegetation structure and the structure of the small mammal assemblage is not surprising as many studies in a variety of habitats globally have found similar relationships (Braithwaite & Gullan 1978; Dueser & Shugart 1978; Hockings 1981; August 1983; Friend & Taylor 1985; Williams 1990; Williams & Marsh in review).

The small mammal diversity at a grid (point species richness and H') was related to both the mean vegetation complexity at the grid and the spatial heterogeneity within the grid; however, only about 20% of the variance in species richness was explained by complexity and even less of the variance (~15%) was explained by the within-grid heterogeneity of vegetation (Table 5.9). It is not surprising that spatial variability over a distance of 50 m does not have a large effect on the mammal assemblage, as individuals of most species operate on a spatial scale larger than the grid, or at least utilise nearby areas. Demonstrating a relationship between habitat structure and the small mammal diversity at a point has not always been successful in forest environments (Hockings 1981; August 1983), although spatial heterogeneity and complexity have been found to be significant factors in simpler environments (M'Closkey 1976; Brown 1973).

Vegetation structure and mammal assemblage structure - site scale

The species richness of small mammals at a site (local species richness) was primarily the result of spatial variation in assemblage structure within the site (Figure 5.8). This type of within-habitat variation in assemblage structure is referred to as internal beta diversity (Whittaker 1977). Although species richness at a site was also correlated with the levels of species richness at a point within the site (alpha diversity), more of the variance was explained by spatial heterogeneity in assemblage structure, and multiple regression analyses show that point diversity did not explain a significant amount of the variance beyond that already explained by spatial heterogeneity.

The number of small, predominantly ground-dwelling, mammal species at a site (local species richness) was primarily associated with the degree of spatial patchiness in vegetation structure, rather than vegetation complexity. Although the total species richness of small mammals at each site was correlated with both vegetation complexity and vegetation heterogeneity (Table 5.10), multiple regression analysis suggests that complexity did not significantly add to the amount of variance in species richness (or beta diversity) already explained by vegetation heterogeneity. There was no relationship between vegetation structure and small mammal diversity across a similar vegetation gradient in Venezuela (August 1983); however, M'Closkey (1976) found that vegetation patchiness was an important correlate of small mammal diversity in a shrubland in southern California. One of the problems with many studies attempting to demonstrate relationships between diversity and habitat structure is the use of an inappropriate scale of sampling. This was recognised by August (1983) who discussed the effects of the spatial scale of sampling with respect to the grain size of the habitat patches. Since it is often impossible to predict the appropriate spatial scale of analysis, a sampling design which is spatially nested, as in this study, allows an examination of observed patterns at several spatial scales.

Sampling considerations

The selection of grids which sampled as much as possible of the variability in vegetation structure within a site, was a key factor in showing the close relationship between vegetation and the structure of the small mammal assemblage. This is shown by the gradient of changes exhibited both in the vegetation structure and the mammal assemblage structure in the MDS analyses (Figures 5.4 & 5.7), rather than a clumped pattern which would have been the likely result had the grids been selected randomly within the sites, with less variability between grids. Morris (1992) expressed concern over the use of ecotones in studying habitat selection due to the difficulty in determining whether observed patterns of movement are due to foraging or dispersal movements. This is not a concern in this study since the distance between sampling points (grids) was greater than the foraging movements of most species (there were very few captures of the same individual at different grids) and the distance between sites was greater than the dispersal distances of most species (there was no observed movement of an individual of any species between sites). This represents another advantage of the use of a sampling design which is spatially nested and spans a spatial scale large enough to minimise effects due to the movements of individuals, as opposed to only examining a small section of the gradient as in Williams & Marsh (in review).

It is interesting that within-habitat variation in assemblage structure (s.d. of MDS scores axis 2, Figure 5.7), and not between-habitat variation (s.d. of MDS scores axis 1, Figure 5.7), explains most of the variation in species richness. There was a high degree of between-habitat beta diversity across the primary habitat gradient; that is, the assemblage underwent a complete change in species composition (Table 5.5, Figure 5.7). However, point species richness (alpha diversity) remained relatively constant within all of the sites. The lack of a relationship between species richness and between-habitat variation in assemblage structure (MDS axis 1 in Figure 5.7 and Table 5.5) was partially a product of the sampling design: the five sampling points within each site were all within the same habitat, thereby limiting the observed between-habitat variability. If sites had been chosen with sampling points in both open and closed forest, the local species richness of those sites would have been very high, due to the inclusion of both open and closed forest species. However, the high local species richness at a local site which spanned the rainforest / open forest boundary would be spurious, confounding the patterns and processes of two completely different habitats and assemblages.

Inadequate sampling can artificially inflate estimates of beta diversity because low numbers of individuals cause higher variance, and increase the influence of stochastic captures of rare species. This is unlikely to be a significant problem in these analyses for three reasons:

1. species which were inadequately sampled by both sampling methods were excluded from the quantitative analyses to reduce the problems caused by stochastic captures of rarely observed species;
2. it would also be expected that if the patterns of beta diversity were an artifact of low numbers of individuals, then beta diversity and the number of individuals would be inversely correlated, and this was not the case (correlation with s.d. of MDS axes:

first axis r = 0.119, p = 0.780; second axis r = -0.495, p = 0.213, NB. relationship were checked for non-linear trends also);

3. the close relationship between species richness (and beta diversity) with spatial heterogeneity of the vegetation structure provides a plausible explanation for the observed patterns: that is, it demonstrates a classic relationship between habitat heterogeneity and diversity (Pianka 1966).

Spotlighting

Vegetation structure and mammal assemblage structure - site scale

There was a tight association between vegetation structure and the mammal assemblage structure described by the spotlighting data (Table 5.11); however, the only correlation between any of the diversity measures and the gradients of vegetation complexity and heterogeneity was between assemblage evenness and the second vegetation gradient. This suggests that assemblage evenness is promoted by a high density of shrubs. The general lack of relationships between canopy structure and arboreal diversity is interesting, since diversity theory would predict that the more complex canopy in the rainforest should support more niches and, therefore, more arboreal species (Southwood 1996). In contrast with my results, a study of mammal assemblages across a similar vegetation gradient in Venezuela found that arboreal species richness increased with vegetation complexity (August 1983). The lack of diversity patterns within the arboreal mammals is probably related to the relative spatial homogeneity of the subcanopy and canopy structure within a site. This implies that the number of arboreal species is not related to the structural complexity of the canopy, which varies enormously across the primary gradient, but may be related to spatial heterogeneity in canopy structure.

The degree of spatial variability in the arboreal assemblage structure was similar in rainforest and open forest (Figure 5.9). This pattern contrasts markedly with those of the ground-dwelling assemblage in which there was more heterogeneity in the open forest than in the rainforest (Figure 5.7). As the sites were deliberately chosen to represent a particular habitat, predisposing the spatial heterogeneity of the canopy within a site to be relatively low, it is impossible to determine from these data whether arboreal diversity is related to spatial heterogeneity in canopy structure. The fact that there was a strong correlation between mammal assemblage structure and vegetation structure, on both vegetation gradients (Table 5.9), indicates that there was a real relationship between mammal assemblage structure and vegetation structure; however, the analysis of the relationship between species richness (spotlighting) and spatial variability in mammal assemblage structure (beta diversity) is limited by two facts:

1. the vegetation was measured at the trapping grids which are only partly representative of the whole spotlighting transect and, given the relatively small spatial scale over which the vegetation structure can change, it is not surprising that no relationships were found between vegetation structure and mammal diversity; and
2. the definition of vegetation strata was biased towards picking up heterogeneity in the middle and lower layers, whereas most of the species sampled by spotlighting were canopy dwellers (structural description limited to two layers).

Alternatively, arboreal assemblage structure may not be related to canopy structure at all and may be related to other resources or processes (see discussion on guilds below).

Combined trapping / spotlighting data - site scale

Combining the data from trapping and spotlighting shows that total mammal diversity (species richness, H', evenness, number of guilds, number of species per guild) was not correlated with either complexity or heterogeneity, and that mammal diversity was relatively constant across the primary habitat gradient. However, the constancy of species richness across the gradient is really the result of three, very different, trends:

1. the species richness of scansorial species was positively associated with complexity, which is not surprising given the increased foraging area produced in high complexity habitats;
2. the species richness of ground-dwelling species shows the opposite trend and seems to mostly be the product of the higher heterogeneity in the open forest rather than lower complexity *per se*. The open forest has a patchy ground, shrub and subcanopy which allows species which are primarily rainforest species to utilise those areas with dense middle-level vegetation. The resulting mixture of both rainforest and open forest small mammals produces the high species richness in the open forest;

3. in contrast, the species richness of arboreal mammals does not vary across the gradient; this is surprising as it could be expected that there would be more arboreal niches and hence a higher species richness in the habitat with a more complex canopy. However, the canopy in open forest is dominated by eucalypts and, unlike the ground vegetation, there is very little intrusion by rainforest species, so there is little mixing of canopy habitats, and hence no mixing of the arboreal faunas.

Although there was little change in the total species richness of arboreal mammals, the number of guilds or the mean number of species per guild over the primary vegetation gradient, there were large differences in the distributions of species within guilds. In contrast to the results of this study, August (1983) found that both the number of guilds and the number of species per guild increased with vegetation complexity; however, both studies found that higher species richness was the result of both more guilds and higher species packing, with more of the variation in species richness being explained by species packing (species per guild). The higher number of species of arboreal folivores (Guild 7) in the rainforest was due to three species which have no open forest equivalent (*Dendrolagus lumholtzi*, *Pseudochirops archeri* and *Pogonomys mollipilosus*). There were two examples of species replacement across the gradient: *Hemibelideus lemuroides* with *Petauroides volans*; and *Pseudocheirulus herbertensis* with *Pseudocheirus peregrinus*. There is some controversy over the taxonomic status of the two sub-species of *Trichosurus vulpecula* but there was a turnover in this species across the gradient as well (*T. v. johnstoni* with *T. v. vulpecula*). One species in this guild occured across the gradient (*Melomys cervinipes*). The higher numbers of species and numbers of individuals of this guild within rainforest was probably related to the greater resource levels, that is a greater productivity and floristic diversity of canopy foliage.

Scansorial insectivores (Guild 3) were mostly restricted to rainforest. This is not surprising since there was a much greater architectural complexity and ostensibly a larger number of foraging niches in rainforest (Southwood 1996). There were no species in this guild that were restricted to open forest, although *Antechinus flavipes* was most common in the wet sclerophyll (WS).

There were three guilds which were primarily found in the open forest:

1. Arboreal nectarivores (Guild 1) consisted of three species of gliding possums (*Acrobates pygmaeus, Petaurus australis, P.breviceps*) in the open forest and the northern pygmy-possum (*Cercatetus caudatus)* in the rainforest. The diversity of this guild in open forest was probably related to a specific resource; that is, the nectar and sap produced by myrtaceous plants (mostly eucalypts and banksias) in the open forest.
2. Large, grazing macropods (Guild 12, three species; *Macropus giganteus, M.parryi, Wallabia bicolor*); and
3. Herbivorous rodents (Guild 11, two species; *Rattus lutreolus, R.sordidus*) were only found in the open forest because there is very little ground vegetation (grasses) in the rainforest.

Community saturation?

The relative constancy of point diversity of mammals across the study area, shown by most of the analyses, suggests local assemblage saturation. It is interesting that the levels of species richness are the same despite the large differences in the habitat structure, given that many studies have shown increased diversity with increases in architectural complexity of the habitat (Southwood 1996). Local species richness is primarily associated with the level of spatial variability in assemblage structure (beta diversity) which is related to habitat heterogeneity, although the upper ceiling has to be limited by the available pool of species. The analysis of guild structure, which was successful in interpreting regional patterns in species richness (Chapter 4), did not help to explain any of the patterns of diversity at the local scale. However, there were large differences in the guild structure across the gradient despite the constancy in numbers of guilds and mean species richness per guild. This may indicate that the relative constancy of diversity across the vegetation gradient (total species richness, number of guilds, number of species per guild) is spurious and does not suggest a consistent pattern of community saturation. If community saturation was the cause of the observed pattern of constant local diversity, then a consistent trend of species turnover within guilds would be expected. However, the observed pattern is mostly a turnover of guilds relating to the specific resource requirements of each guild. The guild structure may be limited by the available species pool which has been determined by historical biogeographic processes at a regional scale (Chapter 4), and the available resources within each habitat at the landscape scale. The constancy of local diversity may thus be spurious and not a product of community saturation.

The relationships between mammal assemblage structure and vegetation structure

I have demonstrated that there is a close association between mammal assemblage structure and the structure of the vegetation at all of the spatial scales examined (point, local, habitat). Most previous studies on the relationships between mammal assemblages and habitat structure have found that habitat structure is a good predictor of assemblage composition (Rosenzweig & Winakur 1969; Brown 1973; M'Closkey 1976; Barnett *et al.* 1978; Fox 1981; Hockings 1981; August 1983; Schwarzkopf & Ryland 1989; Kelt *et al.* 1994; Williams & Marsh in review). However, the effect of habitat structure on measures of diversity have been quite variable; some studies have shown close relationships between mammal diversity and habitat structure (Rosenzweig & Winakur 1969; M'Closkey 1976) while others have found no relationship (Brown 1973; Hockings 1981; August 1983). Few studies have examined the total mammal fauna and many have examined only the small mammal assemblage.

August (1983) examined the total mammal assemblage across a gradient in vegetation complexity from rainforest to savanna in Venezuela. Although that study had many similarities with this study, the results are quite different. August (1983) found that total mammal species richness increased with vegetation complexity and to a lesser degree with spatial heterogeneity, and that small mammal species richness was not related to either complexity or heterogeneity. The increased species richness in more complex vegetation was due to more scansorial and arboreal species. My results also show that scansorial species richness increases with complexity (Table 5.14); however, the other results are quite different, with a strong effect of heterogeneity on ground-dwelling small mammals and no effect of complexity on arboreal species richness (Table 5.14), although this is really a complex interaction between several guilds with opposite trends across the gradient (see above discussion). A single trapping grid in each of five habitat types was used in the study by August (1983). The use of a large grid with no within-habitat replication, and analysis at the trap scale may have had a significant effect on the findings. August attributed the lack of an effect of heterogeneity to a sampling scale which was inappropriate to the grain size of the assemblage patchiness. The multiscale approach used in this study, with five grids in each of eight sites, allows a higher resolution of patterns of spatial variability. The lack of a relationship between vegetation complexity and arboreal species richness in this study, as compared to August (1983), seems to be a result of the high diversity of arboreal mammals in the open forest. This may be a product of the many species of gliding possums which are able to utilise resources more efficiently within the simpler vegetation. Without gliding, arboreal species must climb down a tree and cross the ground in order to reach another tree, an alternative which is both energy intensive and dangerous due to predation on the ground. Demonstration of a relationship between spatial heterogeneity and faunal diversity is more problematic as the spatial scale of observation can have a large effect on the observed patterns (Morris 1992).

I have shown that vegetation complexity and spatial heterogeneity both contribute to patterns of species richness; however, the relationships are a complex interaction between habitat structure and different subsets of the total mammal assemblage. Habitat complexity and heterogeneity should both contribute to faunal diversity according to the theories of niche relations and habitat capacity (Southwood 1996); this study supports this hypothesis for the mammals in the forests of the southern Atherton Tableland. Simple, all-encompassing generalities are rarely possible, and relationships must be set within a framework of initial conditions (MacArthur 1972; May 1986). MacArthur (1972) predicted that ecological relationships must be described within initial conditions, that is "for organisms of type A, in environments of structure B, such and such relations will hold". This is very much the case in the results of this whole study. For example, for scansorial species, across a gradient of vegetation complexity, there will be an increase in species richness in the more complex vegetation.

Mass effect

Williams and Marsh (in review) suggested that the higher diversity (H') of small mammals in the wet sclerophyll forest was the result of a mass effect (Shmida and Wilson 1985), where rainforest species are intruding into the open forest. A "mass effect" occurs when species, which are really part of an assemblage in an adjoining habitat, are observed and their presence is not self-maintaining. The presence of rainforest species in the wet sclerophyll is made possible by the patches of suitable, albeit sub-optimal, habitat within the wet sclerophyll. This patchiness becomes evident in the high heterogeneity in vegetation structure observed by Williams and Marsh (in review) and in this study. In this study, there was a significant relationship between the habitat heterogeneity and small mammal species richness, whereas in the previous study (Williams and Marsh, in review) there was no relationship with species richness, only with species diversity, which in that study, was primarily a function of high evenness. However, the study by Williams and Marsh (in review) was conducted on the western edge of the Paluma Range, an area of the Wet Tropics with a very similar habitat gradient to this study, but a much lower species richness of mammals due to differing effects of biogeographic history (Chapter 4). In both studies, the diversity of the small mammal assemblage was significantly related to the spatial variability in vegetation structure: in the less diverse assemblage (Williams & Marsh, in review) this was manifest in spatial patterns of abundances, where habitat heterogeneity promoted evenness, while in the more diverse assemblage (this study) it was manifest in all measures of diversity (species richness, diversity and evenness). Previous studies have shown that niche overlap is inversely dependent on species richness (Pianka 1972; M'Closkey 1976; Fox 1981), so it would be interesting to compare these two areas (Paluma and Atherton), using similar sampling designs, in order to compare the effect of the different levels of species richness on patterns of niche overlap. Without detailed studies of the movement patterns of individuals, it is difficult to determine if the patterns observed during this study are the result of a mass effect. Several factors suggest that it is not entirely a mass effect:

1. In this study, some "rainforest" species were observed at a much greater distance (>1 km) from the rainforest, than in the study by Williams and Marsh (in review) where the maximum distance was 200 m.
2. Several rainforest species were successfully bred on non-rainforest sites, with marked juveniles growing into adults during the study (*Rattus fuscipes, Melomys cervinipes*).
3. The pervasiveness of a relationship between habitat heterogeneity and mammal diversity in areas with quite different levels of species richness suggests that habitat

diversity has a real influence on the small mammal assemblage. The presence of rainforest species in the wet sclerophyll forest is related to this habitat heterogeneity and is not a simple mass effect.

