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Multiple determinants of Australian tropical frog biodiversity

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Abstract

Distribution data on rainforest frogs within 22 subregions of the Australian Wet Tropics were used to analyse biogeographic patterns in assemblage composition and diversity, and to relate these patterns to environmental factors. The ecological correlates of species richness and spatial patterns of assemblage structure suggested that the patterns of species richness fell into three categories, each being influenced by different processes. The species richness of habitat generalists was largely unaffected by rainforest variables and was primarily related to broad habitat diversity and climate. The spatial patterns of species richness of non-microhylid rainforest frogs were the result of processes associated with historical biogeography, especially extinctions and subsequent recolonisations in those subregions most affected by Quaternary fluctuations in rainforest area. This group of frogs has undergone severe population declines in recent years and the declines represent a significant loss in regional biodiversity since it is this group that produces the majority of regional variability in frog diversity. In contrast, the most significant influence on spatial patterns of microhylid species richness may have been in situ speciation in areas of consistent rainfall, driven by altitudinal gradients, isolation and low dispersal ability. These results stress the necessity of using meaningful and objective groups based on functional ecology in order to understand the determinants of biodiversity: it is not sufficient to examine patterns based purely on species richness within a broad taxonomic group. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

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 conservation biology. 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. 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 first step in the effective conservation and management of the biodiversity of the region is to increase our understanding of the determinants of the spatial patterns of diversity.

Few other fields within ecology have received as much attention as the study of the generation and maintenance of patterns of diversity and assemblage structure and the subject has been comprehensively reviewed many times (e.g. Wiens 1989a,b; Ricklefs and Schluter, 1993; Rosenzweig, 1995; Southwood, 1996). It has become widely recognised that current patterns in assemblage structure are dependent on both contemporary processes and biogeographic history and that the causal processes may vary dependent on the spatial scale and the biodiversity scale (genetic, species or ecological diversity) being examined (Ricklefs, 1987; Ricklefs and Schluter, 1993; Rosenzweig, 1995). Cornell (1993) hypothesised that the “key to community structure may be found in evolutionary history and extrinsic biogeography rather than in intrinsic local processes”. It

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is often difficult to disentangle the relative effects of current ecological interactions and biogeographic history. The Wet Tropics of north-eastern Queensland provides an ideal opportunity to study this interesting question because there is a number of isolated rainforest blocks that represent a natural experiment covering a gradient of sub-regional species diversity, environmental characteristics and differing biogeographic history (Williams et al., 1996; Schneider et al., 1999).

The rainforests of the Wet Tropics contain the most diverse frog assemblage in Australia with high levels of regional endemism (McDonald, 1992; Williams et al., 1996). Distributions of rainforest frogs have been relatively well documented throughout the Wet Tropics (Covacevich et al., 1982; Covacevich and McDonald, 1991, 1993; Ingram and Longmore, 1991; McDonald, 1991, 1992; McDonald et al., 1991; Richards et al., 1993; Williams et al., 1996). The high levels of regional endemism, compared to other regions within Australia, have been largely attributed to altitudinal gradients, dispersal from New Guinea, and the fluctuations in the size of rainforest refugia over the last 25 000 years (Schodde and Calaby, 1972; Winter et al., 1984; Winter, 1988; House and Moritz, 1991; Nix and Switzer, 1991; Hopkins et al., 1993; Walter and Paterson, 1994; Joseph et al., 1995; Williams et al., 1996; Williams and Pearson, 1997). The regionally endemic rainforest specialists of the Wet Tropics are considered to be “relict species of a once more widespread community” primarily restricted to upland, cooler rainforest (Winter, 1988; Nix, 1991) that have survived a series of rainforest contractions and expansions. However, little is known about what factors determine the spatial patterns of frog diversity *within* the region.

McDonald (1992) suggested that the areas of highest species richness within the Wet Tropics were “characterised by high rainfall, granite parent rock and high altitude” with core areas of high diversity in the Atherton Uplands, Carbine Uplands and Thornton Uplands. McDonald (1992) postulated that the lower diversity of frogs in the southern uplands of the Wet Tropics was due to smaller areas of rainforest, limited altitudinal range, disjunct blocks of rainforest and insufficient sampling. Functional niches based on microhabitat compartmentalisation have also been suggested as a significant factor in maintaining the diversity of frogs in the Wet Tropics (Dennis and Trenerry, 1991). In a review of the distributions and biodiversity of all rainforest vertebrates in the region, Williams et al. (1996) found that there was no significant difference in frog species richness between the upland (> 300 m altitude) and lowland (< 300 m) rainforest. The core areas of frog diversity identified by Williams et al. (1996) broadly agreed with those discussed by McDonald (1992).

The spatial patterns of species richness of regionally endemic vertebrates, including frogs, have been shown

to be closely related to the combination of the area and shape of rainforest within each sub-region of the Wet Tropics (Williams and Pearson, 1997). Williams and Pearson suggested that the largest influence on patterns of endemism within the region had been extinctions related to the contraction in rainforest area during the Pleistocene. The severity of these contractions in any subregion is indexed by the combination of current area and shape (Williams and Pearson, 1997). This hypothesis is supported by genetic studies that indicate that the populations in the subregions where contractions would have been severe are the result of recent recolonisations and that most speciation occurred much earlier than the Pleistocene, that is, allopatric speciation during the Pleistocene has not been a significant process affecting contemporary patterns of biodiversity (House and Moritz, 1991; Moritz et al., 1993; Joseph and Moritz, 1994; Joseph et al., 1995; Schneider et al., 1999). The significant non-random patterns of assemblage nestedness exhibited by the vertebrate assemblages over the region provide additional support for the Pleistocene extinction hypothesis (Williams and Pearson, 1997). These facts suggest that the non-random sifting of species, via local extinction and recolonisation during the long series of expansions and contractions in the last 2–3 million years, has been the most significant process shaping contemporary patterns of vertebrate biodiversity in the region. This hypothesis contrasts with the original Pleistocene refugia hypothesis that suggested allopatric speciation in isolated refugia was the most important process shaping contemporary patterns of diversity (Haffer, 1969).