Edge effects

Edge rainforest had the lowest mean point species richness of small mammals of the four habitats (Figure 5.5b), and within the rainforest there was a significant increase in species richness, diversity, number of individuals and biomass from edge to interior rainforest (Figure 5.7, Table 5.5). The lower point diversity in edge rainforest may have been the result of the low numbers of individuals in edge rainforest because at the spatial scale of a site, the total number of species observed in edge rainforest was not significantly different to the number in interior rainforest in the trapping, spotlighting or combined analyses. Therefore, the lower point diversity but similar site diversity, observed in the edge rainforest, was the result of either a low point diversity with a spatially patchy assemblage structure, or it was an artifact produced by the low numbers of individuals causing high spatial and temporal stochastity and the subsequent over-estimation of spatial heterogeneity. Only *Antechinus stuartii* was not observed in the edge rainforest and it is probable that even this species was present in very low numbers (Watt 1997). Spotlighting data suggested that the difference between the northern and southern rainforest sites was greater than the difference between the interior and edge sites (Figure 5.9). The analyses showed that the difference between interior and edge rainforest sites was due to a lower abundance of all rainforest species in the edge sites. Of the four rainforest sites, site E was the most different: it had the highest species richness, the highest beta diversity, the highest number of individuals and the highest vegetation complexity and patchiness in both MDS axes. The other interior rainforest site (A) had the lowest levels of mammal diversity of all eight of the sites. Therefore, it must be concluded that the edge effects at this natural rainforest/wet sclerophyll boundary were not particularly pronounced and that there was more variation in the assemblage structure within rainforest, related to vegetation complexity and heterogeneity, than to an edge effect *per se*. This result is quite different from the results found at anthropogenic edges in the Wet Tropics, where there were significant differences in the mammal assemblage structure between edge rainforest and core rainforest (Laurance 1990; 1991a; 1991b; 1994; Laurance & Yensen 1991). Several studies have demonstrated that habitat edges differ in their relative permeability, with 'soft' edges producing less marked and more gradual effects on the fauna (Stamps *et al.* 1987). The natural rainforest ecotone is expected to be a much 'softer' edge than an anthropogenically cleared edge, and the less pronounced edge-effects observed in this study, compared to fragmentation studies, are probably the result of this "softness".

Spatial scale

Analysis at the point scale (grid, 200m segment) showed that species richness at a point was negatively correlated with vegetation complexity and positively correlated with the variability of the density of ground cover and low shrubs within the grid (Table 5.9). However, at this spatial scale it is unrealistic to examine the spatial variability in mammal assemblage structure since the sampling scale is smaller than the scale of the movements of individuals of most species. Using the larger spatial scale represented by a site (local), it was still possible to relate species richness and assemblage structure to vegetation complexity and heterogeneity. Additionally, within-site variability in mammal assemblage structure (beta diversity) could be assessed. Analysis of these patterns showed that beta diversity was responsible for most of the variation in local species richness and that beta diversity was closely related to vegetation heterogeneity. This would have been missed if only the grid scale was used; that is, the most appropriate spatial scale to examine within-habitat variability in mammal assemblages is the site, or local, scale. Combining sites into broad habitat categories allowed the examination of trends across the open forest / closed forest gradient and highlighted several factors and trends not obvious at the smaller spatial scales:

1. sample species richness was quite different to cumulative species richness over time and sample species richness was heavily influenced by the number of individuals;
2. the low point species richness of edge rainforest; and
3. the high total species richness of the open forest.

The examination of assemblage patterns at several nested spatial and temporal scales reveals more about the relationships between the assemblage and the habitat, than is evident when only one spatial scale is used.

Inappropriate spatial scale of sampling with respect to the grain size of habitat patchiness may explain the lack of studies which demonstrate a significant effect of heterogeneity (Bond *et al.* 1980; Hockings 1981; August 1983; but see M'Closkey 1976 for a positive relationship). The multiscale approach used here, combined with the deliberate nesting of as much spatial variability in within-habitat vegetation structure as possible, are probably the key factors enabling the demonstration of the effects of spatial habitat heterogeneity on the mammal assemblage structure and diversity.

Productivity

Vegetation productivity was not explicitly examined in this study; however, the gradient in vegetation complexity from open forest into rainforest represents a large change in the biomass of vegetation, and productivity is generally related to vegetation biomass (Southwood 1996). The relationship between diversity and productivity has been intensively studied with quite variable results and no universal rule has been found (Southwood 1996). However, there is considerable evidence that there is a humped relationship between diversity and productivity with the highest diversity at intermediate levels of productivity (Abramsky & Rosenzweig 1984; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993). Tilman & Pacala (1993) suggest that the reason for lower diversity at high levels of productivity is related to the tendency for high productivity to lead to high homogeneity and an uneven assemblage structure. This may be the case with the ground dwelling mammals in this study, where the high productivity of the rainforest (compared with open forest) produces a homogeneous and dense canopy which restricts vegetative growth in the lower levels of the forest. The resulting homogeneous vegetation is shown in this study to be related to lower species richness, which supports the hypothesis suggested by Tilman & Pacala (1993). Extending the sampling further into the dry woodland where productivity is even lower would be very likely to produce a humped diversity pattern, as small mammal diversity is lower in the dry woodlands than in the study area (Williams *et al.* 1993). Additionally, the significantly higher number of individuals and the higher biomass of small mammals in the rainforest may be related to higher levels of productivity (August 1983; Tilman & Pacala 1993; Southwood 1996).

The benefits of using a multi-technique sampling approach

The use of the ordinal scale of abundance allowed the inclusion of incidental records and, more importantly, the data from the two principal methods could be combined to analyse the mammal assemblage as a whole. Most of the patterns found in the combined analyses were analogous to those found in the separate analyses. For example, the increase in the species richness of ground-dwelling species in the open forest came out in both the trapping and the combined analyses. The lack of a gradient in the species richness of arboreal mammals was confirmed in both spotlighting and combined analyses. However, the combined analyses produced several results which could not be examined in the separate analyses. Analysis of the guild structure is only realistic using the entire mammal assemblage. Additionally, the pattern of higher species richness of scansorial species in the rainforest was highlighted by the combined analysis. The combined analysis added further support for the relative constancy of species richness across the gradient. Most importantly, the analysis increased the generality of the observed patterns: for example, if only trapping was used, the result would have been that there is an increase in diversity with habitat heterogeneity, yet this is not the case in the scansorial species (where there is a decrease) or the arboreal species of the assemblage (where there was no change in species richness). The use of a single sampling technique is common in many studies and the generality of the results is limited when compared to the results obtained when most of the species in the assemblage are sampled by the use of several techniques.

Summary

Processes which contribute to spatial patterns of diversity at the local / landscape spatial scale can be classified into three types, namely: local ecological interactions, within-habitat dynamics and the interaction between habitats (Schluter & Ricklefs 1993). The results presented in this chapter identified the effects of all three types of process and showed them to be significantly related to the spatial patterns of local mammal diversity:

1. *Ecological interactions*: The spatial patterns in the structure of the mammal assemblage were closely related to the complexity and spatial variability in vegetation structure. Species turnover within guilds across the gradient suggests an effect of diffuse competition within some guilds (Fox 1981) and that the diversity within some guilds was related to the availability of specific resources.
2. *Within-habitat dynamics*: Spatial variability in assemblage structure within a habitat was shown to be the most significant factor relating to local species richness of small

mammals and this internal beta diversity was highly correlated with spatial variability in the vegetation structure.

3. *Interaction between habitats*: The intrusion of rainforest species into the wet sclerophyll forest had significant influences on patterns of assemblage structure and was probably due to the combined influence of a mass-effect (movement between habitats) (Shmida & Wilson 1985) and high habitat diversity in the wet sclerophyll. Guild turnover across the gradient showed a significant effect of different resources and habitats within the landscape and highlighted the large effect that guild turnover has on diversity at the landscape scale.

This chapter addressed several specific questions, which can now be answered:

1. *Can the spatial patterns in the structure of the mammal assemblage (composition, abundances, diversity, biomass, numbers of individuals, guild structure) be explained by vegetation structure?* Yes, all aspects of assemblage structure were significantly related to vegetation structure.
2. *Do habitat complexity or spatial heterogeneity have a significant influence on mammal diversity?* Yes, both complexity and heterogeneity influence patterns of diversity; however, the relationships are variable and specific to particular guilds or ecological subsets of the mammal assemblage.
3. *Are relationships consistent across spatial scales and taxonomic/ecological subsets of the mammal assemblage?* No, patterns of diversity were not always consistent between taxonomic or ecological groups and the spatial scale of sampling had a great influence on the results. Different ecological interactions become apparent at different spatial scales, although some factors were consistent across spatial scales, e.g. the effect of habitat heterogeneity. There were large differences in the relationship between habitat and assemblage structure between different ecological subsets of the assemblage. This is highlighted in the discussion on the various guilds. This chapter confirms the necessity of examining diversity within meaningful ecological groups; it is simply not adequate to examine total species richness alone if the determinants of spatial patterns of diversity are to be understood.
4. *Does habitat structure affect arboreal and ground-dwelling species in a similar way?* This is unclear because, although the diversity of ground-dwelling species was closely related to spatial heterogeneity and the diversity of arboreal mammals was

not, there was insufficient within-site variability in canopy structure to be sure of the lack of a relationship in the latter. Scansorial species were the only group to show an association with vegetation complexity.

5. *Do the local patterns match the regional patterns discussed in previous chapters?* Although regional-scale processes may be the key processes in determining the available species pool in a landscape or local area (Chapter 4), these results demonstrate that local scale processes are extremely significant in structuring mammal assemblages and determining levels of local diversity.

Chapter 6: General Discussion

This study examined spatial patterns of vertebrate biodiversity over a range of spatial scales and has significantly increased our understanding of the determinants of biodiversity in the rainforests of the Australian Wet Tropics. The first part of this discussion will summarise the main conclusions from each chapter, the second part will answer the specific questions asked in the general introduction and the third part will discuss the implications of spatial scale in the examination of the determinants of vertebrate diversity.

Summary of main conclusions

Chapter 2 presents the first complete review, compilation and summary of the distributional patterns of the terrestrial vertebrates of the Wet Tropics. The compiled data represent a significant management resource detailing the biogeographic patterns of diversity, regional endemism and conservation significance of terrestrial vertebrates within the region. The analyses presented in Chapter 2 showed that total species richness in rainforest at the subregional level was related to the coarse, landscape-scale habitat heterogeneity. Rainforest was also shown to have a higher number of species in those subregions where other habitats were present, suggesting that the species richness in rainforest was enhanced by between-habitat movements from the adjacent sclerophyll habitats of species which cannot survive in rainforest alone. Therefore, landscape-level habitat heterogeneity was an important factor in the spatial patterns of subregional biodiversity.

The analyses of the patterns of endemism (Chapter 3) suggested that historical fluctuations in rainforest area have been an important process, via sub-regional extinctions of rainforest endemics (species sifting), in determining current patterns of distributions, species richness and endemism in the vertebrates of Australian tropical rainforests. The results also supported the hypothesis that habitat heterogeneity promotes diversity and demonstrate that different ecological groups relate to different aspects of habitat heterogeneity. The loss of habitat heterogeneity (microhabitats, specific resources etc.) during historical rainforest contractions was suggested as the cause of the localised extinctions.

In the analyses of regional patterns of mammal diversity (Chapter 4), habitat heterogeneity was again shown to be closely related to patterns of species richness. Analyses of the guild structure of rainforest mammals showed that most of the variability in patterns of species richness was related to the degree of species packing within three, primarily arboreal, guilds (arboreal folivores, arboreal insectivore/nectarivores and scansorial guilds). I suggested the hypothesis that the geographic patterns in the species richness of rainforest mammals within the Australian Wet Tropics biogeographic region are largely the result of historical extinctions in these guilds. These extinctions have resulted from rainforest contractions due to climatic fluctuations, as discussed in Chapter 3, leading to historical bottlenecks in rainforest area and therefore habitat heterogeneity.

Chapter 5 showed that the structure of the mammal assemblage at the local scale was strongly correlated with the vegetation structure. Vegetation complexity was closely related to the presence or absence of specific guilds but not to total species richness. The spatial heterogeniety of vegetation structure was significantly related to the spatial variability in assemblage structure (beta diversity), and this beta diversity was the main contributor to the local species richness of mammals. The interactions between microhabitat structure and the local assemblage structure suggested that local scale processes were extremely significant in structuring mammal assemblages at the local scale. Edge effects were shown to be relatively weak across the natural rainforest boundary.

Specific questions posed in the General Introduction

Which environmental factors are related to spatial patterns of diversity and do they vary between taxonomic or ecological groups?

Habitat heterogeneity consistently explained significant amounts of the variance in patterns of vertebrate species richness across most taxonomic and ecological groups, and at all of the spatial scales examined. Habitat area also explained significant amounts of the variance in patterns of species richness within most taxonomic and ecological groups. However, the analyses that excluded area (Chapters 2 and 4) indicated that area acted as the sum of the various measures of habitat heterogeneity, and it was shown that rainfall diversity (an index of coarse habitat diversity) explained more of the variance in patterns of species richness than did area for birds and reptiles. The spatial heterogeneity of vegetation structure was also shown to be important in explaining patterns of mammalian species richness at the local and point spatial scales (Chapter 5). Rainforest shape was also consistently negatively correlated with the number of regional endemics and the proportion of endemism; the importance of shape is that the combination of area and shape reflect the relative effects of historical rainforest contractions and subsequent localised (subregional) extinctions (Chapters 3 and 4). Other variables were more taxon-specific: for example, altitude was of particular importance to mammals, and there were indications that frog species richness increased with rainfall and decreased with latitude (Chapter 2).

Are specific subsets of the fauna, a particular guild for example, responsible for variation in the spatial patterns of diversity?

The results suggest that spatial patterns of species richness can be largely driven by variation in the number of species within a few important guilds. Chapter 4 showed that 96% of the variation in mammal species richness could be explained by the species richness of three guilds, with 73% being explained by one guild (arboreal folivores). The guilds involved were those which would be most affected by extinctions resulting from historical contractions of rainforest. Similarly, the endemic species of each taxonomic group had a large influence on the assemblage structure within each subregion (Chapter 3). Most of the variation in subregional species richness of frogs was also explained by a single guild (Williams & Hero in review - Appendix 8).

How are patterns of diversity related to local ecological interactions with habitat structure, within-habitat movements and spatial variability, or between-habitat movements and species turnover?

Mammal assemblage structure, including patterns of species richness, was closely associated with vegetation structure showing that there were strong ecological interactions between each mammal species and habitat structure. The relationship between spatial variability in small mammal assemblage structure and local species richness demonstrated that within-habitat dynamics were extremely important influences on spatial patterns of diversity (Chapter 5). Low numbers of individuals in the edge rainforest may contribute to artificially high estimates of beta diversity due to the within-habitat movements of individuals. Between-habitat effects were more difficult to determine: regional scale analyses suggested that, since rainforest assemblages were more diverse when other habitats were also present within the subregion, movements between habitats increased the species richness of vertebrates in the rainforest (a "mass-effect"). Movements of individuals across the rainforest / open forest ecotone may be important in increasing species richness in the wet sclerophyll forest; however, the results in Chapter 5 suggest that this was probably not a straightforward "mass-effect" and that the higher levels of species richness in the wet sclerophyll forest were largely due to higher habitat heterogeneity.

Are patterns in local diversity affected by local processes or are they simply a subset of regional diversity and primarily determined by regional scale processes?

Local scale processes were extremely significant in structuring local assemblages and shaping spatial patterns of local diversity. Local diversity is, by definition, a subset of regional diversity; however, patterns of local diversity are not a static subset of regional diversity. Local diversity is a dynamic combination of the larger scale processes producing an upper limit to local diversity and local scale processes (ecological interactions, within-habitat dynamics, between-habitat movements) producing the spatial patterns within a region.

What has been the effect of the biogeographic history of the region?

Biogeographic history has had a huge influence on the vertebrate fauna of the Wet Tropics. The regional fauna has a long and complicated history of between-region exchange with both the surrounding sclerophyll forests and the rainforests further to the north on Cape York and New Guinea (Chapter 2). Historical rainforest contractions during the Pleistocene have probably been the most significant influence on current patterns of species richness and assemblage structure: the guilds present, the species packing within guilds, the proportion of regional endemism and the total species richness of the mammals have all been affected by biogeographic history (Chapters 3 & 4). Although the contractions have predominantly had a sifting effect, via localised extinctions, there are several examples of allopatric speciation also (Chapter 4). Similarly, rainforest contractions have produced a large degree of phylogeographic structuring of genetic diversity within populations in the Wet Tropics (Joseph *et al.* 1995; Schneider *et al.* 1997).

How do the patterns of species richness and ecological diversity relate to known phylogeographic patterns in genetic diversity?

The patterns of species richness and assemblage structure were closely concordant with the phylogeographic patterns of genetic diversity. Assemblage level analyses of mammals in Chapter 4 showed that the most significant geographic differences in assemblage structure occur across the Black Mountain barrier; this is similar to the patterns exhibited by the genetic structure of many rainforest species (Moritz *et al.* 1993; Schneider *et al.* 1997). The more detailed geographic structuring in assemblage similarity concurs with patterns of genetic similarity that are currently under examination (C. Scneider *pers. comm.*). The hypothesis of historical sifting of assemblages by localised extinctions is supported by molecular data which suggest that extinction and patterns of recolonisation, and not speciation, have been the primary processes behind current phylogeographic patterns of genetic diversity (Schneider *et al.* 1997). Additionally, the location of historical refugia as indicated by patterns of genetic similarity accord with the areas suggested by the combination of current rainforest area and shape and associated patterns of endemism (Chapter 3).

Do the processes associated with the spatial patterns of species diversity vary at different spatial scales?

Yes, the total species richness of a given area may have its upper limit constrained by processes operating at a larger spatial scale; however, patterns of diversity within a particular spatial scale are associated with processes that operate at that scale. Therefore, different processes are important at each spatial scale. For example, historical extinctions have a large effect on regional scale patterns but within a particular landscape or local area the effects of historical biogeography will have been relatively uniform and within-landscape patterns will be the result of within-landscape processes. Even processes which are significant at all spatial scales, for example habitat heterogeneity, operate differently at different spatial scales. For example: on a local scale, the spatial variability of vegetation structure affects both point diversity and the beta diversity of the assemblage, and this beta diversity is closely related to the local species richness; on a landscape scale, the number of rainforest structural types affects the number of species in the rainforest within the landscape via guild packing; and finally, on a regional scale, the number of major habitat types in each subregion affects the regional patterns of species richness via guild addition and species turnover within guilds.

The pervasiveness of the effects of spatial scale: the whole is greater than the sum of the parts

Understanding the effect of spatial scale is crucial to understanding the generality of processes which limit or promote biodiversity. The different spatial scales and the variety of processes which act at each spatial scale are illustrated by the conceptual models presented in Figures 6.1 and 6.2. There is a hierarchy of spatial scale, with each smaller scale nested within a larger scale. This model represents an amalgamation of the hierarchical model proposed by Ricklefs and Schluter (1993b) and the results of this study. The available species pool at a given spatial scale constrains the upper limit of species richness possible at the smaller scales within. A variety of processes determine what portion of the larger species pool is present in each of the smaller scale species pools (Figure 6.1 & 6.2). Species richness at each spatial scale is also increased by various processes (Figure 6.1). The sequence of scales presented in Figure 6.1 is not a linear sequence: each species pool is one possibility of many within the constraints imposed by the larger scale species pool that it is within. Figure 6.2 is a schematic diagram to illustrate the nested, tree-like structure of the model which is simplified in Figure 6.1.

Chapter 2 briefly discussed the biogeographic relationships which have determined the regional species pool; however, detailed consideration at this scale is outside the scope of this study. The model (Figure 6.1) illustrates the hypothesis that the species pool present in any subregion within the region has been filtered by localised extinction due to historical fluctuations in rainforest area (Chapters 3 & 4) and is affected by the area and diversity of the habitats within each subregion. The habitat diversity is largely determined by the spatial variability of the climate and topography within the subregion. Species richness is increased over evolutionary time by vicariant, allopatric speciation within isolated refugia and by recolonisation from other subregions where refugia may have persisted.

The species found in a particular landscape within each subregion are determined by the number, type and area of the constituent habitats and sometimes by the presences of a specific microhabitat, e.g. a creek or rocky outcrop. This spatial scale (landscapes) and its relationships with the larger and smaller spatial scales is the scale which this study has examined least. Future work is needed to examine these mesoscale patterns and processes. The process which probably has the largest influence on increasing species richness at this spatial scale is dispersal between landscapes (Figure 6.1).

Each landscape usually consists of one to many different distinct habitats (rainforest, wet sclerophyll etc.), with the within-habitat spatial and temporal heterogeneity of the environment (e.g. the diversity of rainforest structural types) combined with the specific habitat preferences of individual species determining the number of species found within each habitat species pool (Chapter 5). The species richness of each habitat may be increased by the movements of individuals between habitats, a “mass-effect”.

The local species richness of any given place in a habitat, that is an area where the individuals of an assemblage could interact, is related to the fine scale structure of the habitat, including both the complexity and the spatial heterogeneity of the vegetation (Chapte 5). Local diversity may be enhanced by the movements of individuals within the habitat or by the movements between habitats if the site in question is adjacent to a habitat boundary.

This model supports the hypotheses that diversity is the result of different processes acting at different spatial scales (Ricklefs 1987; Ricklefs and Schluter 1993b; Bohning-Gaese 1997). The major difference between this conceptual model (Figure 6.1) and the models which propose that local diversity is primarily just a static subset of regional diversity (eg. Cornell & Lawton 1992; Griffiths 1997) is that this model recognises that different processes are of primary importance at different spatial scales and that there are dynamic processes causing patterns within any given spatial scale. This is the noise around a regression of local versus regional diversity: it is a tautology that local diversity is a proportion of regional diversity (so called 'proportional sampling'): local diversity is, by definition, a subset of, and is constrained by, regional diversity. However, the patterns within a region are very much dependent on dynamic processes at the landscape, habitat and local spatial scales.

Another problem with many comparisons of local and regional diversity is that they in fact compare regional and landscape diversity for the particular study organisms (Caley & Schluter 1997; Griffiths 1997). The smallest 'local scale' used in the study by Caley and Schluter (1997) was still 2500 km^2 which is not an appropriate scale for the examination of local ecological interactions. Griffiths (1997), in a study on the diversity of lacustrine fish assemblages, defined the local scale to be an individual lake. A lake may be more analogous to a landscape (Figures 6.1 & 6.2) and a more realistic 'local' scale may be a much smaller area within the lake: for example, fish species richness was found to be remarkably constant at small spatial scales (approx. 100 m) in streams in northern Australia (B. Pusey *pers. comm.*). It is not surprising that local scale processes such as microhabitat selection (inferring competition) are not significant when comparing landscape and regional diversity. The scale of comparison is crucial the regional habitat complement (Figure 6.1). Dismissing community saturation is not possible with a comparison between the diversity of regions and landscapes. Saturation, if it does occur, can only be examined at a truly local scale where individuals interact, which for most terrestrial vertebrates is a spatial scale in the order of hundreds of metres, and not tens of kilometres. Careful consideration of appropriate spatial scale is crucial in studying the determinants of biodiversity and attempting to determine causal processes in the observed patterns. Research aimed at examining the determinants of patterns of diversity needs to be very careful to address questions at an appropriate scale or, alternatively, because the appropriate scale is not known, it is necessary to examine patterns over a range of nested spatial scales to gain an understanding of the effects of scale. The success of this study in elucidating the patterns and processes influencing the spatial patterns of vertebrate biodiversity in the Wet Tropics resides, to a large extent, in the spatially nested sampling regime.

Figure 6.1: Conceptual model of the processes which affect species richness over a range of spatial scales.

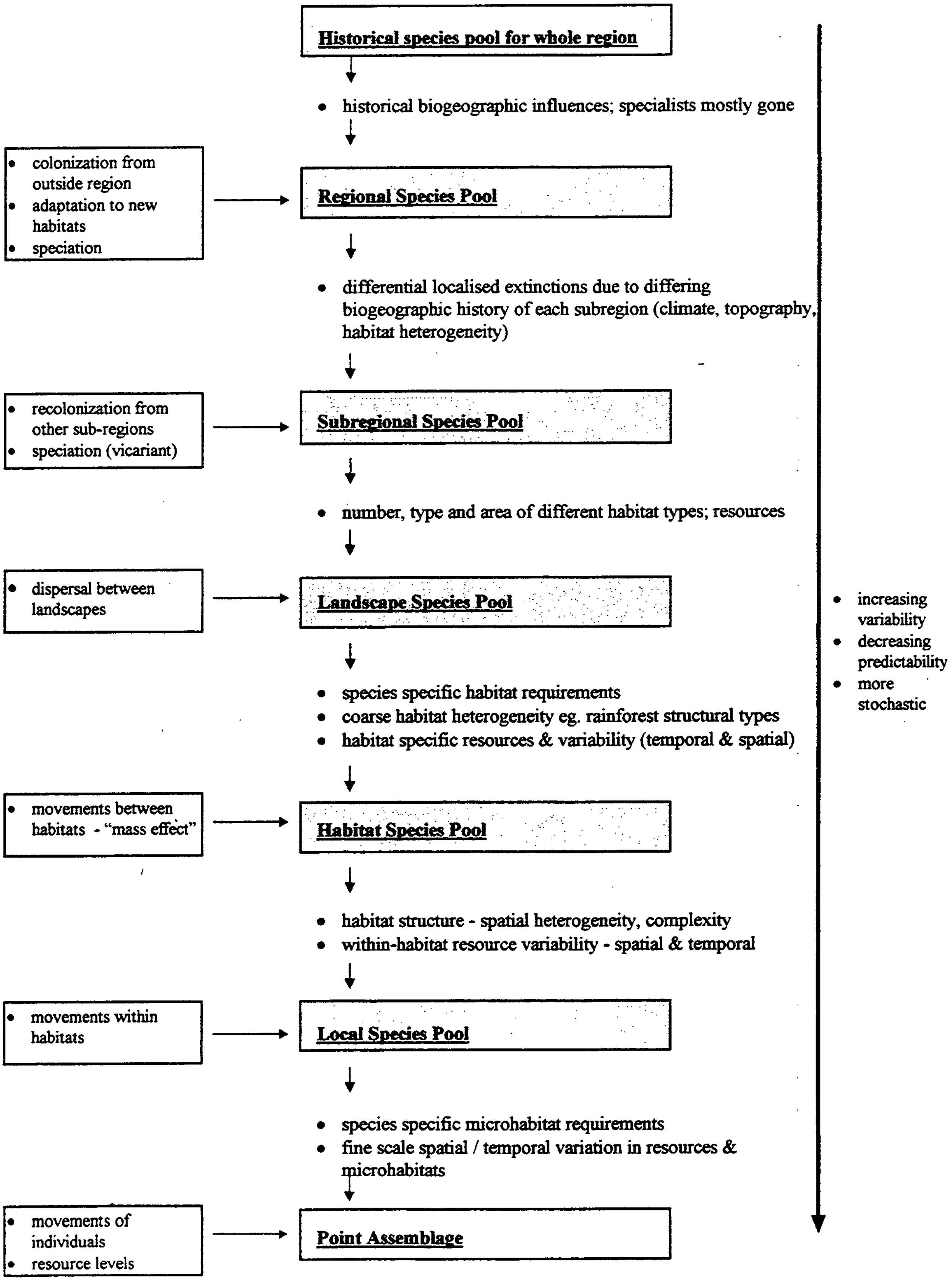
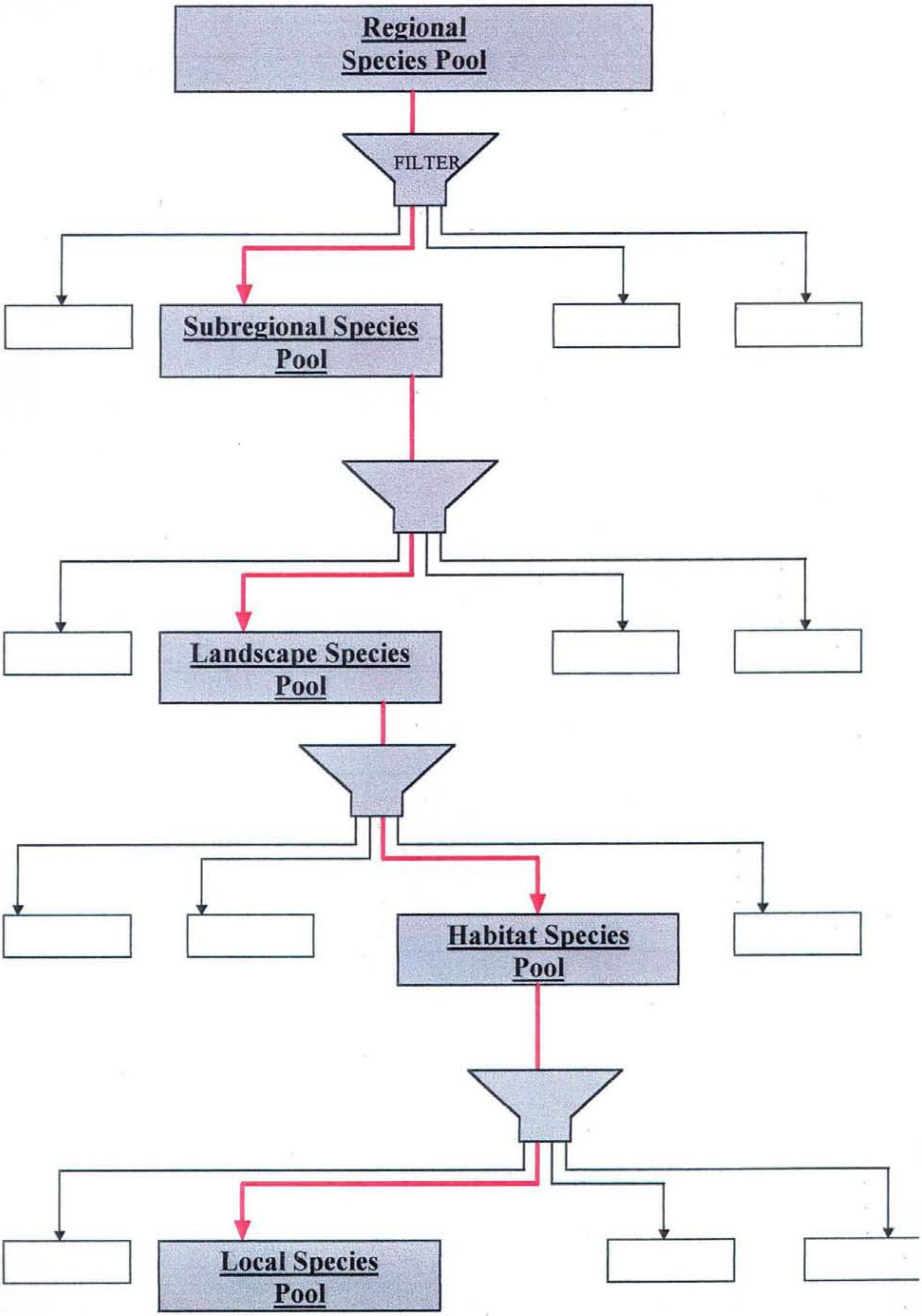


Figure 6.2: Schematic to show the branched nature of the nested hierarchy of spatial scales.

The funnel symbol represents a differential filter which determines the subset of the species pool at each larger spatial scale which goes into each species pool at the smaller spatial scale. The red line shows one of many alternative paths to local diversity. See Figure 6.1 for inputs to the species pools.



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Appendix 1: Mammal distributions within the Wet Tropics biogeographic region by faunal subregions. List compiled from the sources in the Special References (Appendix 5). Refer to Figure 2.1 for subregion codes. Key: * - definite record, P - highly probable occurrence, L - possibly present. Species of particular importance to conservation and management are designated Very Important Species (VIS): VIS = 1 if either the species or subspecies is endemic to the region and/or has a rare and endangered listing (refer text). E = edge species (not true Wet Tropics species, refer text). Names follow Strahn (1995).

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Ornithorhyncidae																										
Ornithorhyncus anatinus		Platypus	_	*	*	*	*	*	*	L	L	_	*	*	*	*	*	P	*	*	_	_	_	*	_	1
Tachyglossidae																										
Tachyglossus aculeatus		Short-beaked Echidna	*	*	*	*	*	*	*	*	P	P	*	*	*	*	*	P	P	*	P	P	*	*	*	0
Dasyuridae																										
Antechinus flavipes		Yellow-footed Antechinus	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	L	*	_	_	1
Antechinus godmani		Atherton Antechinus	_	_	_	L	_	L	L	_	_	_	*	*	*	*	_	_	_	_	_	_	_	_	_	1
Antechinus stuartii		Brown Antechinus	_	L	_	L	*	*	*	_	P	_	*	*	*	*	*	L	P	*	*	_	_	_	_	1
Dasyurus hallucatus		Northern Quoll	*	*	*	*	P	*	P	P	*	*	*	_	*	P	*	L	P	P	P	*	_	*	_	0
Dasyurus maculatus		Spotted-tailed Quoll	_	*	*	*	*	*	*	L	L	_	*	*	*	P	L	L	L	L	L	_	_	_	_	1
Phascogale tapoatafa		Brush-tailed Phascogale	*	_	P	_	_	L	L	_	L	_	*	_	L	L	_	_	_	_	_	_	_	_	_	1
Planigale ingrami	E	Long-tailed Planigale	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Planigale maculata		Common Planigale	*	_	L	_	_	P	_	P	*	_	*	_	*	*	_	_	_	_	_	*	*	*	_	0
Sminthopsis leucopus		White-footed Dunnart	_	_	_	_	_	_	_	_	_	_	L	P	*	P	_	_	_	*	_	_	_	_	_	1
Sminthopsis macroura		Stripe-faced Dunnart	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	0
Sminthopsis murina		Common Dunnart	_	_	_	_	_	*	P	_	_	L	*	_	*	P	_	_	_	_	_	_	_	_	_	0
Sminthopsis virginiae		Red-cheeked Dunnart	*	*	*	_	_	_	_	_	_	L	_	_	_	_	*	_	_	_	_	_	*	_	_	1
Peramelidae																										
Isoodon macrourus		Northern Brown Bandicoot	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	*	*	*	*	0
Perameles nasuta		Long-nosed Bandicoot	*	*	*	*	*	*	*	P	*	L	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Phascolarctidae																										
Phascolarctus cinereus		Koala	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	_	*	*	1
Petauridae																										
Dactylopsila trivirgata		Striped Possum	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	*	_	_	0
Petaurus australis		Yellow-bellied Glider	_	_	_	_	_	*	*	_	_	_	_	_	*	*	_	_	_	_	_	_	_	_	_	1
Petaurus breviceps		Sugar Glider	*	*	*	*	*	*	*	*	P	*	*	P	*	*	*	P	*	*	*	P	P	*	P	0
Petaurus gracilis		Mahogany Glider	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	*	_	_	1
Petaurus norfolcensis	E	Squirrel Glider	L	L	_	_	_	L	L	_	_	_	L	_	P	P	_	_	L	*	L	L	_	P	_	1
Pseudocheiridae																										
Hemibelideus lemuroides		Lemuroid Ringtail Possum	_	_	_	_	_	_	*	_	_	_	*	P	*	*	_	_	_	_	_	_	_	_	_	1
Petauroides volans		Greater Glider	_	_	_	_	_	*	*	*	*	_	*	_	*	*	_	_	P	*	*	_	*	_	_	1
Pseudocheirops archeri		Green Ringtail Possum	_	_	_	_	_	*	*	*	*	_	*	*	*	*	_	L	*	*	L	_	*	_	_	1
Pseudocheirus peregrinus		Common Ringtail Possum	_	_	_	_	_	*	*	_	P	_	*	_	*	*	_	_	P	*	*	*	_	*	_	0

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Pseudochirulus cinereus	Daintree River Ringtail Possum	_	_	_	*	_	*	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Pseudochirulus herbertensis	Herbert River Ringtail Possum	_	_	_	_	_	_	_	_	_	_	*	*	*	*	_	_	*	_	_	_	_	_	_	1
Phalangeridae																									
Trichosurus vulpecula	Common Brushtail Possum	*	_	L	_	L	*	*	_	P	_	*	_	*	*	*	*	*	*	*	*	*	*	*	0
Trichosurus vulpecula j.	Coppery Brushtail Possum	_	_	_	_	_	_	_	_	_	_	*	_	*	P	_	_	_	_	_	_	_	_	_	1
Burryamyidae																									
Cercartetus caudatus	Long-tailed Pygmy Possum	_	P	*	*	*	*	*	P	*	_	*	*	*	P	*	P	P	*	P	_	_	_	_	0
Acrobatidae																									
Acrobates pygmaeus	Feather-tail Glider	*	*	*	_	P	*	*	L	P	P	*	_	*	*	*	P	P	P	P	P	*	P	_	0
Potoroidae																									
Aepyprymnus rufescens	Rufous Bettong	L	_	L	_	_	*	*	_	P	_	*	_	*	*	_	_	*	*	*	L	L	*	_	1
Bettongia tropica	Northern Bettong	_	_	_	_	_	*	*	_	_	_	*	_	L	_	_	_	_	_	_	_	_	_	_	1
Hypsiprymnodon moschatus	Musky Rat-kangaroo	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	_	_	*	_	_	1
Macropodidae																									
Dendrolagus bennettianus	Bennett's Tree-kangaroo	P	*	*	*	*	*	L	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Dendrolagus lumholtzi	Lumholtz's Tree-kangaroo	_	_	_	_	_	_	*	*	*	*	*	*	*	*	*	*	_	_	_	_	_	_	_	1
Lagorchestes conspicillatus E	Spectacled Hare-wallaby	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	1
Macropus agilis	Agile Wallaby	*	_	*	_	*	_	P	*	*	*	*	_	*	*	*	_	*	_	_	_	*	*	*	0
Macropus antilopinus	Antilopine Kangaroo	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Macropus giganteus	Eastern Grey Kangaroo	*	_	*	_	_	_	_	_	L	_	*	_	*	*	*	_	*	*	_	_	_	*	*	0
Macropus parryi	Whiptail Wallaby	*	_	*	_	_	_	_	_	_	_	*	_	*	*	_	_	*	_	_	_	_	*	_	0
Macropus robustus	Wallaroo	*	*	P	_	_	*	P	_	L	_	*	_	_	_	_	_	*	_	_	_	_	*	*	0
Petrogale assimilis	Allied Rock Wallaby	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	*	0
Petrogale godmani	Godman's Rock Wallaby	*	*	*	_	*	*	*	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Petrogale mareeba	Mareeba Rock Wallaby	_	_	_	_	_	_	*	_	_	_	*	_	*	_	_	_	_	_	_	_	_	_	_	1
Petrogale sharmani	Sharman's Rock Wallaby	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	*	_	_	1
Thylogale stigmatica	Red-legged Pademelon	_	*	*	*	*	*	*	*	*	L	*	*	*	*	*	*	*	*	*	_	*	_	_	0
Wallabia bicolor	Swamp Wallaby	*	*	P	P	*	*	P	*	P	L	*	_	*	*	*	_	*	*	P	*	_	*	_	0
Megadermatidae																									
Macroderma gigas	Ghost Bat	*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Pteropidae																									
Dobsonia moluccensis	Bare-backed Fruit-bat	*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Macroglossus minimus	Northern Blossum Bat	*	*	*	*	*	_	*	L	*	*	*	_	P	P	*	_	_	_	_	_	_	_	_	0
Nyctimene robinsoni	Queensland Tube-nosed Bat	*	*	P	*	*	*	*	P	*	P	P	P	*	*	*	_	_	_	_	_	_	*	*	0
Pteropus alecto	Black Flying-fox	*	_	P	_	*	_	_	P	L	P	_	_	_	_	*	_	_	_	_	_	*	*	*	0
Pteropus conspicillatus	Spectacled Flying-fox	*	P	*	P	*	*	*	*	*	*	*	*	*	*	*	_	_	_	_	_	_	_	_	0
Pteropus scapulatus	Little Red Flying-fox	*	*	*	_	*	*	P	*	P	*	P	_	*	P	*	_	P	*	*	_	_	*	_	0
Syconycterus australis	Queensland Blossum-bat	P	*	*	P	*	*	P	P	*	*	*	L	*	P	*	_	_	_	*	_	_	*	*	0

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Emballonuridae																									
Saccolaimus flaviventris E	Yellow-bellied Sheathtailed-ba	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Saccolaimus saccolaimus	Naked-rumped Sheathtail-bat	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	0
Taphozous australis	Northern Sheathtail-bat	_	_	_	_	*	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	*	*	*	1
Taphozous georgianus	Common Sheathtail-bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	*	_	0
Molossidae																									
Mormopterus beccarii	Beccari's Mastif Bat	_	_	_	_	_	*	_	_	_	_	_	_	_	_	*	_	_	_	_	_	*	*	_	0
Mormopterus loriae	Little Northern Mastiff-bat	_	*	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Nyctinomus australis	White-striped Mastiff-bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	0
Rhinolophidae																									
Rhinolophus megaphyllus	Eastern Horseshoe-bat	*	*	_	*	*	*	*	*	*	_	_	_	_	*	*	_	_	*	_	_	*	*	_	0
Rhinolophus philipinensis	Large-eared Horseshoe-bat	*	*	*	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	1
Hipposideridae																									
Hipposideros ater	Dusky Horseshoe-bat	_	_	_	_	_	*	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	*	_	0
Hipposideros cervinus	Fawn Horseshoe-bat	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Hipposideros diadema	Diadem Horseshoe-bat	*	_	_	_	*	*	_	_	_	_	_	_	*	*	_	_	_	_	_	_	*	_	*	1
Hipposideros semoni	Semon's Leafnosed-bat	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Vespertilionidae																									
Chalinolobus gouldii	Gould's Wattled Bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	*	*	_	0
Chalinolobus morio	Chocolate Wattled Bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Chalinolobus nigrogriseus	Hoary Wattled Bat	_	_	_	_	_	*	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	*	_	0
Kerivoula papuensis	Golden-tipped Bat	_	_	_	_	_	_	_	_	_	*	*	_	*	_	_	_	_	_	_	_	_	_	_	1
Miniopterus australis	Little Bent-wing Bat	_	*	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	*	_	_	*	*	0
Miniopterus schreibersii	Common Bent-wing Bat	*	_	_	*	_	*	*	_	*	_	_	_	_	*	*	_	_	*	*	_	*	*	*	0
Murina florium	Flute-nosed Bat	_	L	L	L	L	L	L	_	_	_	L	L	*	_	_	_	_	_	_	_	_	_	_	1
Myotis adversus	Pond Bat	P	*	P	P	*	*	*	P	P	L	*	P	P	*	*	_	_	_	*	_	_	*	*	0
Nyctophilus bifax	North Queensland Long-eared Ba	_	_	_	_	_	*	_	_	*	_	_	_	*	*	*	_	_	_	*	_	_	*	*	0
Nyctophilus geofroyii	Lesser Long-eared Bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Scoteanax ruepellii	Greater Broad-nosed Bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Scotorepens balstoni	Inland Broad-nosed Bat	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Scotorepens sanborni	Northern Broad-nosed Ba	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Vespadelus pumilis	Eastern Forest Bat	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Vespadelus troughtoni	Eastern Cave Bat	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	*	*	*	0
Leporidae																									
Lepus capensis	Brown Hare	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Oryctolagus cuniculus	Rabbit	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	*	_	_	_	_	*	_	0
Muridae																									
Hydromys chrysogaster	Water Rat	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	P	*	*	*	0

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Melomys burtoni		Grassland Melomys	*	*	*	_	*	*	*	*	*	*	*	_	*	*	*	_	P	*	*	_	*	*	*	0
Melomys cervinipes		Fawn-footed Melomys	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Mesembriomys gouldii		Black-footed Tree-rat	*	_	L	_	_	_	_	_	_	L	*	_	*	_	_	_	_	_	_	_	_	_	_	0
Mus musculus		House Mouse	*	_	*	_	*	_	_	*	*	*	*	*	*	*	*	_	_	_	_	*	*	*	P	0
Pogonomys mollipilosus		Prehensile-tailed Rat	_	*	P	*	*	*	*	P	*	_	*	*	*	P	*	P	_	_	_	_	_	_	_	1
Pseudomys delicatulus		Delicate Mouse	L	_	L	_	_	P	P	_	P	_	*	_	*	P	_	_	_	_	_	_	*	*	_	0
Pseudomys gracilicaudatus		Eastern Chestnut Mouse	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	L	L	*	_	_	*	_	0
Rattus fuscipes		Bush Rat	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Rattus leucopus		Cape York Rat	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	L	L	L	_	*	*	_	0
Rattus lutreolus		Swamp Rat	_	_	_	_	_	_	_	_	_	_	L	_	*	*	_	_	P	*	*	_	_	_	_	1
Rattus norvegicus		Brown Rat															*								*	0
Rattus rattus		Black Rat	P	_	P	_	*	_	_	*	_	P	_	_	*	*	*	_	_	_	_	_	*	*	_	0
Rattus sordidus		Canefield Rat	*	*	*	_	*	*	P	*	*	*	*	*	*	P	*	_	_	L	_	_	*	*	_	0
Rattus tunneyi		Pale Field Rat	*	_	_	_	_	_	_	_	_	_	_	_	*	*	*	_	_	_	_	_	_	L	_	0
Uromys caudimaculatus		Giant White-tailed Rat	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	L	*	*	*	0
Uromys hadrourus		Masked White-tailed Rat	_	L	_	*	*	_	*	_	_	_	P	*	*	_	_	_	_	_	_	_	_	_	_	1
Zyzomys argurus	E	Common Rock-rat	*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Canidae																										
Canis familiaris dingo		Dingo	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Felidae																										
Felis catus		Feral Cat	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	0
Equidae																										
Equus caballus		Feral Horse	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Suidae																										
Sus scrofa		Feral Pig	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0

Appendix 2: Bird distributions within the Wet Tropics biogeographic region by faunal subregions. List compiled from the sources in the Special References (Appendix 5). Refer to Figure 2.1 for subregion codes. Key: * - definite record, P - highly probable occurrence, L - possibly present. Species of particular importance to conservation and management are designated Very Important Species (VIS): VIS = 1 if either the species or subspecies is endemic to the region and/or has a rare and endangered listing (refer text). E = edge species (not true Wet Tropics species, refer text). Names follow Christidis and Boles (1995).

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Casuariidae																									
Casuaris casuaris	Southern Cassowary	_	*	*	*	*	_	*	*	*	_	*	*	*	*	*	*	*	*	*	_	*	_	*	1
Dromaius novahollandiae	Emu	P	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	*	_	_	P	*	_	0
Podicipedidae																									
Podiceps cristatus	Great-crested Grebe	_	_	_	_	_	_	_	_	*	_	_	_	*	_	*	*	_	_	_	_	_	*	_	1
Poliocephalus poliocephalus	Hoary-headed Grebe	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	*	_	_	_	*	_	0
Tachybaptus novaehollandiae	Australasian Grebe	P	_	_	_	*	_	_	*	*	*	*	_	*	_	*	_	_	_	_	_	*	*	*	0
Pelicanidae																									
Pelecanus conspicillatus	Australian Pelican	*	_	*	_	*	_	_	*	P	P	*	_	*	_	*	*	_	P	_	_	*	*	*	0
Phalacrocoracidae																									
Phalacrocorax carbo	Great Cormorant	P	_	_	_	*	_	_	*	_	P	*	_	*	_	*	*	_	_	_	_	*	*	*	0
Phalacrocorax melanoleucos	Little Pied Cormorant	*	_	*	_	*	*	_	*	*	*	*	_	*	_	*	*	_	_	_	_	*	*	*	0
Phalacrocorax sulcirostris	Little Black Cormorant	P	_	*	_	*	_	_	P	*	P	*	_	*	*	*	*	_	_	_	_	*	*	_	0
Phalacrocorax varius	Pied Cormorant	P	_	*	_	*	_	_	*	*	P	_	_	*	_	*	*	_	_	_	_	P	*	*	0
Anhingidae																									
Anhinga melanogaster	Darter	*	_	*	_	*	_	_	*	P	_	_	_	*	_	*	*	_	_	_	_	*	*	*	0
Ardeidae																									
Ardea alba	Great Egret	P	_	_	_	*	_	_	*	_	*	_	_	*	_	*	_	*	_	_	_	*	*	*	0
Ardea ibis	Cattle Egret	P	_	_	_	*	_	_	*	_	_	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Ardea intermedia	Intermediate Egret	P	_	_	_	_	_	_	*	*	*	_	_	*	*	*	_	_	_	_	_	*	*	*	0
Ardea pacifica	White-necked Heron	P	_	P	_	*	*	_	*	*	P	*	_	*	*	*	*	_	_	*	_	_	*	*	0
Ardea picata	Pied Heron	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	P	*	_	0
Ardea sumatrana	Great-billed Heron	P	_	_	_	*	_	_	*	_	_	_	_	_	_	*	_	_	_	_	_	_	*	*	0
Butorides striatus	Striated Heron	P	_	P	_	*	_	_	*	_	P	_	_	_	_	*	_	_	_	_	_	*	*	*	0
Egretta garzetta	Little Egret	P	_	_	_	*	_	_	*	_	P	*	_	*	_	*	_	_	_	_	_	P	*	P	0
Egretta novaehollandiae	White-faced Heron	*	_	P	_	*	_	_	*	*	*	*	_	*	*	*	*	*	_	_	_	*	*	*	0
Egretta sacra	Eastern Reef Egret	P	_	*	_	*	_	_	*	_	_	_	_	P	_	*	_	_	_	_	_	*	*	*	0
Ixobrychus flavicollis	Black Bittern	P	_	_	_	_	*	_	_	_	_	*	_	*	_	*	_	_	_	_	_	P	*	*	0
Ixobrychus minutus	Little Bittern	_	_	_	_	_	_	_	_	_	_	_	_	L	_	*	_	_	_	_	_	P	*	_	0
Nycticorax caledonicus	Nankeen Night Heron	P	_	P	_	*	_	_	*	_	P	*	*	*	_	*	_	_	_	*	_	P	*	*	0
Ciconiidae																									
Ephippiorhynchus asiaticus	Black-necked Stork	*	_	_	_	*	_	_	*	*	P	_	_	*	_	*	_	_	_	_	_	*	*	*	1
Threskiornithidae																									

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Platalea flavipes	Yellow-billed Spoonbill	P	_	_	_	*	_	_	*	_	_	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Platalea regia	Royal Spoonbill	P	_	_	_	_	_	_	*	_	_	_	_	*	_	*	_	_	_	_	_	P	*	*	0
Plegadis falcinellus	Glossy Ibis	P	_	_	_	P	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	P	*	_	0
Threskiornis molucca	Australian White Ibis	*	_	*	_	*	_	_	*	*	*	*	_	*	*	*	_	*	_	_	_	P	*	*	0
Threskiornis spinicollis	Straw-necked Ibis	*	_	*	_	*	_	_	*	*	*	*	_	*	*	*	_	*	_	_	_	*	*	*	0
Anseranatidae																									
Anseranas semipalmata	Magpie Goose	*	_	_	_	*	_	_	*	*	_	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Anatidae																									
Anas gracilis	Grey Teal	P	_	*	_	*	_	_	*	*	_	_	_	*	_	*	_	_	*	_	_	*	*	P	0
Anas rhynchotis	Australasian Shoveller													P									*		0
Anas superciliosa	Pacific Black Duck	P	_	*	_	*	_	*	*	*	*	*	*	*	*	*	*	*	P	_	_	*	*	P	0
Aythya australis	Hardhead	P	_	_	_	*	_	_	*	*	_	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Chenonetta jubata	Australian Wood Duck	_	_	_	_	_	*	_	_	*	_	_	_	*	_	*	_	*	P	_	_	*	*	P	0
Cygnus atratus	Black Swan	_	_	_	_	_	_	_	*	_	_	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Dendrocygna arcuata	Wandering Whistling-Duck	P	_	_	_	_	_	_	_	*	*	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Dendrocygna eytoni	Plumed Whistling-Duck	_	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	_	_	_	P	*	_	0
Malacorhynchus membranaceus	Pink-eared Duck	_	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	_	_	_	_	*	_	0
Nettapus coromandelianus	Cotton Pygmy-Goose	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	*	P	1
Nettapus pulchellus	Green Pygmy-Goose	P	_	_	_	_	_	_	*	*	_	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Tadorna radjah	Radjah Shelduck	P	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	*	_	1
Accipitridae																									
Accipiter cirrhocephalus	Collared Sparrowhawk	P	_	_	_	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	P	*	*	*	0
Accipiter fasciatus	Brown Goshawk	_	_	_	_	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	*	*	*	0
Accipiter novaehollandiae	Grey Goshawk	P	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	_	*	*	*	1
Aquila audax	Wedge-tailed Eagle	*	_	*	_	_	*	*	*	*	_	P	*	*	*	*	_	P	*	*	*	*	*	*	0
Aviceda subcristata	Pacific Baza	*	*	P	_	*	_	*	*	*	*	*	*	*	*	*	_	P	*	*	_	*	*	*	0
Circus assimilis	Spotted Harrier	_	_	_	_	_	_	*	*	*	_	*	_	*	*	*	_	_	_	_	_	*	*	_	0
Elanus axillaris	Black-shouldered Kite	*	_	_	_	*	_	*	*	*	*	*	*	*	*	*	_	*	*	P	_	*	*	P	0
Erythrotriorchis radiatus	Red Goshawk	P	_	*	_	_	_	_	_	*	_	_	+	*	_	_	_	_	_	_	_	_	*	_	1
Haliaeetus leucogaster	White-bellied Sea-Eagle	*	_	*	_	*	_	_	*	_	*	*	_	*	_	*	_	_	_	_	_	*	*	*	0
Haliastur indus	Brahminy Kite	*	_	*	_	*	_	_	*	_	*	*	_	*	*	*	_	*	_	_	_	*	*	*	0
Haliastur sphenurus	Whistling Kite	*	_	*	_	*	_	_	*	*	*	*	*	*	*	*	_	*	*	P	_	*	*	*	0
Hamirostra melanosternon	Black-breasted Buzzard	_	_	_	_	_	*	_	_	*	_	_	_	*	_	*	_	_	_	_	_	_	*	P	0
Hieraaetus morphnoides	Little Eagle	P	_	*	_	_	_	_	*	*	*	*	*	*	*	*	_	_	_	_	_	*	*	P	0
Lophoictinia isura	Square-tailed Kite	*	_	*	_	_	_	_	*	*	_	*	_	*	*	*	_	_	*	_	_	P	*	_	1
Milvus migrans	Black Kite	*	*	*	_	*	_	_	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	0
Pandion haliaetus	Osprey	*	_	*	_	*	_	_	*	_	*	*	_	*	_	*	_	_	_	_	_	*	*	*	0

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Falconidae																									
Falco berigora	Brown Falcon	*	_	_	_	_	_	_	_	*	_	*	*	*	_	*	_	*	_	_	_	*	*	_	0
Falco cenchroides	Nankeen Kestrel	*	_	*	_	_	_	_	*	*	*	*	*	*	_	*	_	*	*	_	_	*	*	*	0
Falco hypoleucos	Grey Falcon	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	1
Falco longipennis	Australian Hobby	P	_	_	_	_	_	_	_	*	P	*	*	*	*	*	_	_	*	_	_	*	*	P	0
Falco peregrinus	Peregrine Falcon	*	_	P	_	*	_	_	_	*	P	*	*	*	*	*	*	P	*	*	_	*	*	*	0
Falco subniger	Black Falcon	P	_	_	_	_	_	_	_	_	P	*	*	*	_	_	_	_	_	_	_	P	*	_	0
Megapodiidae																									
Alecturi lathami	Australian Brush Turkey	P	*	*	P	*	*	*	*	*	P	*	*	*	*	*	*	*	*	*	*	P	*	*	0
Megapodius reinwardt	Orange-footed Scrubfowl	*	_	*	_	*	_	_	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	0
Phasianidae																									
Coturnix chinensis	King Quail	P	_	_	_	_	_	_	_	*	P	_	_	*	_	_	_	*	*	_	_	_	*	_	0
Coturnix pectoralis	Stubble Quail	_	_	_	_	_	*	_	_	_	_	*	_	*	*	_	_	_	L	_	_	_	*	_	0
Coturnix ypsilophora	Brown Quail	P	_	_	_	_	_	_	*	*	*	*	_	*	*	*	*	_	*	*	_	*	*	P	0
Turnicidae																									
Turnix maculosa	Red-backed Button-Quail	P	_	_	*	_	_	_	*	*	*	*	_	*	_	*	_	_	_	_	_	_	*	P	0
Turnix pyrrhothorax	Red-chested Button-Quail	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	0
Turnix varia	Painted Button-Quail	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	0
Turnix velox	Little Button-Quail	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	_	_	_	0
Gruidae																									
Grus antigone	Sarus Crane	_	_	_	_	_	_	_	_	*	_	*	_	*	_	*	_	_	_	_	_	P	*	_	0
Grus rubicunda	Brolga	P	_	*	_	_	_	_	_	*	_	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Rallidae																									
Amaurornis olivaceus	Bush-hen	P	_	_	_	*	_	*	*	*	*	_	_	*	*	*	_	_	*	_	_	*	*	*	0
Fulica atra	Eurasian Coot	P	_	_	_	*	_	_	*	*	P	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Gallinula tenebrosa	Dusky Moorhen	P	_	_	_	*	_	_	*	*	_	_	_	*	_	*	_	_	_	_	_	_	*	_	0
Gallirallus philippensis	Buff-banded Rail	P	_	_	_	_	_	_	*	*	P	*	_	*	*	*	_	_	_	_	_	*	*	P	0
Porphyrio porphyrio	Purple Swamphen	P	_	_	_	*	_	_	*	*	_	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Porzana cinerea	White-browed Crake	P							P					P		*									0
Porzana tabuensis	Spotless Crake	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	_	_	0
Rallina tricolor	Red-necked Crake	P	_	_	_	*	*	_	*	*	*	*	*	*	_	*	_	_	*	*	_	*	_	*	0
Rallus pectoralis	Lewin's Rail	_	_	_	_	_	_	_	_	P	_	_	_	_	_	*	_	_	P	_	_	_	_	_	0
Otididae																									
Ardeotis australis	Australian Bustard	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	*	_	0
Jacanidae																									
Irediparra gallinacea	Comb-crested Jacana	P	_	_	_	_	_	_	*	*	*	_	_	*	_	*	_	_	_	_	_	*	*	P	0
Recurvirostridae																									

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Himantopus himantopus	Black-winged Stilt	P	_	_	_	_	_	_	*	_	*	_	_	*	_	*	_	_	_	_	_	_	*	*	0
Burhinidae																									
Burhinus grallarius	Bush Stone-Curlew	P	_	_	_	*	_	_	*	*	*	*	_	*	*	*	_	*	_	*	P	*	*	*	0
Esacus neglectus	Beach Stone-Curlew	P	_	_	_	*	_	_	*	_	*	_	_	_	_	*	_	_	_	_	_	*	*	*	1
Glareolidae																									
Stiltia isabella	Australian Pratincole	P	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	_	_	0
Charadriidae																									
Charadrius ruficapillus	Red-capped Plover	P	_	_	_	_	_	_	_	_	*	_	_	*	_	*	_	_	_	_	_	_	*	*	0
Charadrius veredus	Oriental Plover	_	_	_	_	_	_	_	_	_	_	_	_	P	_	*	_	_	_	_	_	_	*	_	0
Elseyornis melanops	Black-fronted Dotterel	P	_	_	_	_	_	_	_	*	_	_	_	*	_	*	_	_	_	_	_	P	*	*	0
Erythrogonys cinctus	Red-kneed Dotterel	P	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	*	P	0
Vanellus miles	Masked Lapwing	*	_	*	_	*	_	_	*	*	*	*	_	*	*	*	_	*	*	_	_	*	*	*	0
Scolopacidae																									
Calidris acuminata	Sharp-tailed Sandpiper	P	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	P	P	P	0
Laridae																									
Chlidonias hybrida	Whiskered Tern	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	P	*	P	0
Sterna caspia	Caspian Tern	P	_	_	_	_	_	_	_	_	*	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Columbidae																									
Chalcophaps indica	Emerald Dove	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Columba leucomela	White-headed Pigeon	P	P	_	P	_	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	0
Ducula bicolor	Pied Imperial Pigeon	*	P	*	*	*	*	*	*	*	*	P	*	*	_	*	_	_	_	_	_	*	*	*	0
Geopelia cuneata	Diamond Dove	_	_	_	_	_	_	*	_	*	*	_	_	*	_	_	_	_	_	_	_	P	P	_	0
Geopelia humeralis	Bar-shouldered Dove	*	_	*	_	*	_	_	*	*	*	*	_	*	P	*	_	*	*	_	_	*	*	*	0
Geopelia striata	Peaceful Dove	*	_	*	_	*	*	_	*	*	*	*	_	*	*	*	*	*	*	*	P	*	*	*	0
Geophaps scripta	Squatter Pigeon	_	_	_	_	_	_	_	_	_	_	*	_	*	_	P	_	_	_	_	P	P	*	_	0
Lopholaimus antarcticus	Topknot Pigeon	P	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Macropygia amboinensis	Brown Cuckoo-Dove	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	0
Ocyphaps lophotes	Crested Pigeon	_	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	_	_	_	P	*	_	0
Phaps chalcoptera	Common Bronzewing	_	_	_	_	_	_	_	_	_	P	_	_	*	_	_	_	_	_	_	_	P	*	_	0
Ptilinopus magnificus	Wompoo Fruit-Dove	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	_	_	*	0
Ptilinopus regina	Rose-crowned Fruit-Dove	*	P	_	_	*	_	*	*	P	*	*	*	*	*	*	_	_	*	*	_	L	L	*	0
Ptilinopus superbus	Superb Fruit-Dove	*	P	*	P	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	_	*	0
Streptopelia chinensis	Spotted Turtle-Dove	P	_	_	_	_	_	_	*	_	*	_	_	*	_	*	_	*	_	_	_	*	*	*	0
Streptopelia senegalensis	Flock Bronzewing	*	_	_	_	_	_	_	*	*	*	_	_	*	_	*	_	_	_	_	_	P	*	P	0
Cacatuidae																									
Cacatua galerita	Sulphur-crested Cockatoo	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Cacatua roseicapilla	Galah	*	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	_	_	_	*	*	_	0

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Cacatua sanguiea	Little Corella	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Calyptorhynchus banskii	Red-tailed Black Cockatoo	*	P	*	_	P	*	*	*	*	L	*	*	*	*	*	P	*	*	*	P	*	*	*	0
Nymphicus hollandicus	Cockatiel	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	*	_	0
Psittacidae																									
Alisteris scapularis	Australian King Parrot	P	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	_	_	*	1
Aprosmictus erythropterus	Red-winged Parrot	*	_	_	_	_	*	L	_	*	_	_	_	*	P	*	_	_	_	_	_	_	*	_	0
Cyclopsitta diophthalma	Double-eyed Fig-Parrot	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	_	_	*	P	P	1
Glossopsitta pusilla	Little Lorikeet	*	_	*	_	_	_	_	_	*	*	*	_	*	*	*	_	_	*	_	_	_	*	_	0
Melopsittacus undulatus	Budgerigar	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Platycerus adscitus	Pale-headed Rosella	*	_	*	_	*	*	_	_	*	_	*	_	*	*	*	P	P	*	P	P	*	*	P	0
Platycerus elegans	Crimson Rosella	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	*	_	_	0
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Trichoglossus haematodus	Rainbow Lorikeet	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Cuculidae																									
Cacomantis castaneiventris	Chestnut-breasted Cuckoo	P		*		P								*											0
Cacomantis flabelliformis	Fan-tailed Cuckoo	*	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Cacomantis variolosus	Brush Cuckoo	*	_	*	_	_	*	*	*	*	*	*	_	*	*	*	_	*	*	P	*	*	*	*	0
Chrysococcyx basalis	Horsfield's Bronze-Cuckoo	P	_	_	_	_	_	*	*	*	*	*	_	*	*	*	_	L	L	*	_	*	*	*	0
Chrysococcyx minutillus	Little Bronze-Cuckoo	_	_	_	_	_	_	*	_	*	_	*	_	*	_	*	_	_	*	_	_	_	_	_	0
Chrysococcyx osculans	Black-eared Cuckoo	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	L	_	_	_	*	L	0
Chrysococcyx russatus	Gould's Bronze-Cuckoo	_	_	_	_	_	_	_	_	_	_	*	_	*	_	*	_	*	_	*	_	*	*	*	0
Chyrsococcyx lucidus	Shining Bronze-Cuckoo	*	*	_	_	_	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	0
Cuculus pallidus	Pallid Cuckoo	_	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	_	_	_	*	L	*	0
Cuculus saturatus	Oriental Cuckoo	P	*	_	_	_	_	_	_	*	_	*	_	*	_	*	_	L	L	L	_	_	*	*	0
Eudynamys scolopacea	Common Koel	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	*	P	*	P	P	*	*	*	0
Scythrops novaehollandiae	Channel-billed Cuckoo	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	P	*	P	P	*	*	*	0
Centropodidae																									
Centropus phasianinus	Pheasant Coucal	*	*	*	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Tytonidae																									
Tyto alba	Barn Owl	P	_	P	_	_	_	_	*	*	L	*	_	*	*	*	_	_	_	*	_	*	*	*	0
Tyto capensis	Grass Owl	_	_	_	_	_	_	_	_	_	L	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Tyto multipunctata	Lesser Sooty Owl	_	*	_	*	*	*	*	_	*	_	*	P	*	*	*	P	*	*	*	_	_	_	_	1
Tyto novaehollandiae	Masked Owl	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	*	_	_	1
Strigidae																									
Ninox connivens	Barking Owl	P	_	*	_	_	_	_	_	*	_	*	_	*	*	*	_	_	*	*	_	_	*	_	0
Ninox novaseelandiae	Southern Boobook	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	1
Ninox rufa	Rufous Owl	*	P	P	P	P	*	*	*	*	P	P	*	*	*	*	_	_	*	_	_	_	*	*	1

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Podargidae																									
Podargus papuensis	Papuan Frogmouth	*	P	P	P	*	*	*	*	*	*	*	*	*	P	*	_	*	*	*	_	_	*	*	0
Podargus strigoides	Tawny Frogmouth	*	_	P	_	P	*	*	P	*	*	*	_	*	*	*	P	P	*	P	P	P	*	P	0
Aegothelidae																									
Aegotheles cristatus	Australian Owlet-nightjar	*	_	P	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	*	_	_	*	*	0
Caprimulgidae																									
Caprimulgus macrurus	Large-tailed Nightjar	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	_	P	*	*	*	_	*	*	0
Eurostopodus argus	Spotted Nightjar	_	_	_	_	_	_	_	*	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	0
Eurostopodus mystacalis	White-throated Nightjar	P	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	*	*	_	*	*	*	0
Apodidae																									
Apus pacificus	Fork-tailed Swift	P	_	_	_	_	*	*	*	*	*	*	*	*	*	*	_	P	*	*	P	*	*	P	0
Collocalia spodiopygius	White-rumped Swiftlet	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	*	*	*	1
Collocalia vanikorensis	Uniform Swiftlet	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Hirundapus caudacutus	White-throated Needletail	P	_	_	_	_	*	*	*	*	*	*	*	*	_	*	*	_	*	_	_	*	*	*	0
Alcedinidae																									
Alcedo azurea	Azure Kingfisher	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	P	*	*	*	0
Alcedo pusilla	Little Kingfisher	*	_	*	_	*	_	P	*	*	*	P	*	*	*	*	L	P	*	*	_	P	*	*	0
Halcyonidae																									
Dacelo leachii	Blue-winged Kookaburra	*	_	*	_	*	_	_	P	*	P	*	*	*	*	*	_	*	*	P	P	*	*	*	0
Dacelo novaeguineae	Laughing Kookaburra	*	_	*	_	*	P	*	*	*	*	*	P	*	*	*	_	*	*	*	*	*	*	*	0
Tanysiptera sylvia	Buff-breasted Paradise-Kingfisher	*	*	*	_	*	_	*	*	*	*	*	_	*	_	*	_	_	P	_	_	_	*	*	0
Todirhamphus chloris	Collared Kingfisher	*	_	*	_	*	_	_	*	_	*	_	_	_	_	*	_	_	_	_	_	P	*	*	0
Todirhamphus macleayii	Forest Kingfisher	*	_	*	_	*	_	*	*	*	*	*	_	*	*	*	_	*	*	*	*	*	*	*	0
Todirhamphus pyrrhopygia	Red-backed Kingfisher	*	_	*	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Todirhamphus sanctus	Sacred Kingfisher	*	_	*	_	*	_	*	*	*	*	*	_	*	*	*	_	P	*	P	P	*	*	*	0
Meropidae																									
Merops ornatus	Rainbow Bee-eater	*	P	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Coraciidae																									
Eurystomus orientalis	Dollarbird	*	_	*	_	*	*	*	*	*	*	*	_	*	*	*	_	P	*	P	_	*	*	*	0
Pittidae																									
Pitta versicolor	Noisy Pitta	*	*	*	P	*	P	*	*	*	*	*	*	*	P	*	*	P	*	*	*	_	*	*	0
Alaudidae																									
Mirafra javanica	Singing Bushlark	_	_	_	_	_	_	_	_	_	P	*	_	*	_	*	_	_	P	_	_	*	*	P	0
Hirundinidae																									
Hirundo ariel	Fairy Martin	P	_	_	_	_	*	_	*	_	*	*	_	*	*	*	_	*	*	P	P	*	*	*	0
Hirundo neoxena	Welcome Swallow	P	_	*	_	*	*	*	*	*	*	*	*	*	*	*	_	P	*	P	P	*	*	*	0
Hirundo nigricans	Tree Martin	*	_	*	_	*	*	_	*	_	_	*	_	*	*	*	_	*	*	P	_	*	*	*	0

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Hirundo rustica	Barn Swallow	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	*	_	0
Motacillidae																									
Anthus novaeseelandiae	Richard's Pipit	*	_	*	_	_	_	_	*	*	*	*	_	*	*	*	_	_	*	_	_	*	*	*	0
Campephagidae																									
Coracina lineata	Barred Cuckoo-Shrike	*	*	*	_	*	*	*	*	*	P	*	*	*	*	*	*	P	*	*	_	*	*	P	0
Coracina maxima	Ground Cuckoo-shrike	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	P	*	_	1
Coracina novaehollandiae	Black-faced Cuckoo-shrike	*	_	*	_	*	P	*	*	*	*	*	*	*	*	*	_	_	*	*	_	*	*	*	0
Coracina papuensis	White-bellied Cuckoo-Shrike	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	*	0
Coracina tenuirostris	Cicadabird	P	*	_	_	*	*	*	P	*	P	*	*	*	*	*	*	P	*	P	P	*	*	*	0
Lalage leucomela	Varied Triller	*	_	*	_	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Lalage sueurii	White-winged Triller	*	_	_	_	_	_	_	_	_	P	*	_	*	*	*	_	_	*	_	_	*	*	*	0
Muscicapidae																									
Zoothera lunulata	Bassian Thrush	_	_	_	_	_	*	_	_	*	P	*	*	*	*	P	_	_	*	*	_	P	P	_	0
Orthonychidae																									
Orthonyx spaldingii	Chowchilla	_	*	P	*	*	*	*	*	*	_	*	*	*	*	*	*	P	*	*	_		_	P	0
Cinclosomatidae																									
Psophodes olivaceus	Eastern Whipbird	_	_	_	P	P	*	*	_	*	P	*	*	*	*	*	*	*	*	*	_	_	_	P	1
Pomatostomidae																									
Pomatostomus temporalis	Grey-crowned Babbler	P	_	*	_	_	_	_	_	_	_	*	_	*	_	*	_	_	_	_	_	*	*	_	0
Sylviidae																									
Acrocephalis stentoreus	Clamorous Reed-Warbler	_	_	_	_	_	_	_	*	_	_	_	_	*	_	P	_	_	P	_	_	P	*	*	0
Cinclorhamphus cruralis	Brown Songlark	_	_	_	_	_	_	_	_	_	_	_	_	P	_	*	_	_	_	_	_	_	*	_	0
Cinclorhamphus mathewsi	Rufous Songlark	_	_	_	_	_	_	_	_	_	_	_	_	*	_	P	_	_	P	_	_	P	*	_	0
Cisticola exilis	Golden-headed Cisticola	P	_	P	_	*	_	_	*	*	*	*	_	*	*	*	_	_	*	_	_	*	*	*	0
Megalurus gramineus	Little Grassbird	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	P	*	_	0
Megalurus timoriensis	Tawny Grassbird	P	_	P	_	_	_	_	P	*	P	*	_	*	_	*	_	_	*	_	_	P	*	*	0
Maluridae																									
Malurus lamberti	Varigated Fairy-wren	*	*	*	P	*	P	P	*	*	*	*	*	*	*	*	_	P	*	P	P	P	*	*	0
Malurus melanocephalus	Red-backed Fairy-wren	*	*	*	_	_	_	_	*	*	*	*	*	*	*	*	*	*	*	*	P	P	*	P	0
Pardalotidae																									
Acanthiza katherina	Mountain Thornbill	_	*	_	*	_	*	*	_	*	_	*	*	*	*	_	L	L	*	*	_	_	_	_	1
Acanthiza nana	Yellow Thornbill	_	_	_	_	_	_	_	_	_	_	*	_	*	*	_	_	_	P	_	_	_	_	_	0
Acanthiza reguloides	Buff-rumped Thornbill	_	_	_	_	_	*	_	_	_	_	_	P	*	*	P	_	_	_	_	_	_	P	*	0
Gerygone levigaster	Mangrove Gerygone	_	_	_	_	_	_	_	_	_	P	_	_	_	_	*	_	_	_	_	_	*	*	*	0
Gerygone magnirostris	Large-billed Gerygone	_	_	_	_	*	_	*	*	*	*	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Gerygone mouki	Brown Gerygone	*	*	_	_	*	*	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	1
Gerygone olivacea	White-throated Gerygone	_	*	*	_	_	_	_	_	*	P	*	_	*	*	*	_	_	*	_	_	*	*	P	0

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Gerygone palpebrosa	Fairy Gerygone	*	*	*	_	*	_	_	*	*	*	*	*	*	*	*	_	*	*	*	_	*	*	*	0
Oreoscopus gutteralis	Fernwren	_	*	_	*	_	*	*	_	*	_	*	*	*	*	_	*	_	*	*	_	_	_	_	1
Pardalotus punctatus	Spotted Pardalote	P	_	_	_	_	_	_	_	_	P	*	_	*	*	*	_	*	*	*	_	*	*	_	0
Pardalotus rubricatus	Red-browed Pardalote	_	_	_	_	_	_	_	_	P	_	*	_	*	P	P	_	P	P	P	_	_	_	_	0
Pardalotus striatus	Striated Pardalote	P	_	_	_	_	_	_	_	*	P	*	_	*	*	*	_	*	P	*	P	P	*	*	0
Sericornis beccarii	Tropical Scrubwren	*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Sericornis citreogularis	Yellow-throated Scrubwren	_	*	*	_	*	*	*	_	*	*	*	*	*	*	*	P	P	*	*	L	_	*	*	0
Sericornis frontalis	White-browed Scrubwren	_	_	_	_	_	_	_	_	*	P	*	*	*	*	_	_	P	*	*	*	_	_	*	0
Sericornis keri	Atherton Scrubwren	_	_	_	*	_	*	*	_	P	_	*	*	*	*	_	_	_	_	_	_	_	_	_	1
Sericornis magnirostris	Large-billed Scrubwren	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	0
Smicrornis brevirostris	Weebill	*	_	*	_	_	*	_	*	*	*	*	_	*	*	*	_	_	*	_	_	_	*	_	0
Dicruridae																									
Arses kaupi	Pied Monarch	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	_	*	1
Dicrurus bracteatus	Spangled Drongo	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Grallina cyanoleuca	Magpie Lark	*	_	*	_	*	_	_	*	*	*	*	_	*	*	*	*	*	*	_	_	*	*	*	0
Machaerirhynchus flaviventer	Yellow-breasted Boatbill	_	*	*	P	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	_	*	1
Monarcha leucotis	White-eared Monarch	_	_	_	_	*	_	P	P	*	P	_	_	*	*	*	_	_	P	_	_	P	*	*	0
Monarcha melanopsis	Black-faced Monarch	_	*	*	P	*	*	*	*	*	P	*	*	*	*	*	*	P	*	*	*	_	_	*	0
Monarcha trivirgatus	Spectacled Monarch	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	0
Myiagra alecto	Shining Flycatcher	*	_	_	_	*	_	_	*	_	*	*	_	*	_	*	_	_	_	_	_	P	*	*	0
Myiagra cyanoleuca	Satin Flycatcher	*	_	P	_	*	_	_	_	*	P	_	_	*	_	P	_	P	*	*	_	P	*	*	0
Myiagra inquieta	Restless Flycatcher	P	_	*	_	_	_	_	_	_	_	*	_	*	*	P	_	P	P	P	_	*	*	*	0
Myiagra rubecula	Leaden Flycatcher	P	_	*	_	*	*	_	*	*	*	*	_	*	*	*	_	P	*	*	P	*	*	*	0
Myiagra ruficollis	Broad-billed Flycatcher	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	0
Rhipidura fuliginosa	Grey Fantail	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	1
Rhipidura leucophrys	Willie Wagtail	*	_	*	_	_	_	_	*	*	*	*	_	*	*	*	_	*	P	*	P	*	*	*	0
Rhipidura rufifrons	Rufous Fantail	*	*	*	P	*	*	*	P	*	P	*	*	*	*	*	*	P	*	*	P	*	*	*	0
Rhipidura rufiventris	Northern Fantail	*	_	*	_	_	*	_	_	*	*	*	_	*	_	*	_	*	_	_	_	*	*	*	0
Petroicidae																									
Eopsaltria australis	Eastern Yellow Robin	_	*	*	_	P	*	_	P	*	P	*	_	*	*	*	_	*	*	*	_	*	*	*	0
Eopsaltria pulverulenta	Mangrove Robin	P	_	_	_	*	_	_	P	_	P	_	_	_	_	*	_	_	_	_	_	P	*	*	0
Heteromyias albispecularis	Grey-headed Robin	_	*	*	*	_	*	*	_	*	_	*	*	*	*	*	*	_	*	*	*	_	_	*	1
Microeca fascinans	Jacky Winter	_	_	_	_	_	_	_	_	_	P	*	_	*	*	P	_	_	_	_	_	*	P	P	0
Microeca flavigaster	Lemon-bellied Flycatcher	*	_	*	_	_	_	_	*	*	*	*	_	*	*	*	_	*	P	_	_	*	*	*	0
Poecilodryas superciliosa	White-browed Robin	*	_	*	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	L	*	_	_	0
Tregellasia capito	Pale-yellow Robin	_	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	_	*	1
Pachycephalidae																									

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Colluricincla boweri	Bowers Shrike-Thrush	P	*	_	*	_	*	*	_	*	_	*	*	*	*	_	*	P	*	*		_	_	*	1
Colluricincla harmonica	Grey Shrike-Thrush	*	_	*	_	_	_	_	_	_	P	*	_	*	*	*	_	*	*	*	_	*	*	*	0
Colluricincla megarhyncha	Little Shrike-Thrush	*	*	*	P	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Falcunculus frontatus	Crested Shrike-tit	_	_	_	_	_	*	_	_	_	_	_	_	*	*	*	_	_	*	_	P	_	_	_	1
Pachycephala pectoralis	Golden Whistler	P	*	_	*	_	*	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	L	*	0
Pachycephala rufiventris	Rufous Whistler	*	_	*	_	*	*	_	_	*	P	*	*	*	*	*	_	*	*	*	P	*	*	*	0
Pachycephala simplex	Grey Whistler	P	_	_	_	*	_	_	*	*	P	*	P	*	*	*	*	*	P	*	*	P	_	*	0
Neosittidae																									
Daphoenositta chrysoptera	Varied Sittella	_	_	_	_	_	*	_	_	*	_	*	*	*	*	*	_	_	*	*	_	_	_	_	0
Climacteridae																									
Climacteris picumnus	Brown Treecreeper	P	_	_	_	_	*	_	_	*	_	_	_	*	*	P	_	_	*	_	_	_	*	P	0
Cormobates leucophaeus	White-throated Treecreeper	P	_	_	_	_	*	*	*	*	P	*	*	*	*	*	*	*	*	*	_	_	_	*	0
Dicaeidae																									
Dicaeum hirundinaceum	Mistletoebird	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Nectarinidae																									
Nectarina jugularis	Yellow-bellied Sunbird	*	*	*	_	*	_	_	*	*	*	*	*	*	*	*	_	P	*	P	P	*	*	*	0
Zosteropidae																									
Zosterops lateralis	Silvereye	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	P	*	*	_	*	*	*	0
Meliphagidae																									
Acanthorhynchus tenuirostris	Eastern Spinebill	_	*	_	P	_	*	*	*	*	*	*	*	*	*	*	_	P	*	*	*	*	_	_	0
Certhionyx pectoralis	Banded Honeyeater	P	_	_	_	_	_	_	_	*	P	*	_	*	P	_	_	_	_	_	_	_	_	_	0
Conopophila rufogularis	Rufous-throated Honeyeater	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	P	*	P	0
Entomyzon cyanotis	Blue-faced Honeyeater	*	_	*	_	_	_	_	_	*	P	L	_	*	*	*	_	P	P	P	P	*	*	_	0
Lichenostomus chrysops	Yellow-faced Honeyeater	P	*	*	_	_	*	*	P	*	P	*	*	*	*	*	P	*	*	*	*	P	*	_	0
Lichenostomus flavescens	Yellow-tinted honeyeater	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Lichenostomus flavus	Yellow Honeyeater	*	_	*	_	*	_	_	*	*	*	*	_	*	_	*	_	*	P	_	_	P	*	*	0
Lichenostomus frenatus	Bridled Honeyeater	_	*	*	*	*	*	*	*	*	_	*	*	*	*	*	P	*	*	*	*	P	*	P	1
Lichenostomus fuscus	Fuscous honeyeater	_	_	_	_	_	_	_	_	_	_	_	_	*	P	*	_	*	_	_	_	P	_	_	0
Lichenostomus unicolor	White-gaped Honeyeater	_	_	_	_	_	_	_	_	_	_	_	¬	_	_	*	_	_	_	_	_	_	*	_	0
Lichenostomus versicolor	Varied Honeyeater	_	_	_	_	_	_	_	*	_	*	_	_	_	_	*	_	_	_	_	_	P	_	*	0
Lichmera indistincta	Brown Honeyeater	*	_	*	_	P	_	_	*	*	*	*	_	*	*	*	_	P	*	*	_	*	*	*	0
Manorina flavigula	Yellow-throated Miner	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Manorina melanocephala	Noisy Miner	_	_	_	_	_	_	_	_	_	P	_	_	*	_	_	_	_	_	_	_	P	*	_	0
Meliphaga gracilis	Graceful Honeyeater	P	*	*	P	*	P	*	*	*	*	*	*	*	*	*	*	*	P	*	P	P	P	*	0
Meliphaga lewinii	Lewin's Honeyeater	_	*	P	*	*	*	*	L	*	L	*	*	*	*	*	*	*	*	*	*	_	_	_	0
Meliphaga notata	Yellow-spotted Honeyeater	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	*	P	*	*	*	0
Melithreptus albogularis	White-throated Honeyeater	*	_	*	_	_	_	*	P	*	*	*	*	*		*	_	*	P	_	_	P	*	*	0

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Melithreptus gularis	Black-chinned Honeyeater	P	_	_	_	_	_	_	_	P	_	*	_	*	_	*	_	_	_	_	_	_	*	_	1
Melithreptus lunatus	White-naped Honeyeater	_	_	_	_	_	_	_	_	*	_	*	*	*	*	*	_	P	*	*	_	_	_	_	0
Myzomela obscura	Dusky Honeyeater	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Myzomela sanguinolenta	Scarlet Honeyeater	P	*	*	P	P	*	*	P	*	*	*	*	*	*	*	*	*	*	*	P	P	*	*	0
Philemon argenticeps	Silver-crowned Friarbird	P	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Philemon buceroides	Helmeted Friarbird	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Philemon citreogularis	Little Friarbird	P	_	*	_	*	_	_	*	_	_	*	_	*	*	*	_	_	_	_	_	_	*	_	0
Philemon corniculatus	Noisy Friarbird	P	_	_	_	_	*	_	*	*	P	*	P	*	*	*	_	P	*	*	P	*	*	*	0
Phylidonyris nigra	White-cheeked Honeyeater	_	_	_	_	_	*	*	_	_	_	*	*	*	*	_	_	_	*	*	_	_	_	_	0
Ramsayornis modestus	Brown-backed Honeyeater	*	_	*	_	_	_	_	*	*	*	_	_	*	_	*	_	_	_	_	_	*	*	*	0
Trichodere cockerelli	White-streaked Honeyeater	P		*																					0
Xanthotis macleayana	Macleay's Honeyeater	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	_	_	*	1
Passeridae																									
Erythrura trichroa	Blue-faced Parrot-Finch	_	*	_	_	_	_	*	_	*	L	_	*	P	_	L	_	_	_	_	_	L	_	_	1
Lonchura castaneothorax	Chestnut-breasted Mannikin	P	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	*	*	P	_	*	*	*	0
Lonchura punctulata	Nutmeg Mannikin	P	_	_	_	_	_	_	*	*	*	*	*	*	*	*	_	_	P	_	_	*	*	*	0
Neochmia modesta	Plum-headed Finch	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Neochmia phaeton	Crimson Finch	_	_	_	_	_	_	_	_	_	*	_	_	_	_	*	_	_	_	_	_	_	*	*	1
Neochmia ruficauda	Star Finch	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	1
Neochmia temporalis	Red-browed Finch	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	0
Passer domesticus	House Sparrow	*	_	_	_	_	_	_	*	*	*	_	_	*	_	*	_	_	*	_	_	*	*	*	0
Poephila cincta	Black-throated Finch	P	_	_	_	_	_	_	_	_	P	*	_	*	_	_	_	_	_	_	_	_	*	_	1
Taeniopygia bichenovii	Double-barred Finch	*	_	_	_	_	*	_	*	*	*	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Taeniopygia guttata	Zebra Finch	*	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	*	_	0
Sturnidae																									
Acridotheres tristis	Common Myna	P	_	_	_	_	_	_	*	*	*	_	_	*	_	*	_	_	*	_	_	*	*	P	0
Aplonis metallica	Metallic Starling	*	*	*	P	*	_	*	*	*	*	*	*	*	*	*	_	_	*	_	_	*	P	*	0
Oriolidae																									
Oriolus flavocinctus	Yellow Oriole	*	*	*	_	*	_	_	*	*	*	*	_	*	_	*	_	_	_	_	_	*	_	*	0
Oriolus saggitatus	Olive-backed Oriole	*	_	*	_	*	*	*	*	*	*	*	*	*	*	*	P	P	*	*	_	*	*	*	0
Sphecotheres viridis	Figbird	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	0
Corcoracidae																									
Struthidea cinerea	Apostlebird	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Artamidae																									
Artamus cinereus	Black-faced Woodswallow	P	_	_	_	_	_	_	_	_	*	_	_	*	_	*	_	*	_	_	_	*	*	_	0
Artamus cyanopterus	Dusky Woodswallow	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	L	_	_	_	_	L	0
Artamus leucorhynchus	White-breasted Woodswallow	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	_	*	*	*	0

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Artamus minor	Little Woodswallow	P	_	_	_	_	_	_	_	_	P	_	_	*	_	*	_	_	L	_	_	P	*	_	0
Artamus personatus	Masked Woodswallow	_	_	_	_	_	_	_	_	_	P	_	_	*	_	_	_	_	*	_	_	P	*	_	0
Artamus superciliosus	White-browed Woodswallow	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	P	*	*	0
Cracticus nigrogularis	Pied Butcherbird	L	_	_	_	_	P	P	P	*	P	*	_	*	*	*	_	_	*	_	_	*	*	P	0
Cracticus quoyi	Black Butcherbird	*	*	*	p	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	_	*	_	*	0
Cracticus torquatus	Grey Butcherbird	_	_	_	_	_	_	_	_	*	P	*	_	*	*	_	_	*	P	_	_	P	*	*	0
Gymnorhina tibicen	Australian Magpie	*	_	_	_	_	_	_	*	_	*	*	_	*	*	*	_	_	*	_	_	*	*	*	0
Strepera graculina	Pied Currawong	_	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	0
Ptilonorhynchidae																									
Ailuroedus melanotis	Spotted Catbird	_	*	_	*	*	*	*	*	*	P	*	*	*	*	*	*	*	*	*	_	*	_	*	1
Chlamydera nuchalis	Great Bowerbird	*	_	*	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	*	P	*	_	0
Prionodura newtoniana	Golden Bowerbird	_	L	_	*	_	*	*	_	_	_	*	*	*	*	_	_	_	*	_	_	_	_	_	1
Ptilonorhynchus violaceus	Satin Bowerbird	_	P	_	*	*	*	*	_	*	_	*	*	*	*	*	_	_	*	*	*	P	*	*	1
Scenopoeetes dentirostris	Tooth-billed Bowerbird	_	*	_	*	_	*	*	_	_	_	*	*	*	*	_	*	_	*	*	*	_	_	_	1
Paradisaeidae																									
Ptiloris victoriae	Victoria's Riflebird	_	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	P	*	*	*	*	_	*	1
Corvidae																									
Corvus coronoides	Australian Raven	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	*	_	0
Corvus orru	Torresian Crow	*	_	*	_	_	_	_	*	*	*	*	*	*	*	*	_	P	*	*	P	*	*	*	0

Appendix 3: Reptile distributions within the Wet Tropics biogeographic region by faunal subregions. List compiled from the sources in Special References (Appendix 5). Refer to Figure 2.1 for zone codes. Key: * - definite record, P - highly probable occurrence, L - possibly present. Species of particular importance to conservation and management are designated Very Important Species (VIS): VIS = 1 if either the species or subspecies is endemic to the region and/or has a rare and endangered listing (refer text). E = edge species (not true Wet Tropics species, refer text).

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Crocodylidae																									
Crocodylus porosus	Estuarine Crocodile	*	_	*	_	*	_	_	*	_	*	_	_	_	_	*	_	_	_	_	_	*	*	*	1
Chelidae																									
Chelodina novaeguineae		_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	0
Elseya dentata	Northern Snapping Turtle	_	*	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	_	_	0
Elseya latisternum	Sawshell Tortoise	_	*	*	*	*	_	_	*	_	_	*	_	*	*	*	_	_	_	_	_	*	*	*	0
Emydura kreftii	Krefft's River Tortoise	*	_	_	_	_	*	*	_	_	*	_	_	*	_	*	_	_	_	_	_	_	*	_	0
Gekkonidae																									
Carphodactylus laevis	Chameleon Gecko	_	*	_	*	_	*	*	_	*	_	*	*	*	*	*	*	_	_	_	_	_	_	_	1
Crytodactylus louisiadensis	Ring-tailed Gecko	*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Diplodactylus steindachneri		*	_	*	_	_	*	_	_	_	_	*	_	_	_	_	_	_	_	*	_	_	_	_	0
Diplodactylus williamsi		_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	0
Gehyra dubia		_	*	*	_	_	*	_	_	_	_	_	_	*	_	*	_	_	_	*	_	_	*	*	0
Heteronotia binoei	Bynoe's Gecko	_	_	*	*	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	*	*	0
Lepidodactylus lugubris	Mourning Gecko	*	_	P	_	P	_	_	*	_	P	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Nactus galgajuga		*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Nactus pelagicus	Pelagic Gecko	*	*	*	_	*	*	_	*	_	*	_	_	*	_	*	_	_	_	_	_	_	_	_	0
Nephurus asper		*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Oedura castlenaui	Northern Velvet Gecko	*	_	L	_	_	*	*	_	L	_	*	_	*	*	_	_	_	_	_	_	P	*	_	0
Oedura coggeri	Northern Spotted Velvet Gecko	*	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	_	_	_	_	_	_	0
Oedura monilis	Ocellated Velvet Gecko	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	_	*	*	0
Oedura rhombifer		*	_	L	_	_	*	*	_	*	*	_	_	*	*	*	_	_	_	_	_	P	*	*	0
Saltuarius cornutus	Northern Leaf-tailed Gecko	_	*	P	*	*	*	*	*	*	L	*	P	*	*	*	*	P	*	P	_	*	*	_	1
Pygopodidae																									
Delma labialis		_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	*	*	1
Delma mitella		_	_	_	_	_	_	_	_	_	_	L	L	*	P	_	_	L	*	P	_	_	_	_	1
Delma tincta		*	*	_	_	_	_	_	_	*	_	_	_	_	_	*	_	_	_	_	*	_	*	_	0
Lialis burtonis	Burton's Legless Lizard	*	_	*	_	_	*	_	_	*	*	_	*	*	P	*	_	_	_	_	_	P	*	*	0
Pygopus lepidopodus	Common Scaley Foot	_	*	*	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	0
Scincidae																									
Bartleia jigurru	Bartle Frere Skink	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	1
Calyptotis thorntonensis	Thornton Peak Skink	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Carlia jarnoldae		*	_	*	_	_	*	*	_	*	_	*	_	*	*	L	_	_	P	*	_	L	*	_	0

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Carlia longipes			*	*	*	*	*	_	_	*	*	*	_	_	*	P	*	_	_	_	_	_	_	_	*	0
Carlia munda	E		_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Carlia mundivensis	E		_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Carlia pectoralis	E		_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	*	*	*	0
Carlia rostralis			*	*	*	_	*	_	*	*	*	*	_	_	*	*	*	_	_	_	*	_	*	*	*	0
Carlia rubrigularis		Northern Red-throated Skink	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	_	*	_	*	1
Carlia schmeltzii			*	_	*	_	_	*	_	_	_	*	_	_	_	_	L	_	_	_	_	_	L	*	_	0
Carlia scirtetis			_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Carlia storri			*	*	_	_	_	_	*	_	*	_	_	_	_	_	*	_	_	_	*	_	*	*	*	0
Carlia vivax			*	_	L	_	L	*	_	*	_	_	_	_	_	_	*	_	_	_	_	_	_	*	_	0
Coeranoscincus frontalis			_	P	_	*	*	P	*	P	*	_	P	*	*	*	*	P	L	*	P	P	_	*	_	1
Cryptoblepharus litoralis			*	_	*	_	*	_	_	*	_	_	_	_	_	_	*	_	_	_	_	_	P	*	*	0
Cryptoblepharus plagiocephali			*	_	L	_	L	*	*	*	*	L	*	_	P	P	P	_	_	L	L	_	_	*	_	0
Cryptoblepharus virgatus			*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	_	P	P	*	P	*	*	*	0
Ctenotus eutaenius	E		_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	*	1
Ctenotus monticola	E		_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	1
Ctenotus robustus			*	_	*	_	*	P	P	P	*	*	P	_	*	*	*	_	_	_	*	_	*	*	*	0
Ctenotus spaldingi			_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	0
Ctenotus taeniolatus		Copper-tailed Skink	*	_	L	_	L	_	_	_	_	*	_	_	*	*	*	_	_	_	*	_	*	*	_	0
Ctenotus terrareginae			_	_	_	_	_	_	*	_	_	_	_	_	_	_	*	_	_	*	_	_	_	_	*	1
Egernia frerei		Major Skink	*	*	*	*	*	*	*	*	*	*	*	L	*	*	*	*	_	_	_	_	_	*	*	0
Egernia striolata		Tree Skink	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Eulamprus frerei			_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	1
Eulamprus quoyii		Eastern Water Skink	_	_	_	_	_	_	_	*	_	_	*	_	*	*	*	_	_	*	*	*	_	*	*	0
Eulamprus sokosoma	E		_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	*	_	1
Eulamprus tenuis			*	*	*	_	*	*	_	*	_	_	*	_	*	*	*	_	_	*	_	_	*	_	*	0
Eulamprus tigrinus			_	*	*	*	*	*	*	*	*	_	*	P	*	*	*	_	_	_	*	_	_	_	_	1
Glaphyromorphus crassicaudu			*														*									0
Glaphyromorphus fuscicaudis		Grey-tailed Skink	_	*	*	*	*	*	*	*	*	_	*	_	*	*	*	_	_	*	*	_	_	_	_	1
Glaphyromorphus mjobergi			_	*	_	L	_	_	*	_	_	_	*	*	*	*	_	_	_	_	_	_	_	_	_	1
Glaphyromorphus nigricaudis			*	*	L	_	*	*	*	L	*	*	_	_	_	_	*	_	_	_	_	_	_	_	*	0
Glaphyromorphus pardalis			*	_	_	_	_	*	*	_	_	*	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Glaphyromorphus pumilis			*	_	_	_	_	_	_	_	_	_	*	_	*	_	*	_	_	_	_	_	_	_	_	1
Glaphyromorphus punctulatus			_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	*	*	0
Gnypetoscincus queenslandiae		Prickly Forest Scink	_	*	*	*	*	*	*	*	*	L	*	*	*	*	*	*	_	_	_	_	_	_	_	1
Hemisphaeriodon gerrardii		Ping-tongue Lizard	_	_	_	_	_	_	_	L	*	*	P	_	*	*	*	_	_	*	_	*	*	_	_	0
Lampropholis coggeri			_	*	_	*	*	*	*	*	_	_	*	*	*	*	*	*	_	*	*	*	*	*	*	1
Lampropholis delicata			_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	_	_	_	_	*	*	*	*	0

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Lampropholis mirabilis			_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	*	*	1
Lampropholis robertsi			_	*	_	*	_	_	*	_	_	_	*	*	*	_	*	_	_	_	_	_	_	_	_	1
Lerista zonulata	E		_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Lygisaurus aeratus			*	*	_	_	_	*	_	_	_	_	_	_	*	*	_	_	_	_	_	_	*	_	_	0
Lygisaurus foliorum			_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	*	_	*	*	_	0
Lygisaurus laevis			*	*	*	*	*	_	P	*	*	_	*	_	*	*	*	*	_	_	_	_	_	_	_	1
Lygisaurus tanneri	E		*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Morethia taeniopleura		Fire-tailed Skink	*	_	*	_	_	*	*	_	*	_	*	_	*	L	*	_	_	_	*	_	_	*	_	0
Proablepharus tenuis			*	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	0
Saproscincus basiliscus			*	*	*	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	1
Saproscincus czechurai		Czechura's Litter Skink	_	*	_	*	*	*	*	_	*	_	*	*	*	*	*	_	_	_	_	_	_	_	_	1
Saproscincus tetradactyla		Four-toed Litter Skink	_	_	_	_	_	_	*	*	*	_	*	*	*	*	*	*	*	*	*	_	_	_	_	1
Tiliqua scincoides		Eastern Blue-tongue Lizard	*	_	P	_	_	P	P	_	_	*	P	_	P	P	*	_	_	_	_	_	*	*	_	0
Agamidae																										
Amphibolurus nobbi	E	Nobbi	*	_	_	_	_	*	_	_	_	_	_	_	*	_	_	_	_	*	_	_	_	*	_	0
Chlamydosaurus kingii		Frill-necked Lizard	*	_	*	_	_	*	*	_	*	_	*	_	*	_	_	_	_	_	_	_	*	*	_	0
Diporiphora australis			_	_	_	_	_	*	*	_	*	_	_	_	*	*	*	_	_	_	*	_	*	*	*	0
Diporiphora bilineata		Two-lined Dragon	*	*	*	_	*	*	*	L	*	*	*	_	*	*	*	_	_	_	_	_	*	*	_	0
Hypsilurus boydii		Boyd's Forest Dragon	_	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	P	*	P	_	_	_	_	1
Lophognathus gilberti	E																							*		0
Physignathus lesueurii		Eastern Water Dragon	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	_	*	*	_	_	_	*	0
Varanidae																										
Varanus gouldii	E	Gould's Goanna/Sand Monitor	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Varanus panoptes			_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Varanus scalaris			*	*	*	L	*	*	*	P	*	*	*	P	*	*	*	L	L	*	*	L	*	*	*	0
Varanus semiremex	E	Rusty Monitor	*	_	L	_	L	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	1
Varanus storri	E		*	_	_	_	_	L	L	_	_	_	*	_	*	_	_	_	_	_	_	_	_	_	_	0
Varanus tristis	E		*	*	_	_	_	_	_	_	_	_	_	_	*	P	*	_	_	_	_	_	_	*	_	0
Varanus varius		Lace Monitor	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	_	_	*	*	*	_	_	*	0
Typhlopidae																										
Ramphotyphlops broomi			*																							1
Ramphotyphlops ligatus			_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Ramphotyphlops polygrammici			*	*	_	_	_	_	_	_	_	*	_	_	*	_	*	_	_	*	_	_	_	_	_	0
Acrochordidae																										
Acrochordus granulatus		Little File Snake	*	_	P	_	*	_	_	*	_	*	_	_	_	_	*	_	_	_	_	_	P	*	*	0
Boidae																										
Aspidites melanocephalus		Black-headed Python	*	_	_	_	_	*	_	*	_	*	_	_	P	_	_	_	_	_	_	_	_	*	_	0
Liasis fuscus		Water Python	*	_	P	_	L	_	_	L	P	*	_	_	_	_	*	_	_	_	_	*	*	*	_	0

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Liasis maculosus		Spotted Python	*	_	P	_	P	_	L	L	_	_	*	_	*	_	*	_	_	_	*	L	P	*	*	0
Morelia amethestina		Amethystine Python	*	*	*	P	*	*	*	*	*	*	*	*	*	*	*	P	*	*	*	_	_	*	*	0
Morelia spilota		Carpet Python	*	P	P	*	*	*	*	*	*	*	*	*	*	*	*	_	_	*	P	*	_	*	*	0
Colubridae																										
Boiga irregularis		Brown Tree Snake	*	*	*	_	*	*	*	*	P	P	*	*	*	*	*	P	P	*	*	*	P	*	*	0
Dendrelaphis calligastra		Northern Tree Snake	*	*	P	_	*	_	*	*	*	*	_	_	*	*	*	_	_	*	_	_	_	*	*	0
Dendrolaphis punctulata		Common Tree Snake	*	*	*	_	*	*	*	*	*	*	*	*	*	*	*	_	_	*	*	_	_	*	*	0
Enhydris polylepis		MacLeay's Water Snake	*	_	P	*	_	P	P	_	*	L	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Stegonotus cucullatus		Slaty-grey Snake	*	*	*	_	*	_	*	*	*	*	P	P	*	*	*	_	_	*	_	_	_	_	*	0
Tropidonophis mairii		Keelback	*	_	*	_	*	_	_	*	_	*	*	*	*	*	*	_	_	*	*	*	*	*	_	0
Elapidae																										
Acanthophis antarcticus		Common Death Adder	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	*	*	*	*	1
Acathophis praelongus		Northern Death Adder	*	_	*	_	P	*	P	*	*	*	*	_	*	P	*	*	_	_	_	_	_	_	_	0
Cacophis churchilli			_	_	_	_	*	_	*	*	*	*	*	_	*	*	*	_	_	_	_	_	*	*	_	1
Demansia papuensis			_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	*	_	0
Demansia psammophis		Yellow-faced Whipsnake	_	_	*	_	_	*	_	P	P	*	*	_	*	*	_	_	_	*	*	*	*	*	_	0
Demansia torquata		Collared Whipsnake	_	_	_	_	*	_	_	*	_	_	_	_	_	_	_	_	_	_	_	*	*	*	_	0
Demansia vestigiata		Black Whipsnake	*	_	*	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	*	*	*	_	0
Furina barnardi		Yellow-naped Snake	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	1
Furina ornata		Orange-naped Snake	*	_	_	_	_	_	_	_	_	_	*	_	_	*	_	_	_	_	_	*	_	*	_	0
Furina tristris	E	Brown-headed Snake	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Hemiaspis signata		Black-bellied Swamp Snake	*	*	L	*	*	*	*	*	*	L	*	P	*	*	*	_	L	L	L	L	L	*	_	0
Hoplocephalus bitorquatus	E	Pale-headed Snake	*	_	P	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	0
Oxyuranus scutellatus		Taipan	*	*	P	_	P	*	*	*	*	*	*	_	*	*	*	_	_	_	_	*	*	*	_	0
Pseudechis australis	E	King Brown Snake	*	_	P	_	_	P	*	_	_	_	_	_	*	_	_	_	_	_	_	*	*	P	_	0
Pseudechis porphyriacus		Red-bellied Black Snake	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	*	*	*	_	_	_	*	0
Pseudonaja textilis		Eastern Brown Snake	*	_	P	_	L	*	P	_	*	L	L	_	*	*	*	_	_	_	_	*	*	*	_	0
Rhinoplocephalus boschmai	E	Carpentaria Whip-snake	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Rhinoplocephalus nigrescens		Eastern Smalleyed Snake	_	*	_	*	*	P	*	*	_	_	_	_	*	*	*	_	*	*	*	_	_	_	*	0
Rhinoplocephalus nigrostriatu		Black-striped Snake	*	_	*	_	_	_	_	_	_	_	_	_	_	L	L	_	_	_	_	_	_	*	_	0
Simoselaps warro	E		*	_	_	_	_	P	P	_	*	_	*	_	*	P	_	_	_	_	_	_	P	P	_	1
Suta suta	E	Myall/Curl Snake	*	_	_	_	_	P	P	_	_	_	P	_	*	_	_	_	_	_	_	_	_	_	_	0
Tropidechis carinatus		Rough-scaled Snake	_	P	_	*	*	*	*	_	_	_	*	P	*	P	_	_	_	_	_	_	_	_	_	0
Vermicella annulata		Bandy Bandy	*	_	_	_	_	*	_	_	_	P	*	_	*	*	_	_	_	_	_	_	P	*	_	1

Appendix 4: Frog distributions within the Wet Tropics biogeographic region by faunal subregions. List compiled from the sources in Special References (Appendix 5). Refer to Figure 2.1 for subregion codes. Key: * - definite record, P - highly probable occurrence, L - possibly present. Species of particular importance to conservation and management are designated Very Important Species (VIS): VIS = 1 if either the species or subspecies is endemic to the region and/or has a rare and endangered listing (refer text). E = edge species (not true Wet Tropics species, refer text). Common names follow Ingram et al .1993.

Species		Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Bufonidae																										
Bufo marinus		Cane Toad	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
Hylidae																										
Cyclorana brevipes	E	Superb Collared-Frog	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	*	_	0
Cyclorana novaehollandiae	E	Eastern Snapping-Frog	*	_	_	_	_	P	P	_	_	_	_	_	*	_	_	_	_	_	_	_	P	*	_	0
Litoria alboguttata	E	Greenstripe Frog	*	_	_	_	_	*	*	_	_	_	_	_	*	P	_	_	_	_	_	_	P	*	_	0
Litoria bicolor		Northern Sedgefrog	*	_	L	*	_	*	*	*	*	*	*	_	*	*	*	_	_	_	_	_	*	*	_	0
Litoria caerulea		Green Treefrog	*	_	*	_	*	L	*	*	*	*	*	*	*	*	*	*	_	*	*	_	*	*	*	0
Litoria fallax		Eastern Sedgefrog	_	_	*	*	*	*	_	*	*	_	_	_	*	*	*	_	_	*	_	_	*	*	_	0
Litoria genimaculata		Green-eyed Treefrog	*	*	*	*	*	*	*	*	*	_	*	*	*	*	*	*	*	*	*	_	*	_	*	1
Litoria gracilenta		Graceful Treefrog	*	*	*	_	*	*	*	*	*	*	*	_	*	*	*	_	_	*	_	_	*	*	_	0
Litoria inermis		Bumpy Rocketfrog	*	*	*	_	_	*	*	_	*	P	*	_	*	*	*	_	_	_	_	*	_	*	_	0
Litoria infrafrenata		White-lipped Treefrog	*	_	*	_	*	*	*	*	*	*	P	_	*	*	*	_	_	_	_	_	*	*	_	0
Litoria latopalmata		Broad-palmed Rocketfrog	_	_	_	_	_	*	*	_	_	_	_	_	_	*	*	_	_	_	_	_	*	*	_	0
Litoria leseuri		Stony-creek Frog	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	0
Litoria lorica		Armoured Mistfrog	_	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Litoria microbelos		Pygmy Rocketfrog	*	_	_	_	_	_	_	*	*	*	_	_	_	_	*	_	_	_	*	_	*	_	_	0
Litoria nannotis		Waterfall Frog	_	*	*	*	*	*	*	*	*	_	*	*	*	*	*	_	*	*	*	_	*	_	_	1
Litoria nasuta		Striped Rocketfrog	*	_	*	_	*	*	*	*	*	*	*	_	*	*	*	_	_	_	*	_	*	*	_	0
Litoria nigrofrenata		Tawny Rocketfrog	*	*	*	*	_	_	_	*	*	_	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Litoria nyakalensis		Mountain Mistfrog	_	_	_	*	_	_	*	*	_	_	P	*	*	*	*	_	_	_	_	_	_	_	_	1
Litoria pallida		Peach-sided Rocketfrog	*	_	*	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Litoria revelata		Whirring Treefrog	_	_	_	_	_	_	_	_	_	_	_	*	*	_	_	_	_	_	_	_	_	_	_	1
Litoria rheocola		Common Mistfrog	_	*	*	*	*	*	*	*	*	_	*	*	*	*	*	_	_	_	_	_	*	_	_	1
Litoria rothi		Red-eyed Treefrog	*	_	*	*	*	*	*	*	*	*	*	_	*	*	*	_	_	_	_	_	*	*	_	0
Litoria rubella		Naked Treefrog	*	*	*	_	*	_	*	*	*	*	*	_	*	*	*	*	_	_	_	_	*	*	_	0
Litoria xanthomera		Northern Orange-eyed Treefrog	_	*	*	*	*	*	*	*	*	P	*	*	*	*	*	*	*	*	*	_	_	*	_	1
Nyctimistes dayi		Australian Lace-lid	_	*	*	*	*	*	*	*	*	_	*	*	*	*	*	_	*	*	_	_	*	_	_	1
Microhylidae																										
Cophixalus bombiens		Windsor Nursery-Frog	_	_	*	_	_	*	L	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Cophixalus concinnus		Tapping Nursery-Frog	_	*	_	*	*	P	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Cophixalus exiguus		Bloomfield Nursery-Frog	_	*	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Cophixalus hosmeri		Pipping Nursery-Frog	_	_	_	*	L	_	*	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	1

Species	Common Name	CL	FU	BL	TU	TL	WU	CU	ML	BM	MF	LU	BK	AU	KU	CC	MT	LE	SU	HU	EU	IL	TV	IS	VIS
Cophixalus infacetus	Buzzing Nursery-Frog	_	_	_	_	_	_	_	_	*	L	*	*	*	*	*	*	_	_	_	_	*	_	_	1
Cophixalus mcdonaldi	Southern Nursery-Frog	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	1
Cophixalus monticola								*																	1
Cophixalus neglectus	Tangerine Nursery-Frog	_	_	_	_	*	_	_	_	_	_	_	*	*	_	*	_	_	_	_	_	_	_	_	1
Cophixalus ornatus	Common Nursery-Frog	_	_	_	_	_	_	*	_	*	_	*	*	*	*	*	*	_	*	*	_	_	_	*	1
Cophixalus saxatilis	Boulder Nursery-Frog	_	_	*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1
Sphenophryne fryi	Cricket Chirper	_	*	*	*	*	*	*	*	*	L	*	_	*	_	*	*	_	_	_	_	_	_	_	1
Sphenophryne pluvialis	White-browed Chirper	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	P	*	_	_	_	*	_	_	1
Sphenophryne robusta	Pealing Chirper	_	_	_	_	_	_	_	_	*	_	*	*	*	*	*	*	*	*	*	_	*	_	_	1
Myobatrachidae																									
Crinia deserticola	Chirping Froglet	*	_	_	_	_	_	_	_	*	_	_	_	_	_	*	_	_	_	_	_	*	*	_	0
Crinia remota	Torrid Froglet	_	_	_	_	_	_	_	_	*	_	_	_	_	_	*	_	_	_	_	_	_	_	_	0
Limnodynastes convexiusculus	Marbled Frog	*	_	*	_	*	_	_	*	*	*	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Limnodynastes ornatus	Ornate Burrowing-Frog	*	*	*	_	P	_	_	*	*	*	_	_	*	*	*	_	_	_	_	_	*	*	_	0
Limnodynastes peronii	Striped Marshfrog	_	_	_	*	*	*	*	*	*	*	*	_	*	*	*	_	_	*	*	_	_	_	_	0
Limnodynastes tasmaniensis	Spotted Marshfrog	_	_	_	_	_	_	_	_	_	_	_	_	*	P	*	_	_	_	_	_	*	*	_	0
Limnodynastes terraereginae	Scarlet-sided Pobblebonk	*	_	_	_	_	L	L	_	_	_	L	_	*	L	_	_	L	*	L	_	_	*	_	0
Mixophyes schevilli	Northern Barred-Frog	_	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	_	_	_	_	1
Notaden melanoscaphus E	Brown Orbfrog	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	*	_	0
Pseudophryne covacevichae		_	_	_	_	_	_	_	_	_	_	_	_	*	_	_	_	_	_	_	_	_	_	_	1
Taudactylus acutirostris	Sharp-snouted Dayfrog	_	*	*	*	*	*	*	_	*	_	*	*	*	*	*	*	_	_	_	_	*	_	_	1
Taudactylus rheophilus	Northern Tinkerfrog	_	_	_	*	_	_	*	_	_	_	*	*	_	_	_	_	_	_	_	_	_	_	_	1
Uperoleia altissima	Tableland Gungan	_	_	_	_	_	*	L	_	_	_	L	_	*	L	_	_	_	_	_	_	_	_	_	1
Uperoleia lithomoda	Stonemason Gungan	*	_	_	_	_	*	*	_	_	_	_	_	_	_	*	_	_	_	_	_	*	*	_	0
Uperoleia mimula	Torres Gungan	*	_	_	_	_	*	*	_	_	_	_	_	*	_	*	_	_	_	_	_	*	*	_	0
Ranidae																									
Rana daemeli	Australian Bullfrog	*	*	*	*	*	*	*	*	*	*	*	_	_	_	*	_	_	_	_	_	*	*	*	0

Appendix 5 : Special references: sources of information for distributional data (Appendices 1-4).

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Appendix 6: Non-volant mammal species known to occur on the Atherton Tableland (Williams *et al.* 1996).

The method by which each species was observed in study area is tabulated, with the method used for quantitative estimates of abundance in upper case (T - trapping; S - spotlighting; M - miscellaneous; - not observed). Column headings are (a "1" indicates present in that category): END - Species which are endemic to the Wet Tropics biogeographic region; NCA - listing under the Nature Conservation Act - Wildlife (1994); VIS - Very Important Species, denotes species which are important to conservation in the region either because of NCA listing &/or they are regional endemics; ARB - arboreal species; GRND - ground-dwelling species; scansorial species have a 1 in both ARB & GRND; CF - Closed Forest (rainforest); WS - Wet Sclerophyll; DS - Dry Sclerophyll; OF - Open Forest; W - Woodland; G - Grassland; GUILD - guild classification from Braithwaite *et al.* 1985 with the addition of guild 12 (large grazing macropods).

FAMILY	SPECIES	COMMON NAME	METHOD	END	NCA	VIS	ARB	GRND	CF	WS	DS	OF	W	G	GUILD
Dasyuridae	*Antechinus flavipes*	Yellow-footed Antechinus	T			1	1	1	1	1	1	1			3
Dasyuridae	*Antechinus godmani*	Atherton Antechinus	T	1	R	1	1	1	1						3
Dasyuridae	*Antechinus stuartii*	Brown Antechinus	T, s			1	1	1	1						3
Dasyuridae	*Dasyurus hallucatus*	Northern Quoll	-				1	1			1	1	1		3
Dasyuridae	*Dasyurus maculatus*	Spotted-tailed Quoll	-		R	1	1	1	1						5
Dasyuridae	*Planigale maculata*	Common Planigale	-					1	1	1	1	1	1		4
Dasyuridae	*Sminthopsis leucopus*	White-footed Dunnart	t		R	1		1	1						4
Dasyuridae	*Sminthopsis murina*	Common Dunnart	m					1			1	1	1		4
Peramelidae	*Isoodon macrourus*	Northern Brown Bandicoot	T, s					1		1	1	1	1	1	2
Peramelidae	*Perameles nasuta*	Long-nosed Bandicoot	S, t					1	1	1					2
Phascolarctidae	*Phascolarctus cinereus*	Koala	-			1	1			1	1	1	1		7
Petauridae	*Dactylopsila trivirgata*	Striped Possum	S				1		1	1					3
Petauridae	*Petaurus australis*	Yellow-bellied Glider	S		V	1	1			1					1
Petauridae	*Petaurus breviceps*	Sugar Glider	S				1		1	1	1	1	1		1
Petauridae	*Petaurus norfolcensis*	Squirrel Glider	-			1	1			1	1	1	1		1
Pseudocheiridae	*Hemibelideus lemuroides*	Lemuroid Ringtail Possum	S	1	R	1	1		1						7
Pseudocheiridae	*Petauroides volans*	Greater Glider	S			1	1			1	1	1	1		7
Pseudocheiridae	*Pseudocheirops archeri*	Green Ringtail Possum	S	1	R	1	1		1						7
Pseudocheiridae	*Pseudocheirus peregrinus*	Common Ringtail Possum	S				1		1	1	1	1	1		7
Pseudocheiridae	*Pseudochirulus herbertensis*	Herbert River Ringtail Possum	S	1	R	1	1		1						7
Phalangeridae	*Trichosurus vulpecula*	Common Brushtail Possum	S, t				1		1	1	1	1	1		7
Phalangeridae	*Trichosurus vulpecula j.*	Coppery Brushtail Possum	S, t	1		1	1		1	1					7
Burryamyidae	*Cercartetus caudatus*	Long-tailed Pygmy Possum	S				1		1						1

APPENDIX 6

FAMILY	SPECIES	COMMON NAME	METHOD	END	NCA	VIS	ARB	GRND	CF	WS	DS	OF	W	G	Guild
Acrobatidae	*Acrobates pygmaeus*	Feather-tail Glider	**S**				1			1	1	1			1
Potoroidae	*Aepyprymnus rufescens*	Rufous Bettong	**T**, s			1		1		1	1	1	1		7
Potoroidae	*Hypsiprymnodon moschatus*	Musky Rat-kangaroo	m	1		1		1	1						2
Macropodidae	*Dendrolagus lumholtzi*	Lumholtz's Tree-kangaroo	**S**	1	R	1	1		1						7
Macropodidae	*Macropus agilis*	Agile Wallaby	-					1			1	1	1		12
Macropodidae	*Macropus giganteus*	Eastern Grey Kangaroo	**S**					1		1	1	1	1	1	12
Macropodidae	*Macropus parryi*	Whiptail Wallaby	m					1			1	1			12
Macropodidae	*Petrogale mareeba*	Mareeba Rock Wallaby	-		R	1		1			1	1	1		6
Macropodidae	*Thylogale stigmatica*	Red-legged Pademelon	**S**, t					1	1	1					6
Macropodidae	*Wallabia bicolor*	Swamp Wallaby	**S**					1		1	1	1			12
Leporidae	*Oryctolagus cuniculus*	Rabbit	m					1	1	1	1	1	1	1	6
Muridae	*Hydromys chrysogaster*	Water Rat	s, t					1	1	1	1	1	1		5
Muridae	*Melomys burtoni*	Grassland Melomys	**T**					1		1	1	1	1	1	10
Muridae	*Melomys cervinipes*	Fawn-footed Melomys	**T**,s				1	1	1	1	1	1			7
Muridae	*Mesembriomys gouldii*	Black-footed Tree-rat	-				1	1			1	1	1		10
Muridae	*Mus musculus*	House Mouse	-					1	1	1	1	1	1	1	9
Muridae	*Pogonomys mollipilosus*	Prehensile-tailed Rat	**S**			1	1	1	1						8
Muridae	*Pseudomys delicatulus*	Delicate Mouse	-					1			1	1	1	1	9
Muridae	*Rattus fuscipes*	Bush Rat	**T**, s					1	1	1					2
Muridae	*Rattus leucopus*	Cape York Rat	**T**					1	1						2
Muridae	*Rattus lutreolus*	Swamp Rat	**T**			1		1		1					11
Muridae	*Rattus rattus*	Black Rat	-				1	1							10
Muridae	*Rattus sordidus*	Canefield Rat	**T**					1			1	1	1	1	11
Muridae	*Rattus tunneyi*	Pale Field Rat	-					1		1	1	1	1	1	11
Muridae	*Uromys caudimaculatus*	Giant White-tailed Rat	**T**, s				1	1	1						10
Muridae	*Uromys hadrourus*	Masked White-tailed Rat	-	1	R	1		1	1						8
Canidae	*Canis familiaris dingo*	Dingo	s					1	1	1	1	1	1	1	5
Felidae	*Felis catus*	Feral Cat	m					1	1	1	1	1	1	1	5
Suidae	*Sus scrofa*	Feral Pig	m, s					1	1	1	1	1	1	1	

Appendix 7: Habitat proforma

SITE DESCRIPTION PROFORMA

Site:__ ___ __ ___ ___ AMG: ________________ Observers:________
Habitat : ____________________________________
Altitude:________ Aspect: _________ Slope:_____
Soiltype: _________ Water present:___ Distance to water:____
Distance to drainage line:_____Disturbance:____________________
Notes (special habitats etc):____________________________

Attributes/life forms (scale 0-4)

Flowering:___ Fruiting:___ Stranglers:___ Rocks:___ Logs:___
Caulifory:___ Grasses:___ Mistletoe :___ Ferns:___ Vine:___
W. lianes:___ Mosses:___ Epiphytes :___ Palms:___ Ginger:___
T.ferns :___ Calamus:___ Acacia:___ Eucalypt:___ Alphit.:___
Kauri:___ Treefall gap:___ Canopy Opening: ____
Habitat ecotone:______________

Walker & Hopkins Classification:

____

Foliage Density (modified Braun blanquet scale)

Strata	1	2	3	4	5	6	7	8	9	10
0-1m...........										
1-2m...........										
2-5m...........										
Sub-canopy (5-.)										
Canopy										
Total Cover....										
Canopy height..										
Canopy connect.										
No. tree stems										

0 - Absent
1 - present
2 - common
3 - >5%
4 - 25-50% cover
5 - 50-75%
6 - 75-95%
7 - 95-100%

Notes on general site habitat characterisation

Appendix 8: Additional papers which are a direct result of this study but which were not included as a formal part of the thesis.

Williams, S.E. 1995. Measuring and monitoring wildlife communities: the problem of bias. *pp* 140-144 *in* Conservation through sustainable use of wildlife, ed. by G.C. Grigg, P.T. Hale and D. Lunney. Centre for Conservation Biology, The University of Queensland.

Williams S.E. & Hero J-M. 1998. Rainforest frogs of the Australian Wet tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London B* **265**: 1-6

Williams S.E. & Hero J-M. in review. Rainforest frogs of the Australian Wet tropics: spatial patterns of species richness and assemblage structure. *Proceedings of the Royal Society of London B*

Appendix 9: Mammal guilds used in the analyses (from Braithwaite *et al.* 1985). See also Appendix 6 for individual species.

Guild 1	Small, arboreal insectivore-nectarivores: *Petaurus, Cercatetus, Acrobates*
Guild 2	Medium sized, terrestrial, insectivorous omnivores: *Rattus leucopus/fuscipes, Isoodon, Perameles*
Guild 3	Small scansorial insectivores: *Antechinus, Dactylopsila*
Guild 4	Small, terrestrial insectivores: *Sminthopsis, Planigale*
Guild 5	Large, terrestrial insectivore /carnivore: *Dasyurus, Felis, tachyglossus, Hydromys*
Guild 6	Large, terrestrial grass/leaf eaters: *Thylogale, Wallabia* and lagomorphs
Guild 7	Large, arboreal (mostly), folivore/omnivores: *Trichosurus, Melomys, Hemibelideus, Pseudocheirus, Pseudochirops, Dendrolagus, Aepyprymnus, Petauroides*
Guild 8	Small scansorial folivore/granivore: *Pogonomys*
Guild 9	Small terrestrial granivore/omnivores: *Mus*
Guild 10	Habitat-generalist tree-rats: *Melomys, Uromys*
Guild 11	Small terrestrial omnivores: *Rattus sordidus, R. lutreolus*