In recent years there has been a dramatic decline of seven frog species that are endemic to the Wet Tropics rainforest (Richards et al., 1993). Four species (*Litoria lorica*, *L. nyakalensis*, *Taudactylus rheophilus* and *T. acutirostris*) have not been found for some years and three additional species (*Litoria nannotis*, *L. rheocola* and *Nyctimystes dayi*) have severely declined in many upland areas (above 300 m) where they were once common (Richards et al., 1993). However, two of the missing species are not extinct: one individual of *Taudactylus acutirostris* and 12 individuals of *Taudactylus rheophilus* were recorded in remote localities in north Queensland in late 1996 (Marshall, 1998). Williams and Hero (1998) demonstrated that the species that have declined in the Wet Tropics are all within two ecological guilds characterised by low fecundity, rainforest specialisation and breeding in flowing streams. The cause of these declines has been the subject of much, largely unresolved, debate (Hero and Gillespie, 1996; Alford and Richards, 1997; Laurance et al., 1997): however, there is mounting evidence for the involvement of a disease (Laurance et al., 1996; Berger et al., 1998; Halliday, 1998).

This paper examines the spatial patterns of frog diversity at a regional scale within the Australian Wet Tropics and attempts to elucidate the determinants of

these patterns by not only examining total species richness but also by examining ecological subsets and guilds within the frog fauna. The ecological groups used were defined by Williams and Hero (1998) using an objective, multivariate classification analysis based on what is known about the functional ecology of each species. It is all too common in the conservation-biology literature that total species richness of a taxonomic group is used to make conservation recommendations about biodiversity. We will show here that this is not adequate and that it is absolutely necessary to examine diversity patterns using ecological rather than taxonomic groups.

2. Methods

2.1. Study area

The Australian Wet Tropics biogeographic region consists of a narrow strip of coastal plains and a series of disjunct mountain ranges running parallel to the north Queensland coast between Mount Elliot (Lat. 19° 30' S) and Cooktown (Lat. 15° 30' S) (Fig. 1). The region extends from the coast to the western edge of the wet sclerophyll forests (approx. between the 1000 and 1500 mm annual rainfall isohyet), where the forests give way to more open, drier woodlands (Tracey, 1982). The region has a spatially and seasonally variable rainfall ranging from between 1500 and 4000 mm annually with about 60% of this rainfall usually falling between December and March (Keto and Scott, 1986). Tropical rainforest (approx. 930 000 ha) covers much of the montane areas of the region and the coastal flats in the northern half of the region. Although the region represents only 0.1% of the continent it is the most biologically diverse area in Australia and contains significant proportions of the continental biodiversity of most flora and fauna groups.

The Wet Tropics biogeographic region was divided into 22 sub-regions based on biogeographically distinct upland (> 300m) blocks of rainforest [Fig. 1. see Williams et al. (1996) and Williams and Pearson (1997) for further details]. Presence/absence data from a wide range of sources were collated for all of the vertebrate species present within each of the 22 sub-regions and a complete list of species, their distributions within the region, and the sources of information is contained in Williams et al. (1996).

2.2. Environmental variables

For each sub-region we calculated the total area of rainforest, area of each rainforest structural type, perimeter length of the rainforest within each sub-region (P), latitude (centre of the sub-region), latitudinal range, altitudinal breakdown of area, annual rainfall, number of different rainfall regimes (based on annual mean

rainfall), index of rainfall in the driest quarter (Rainfall Consistency) (Nix, 1991) and an index of the coldest quarter (Temperature) (Nix, 1991). The Shannon–Wiener diversity index was used as a measure of the structural vegetation diversity of rainforest (Vegetation Diversity) and in the distribution of area within a series of altitudinal bands (Altitudinal Diversity). Estimates of area, structural vegetation type, and perimeter length were calculated from 1:100 000 vegetation maps (Tracey and Webb, 1975; Tracey, 1982) using the ARC/INFO GIS system of the Wet Tropics Management Authority.

Analysis of the effects of rainforest shape required an index of shape that is independent of area. The degree to which a shape differs from circular can be indexed using a shape index (SI) (Patton, 1975) that equals 1.0 for a circle and all other shapes will have a larger SI [see Williams and Pearson (1997) for more details on shape calculation]. This index was both theoretically and empirically independent of area ($r = 0.078$, $p = 0.730$, $n = 22$).

2.3. Analytical methods

Rainforest frogs are defined as those species that regularly occur within the rainforest of the Wet Tropics, but that are not necessarily confined to rainforest. Endemic species are those species that occur only in the Wet Tropics biogeographic region. The classification of species into nine ecological guilds or functional groups was described by Williams and Hero (1998) and that classification is used here (Appendix). Multiple regression models detailed in Table 1 used backward-removal of the listed variables to reach an optimal model explaining the relationship between the environmental variables and species richness. These models are intended to be descriptive and hypothesis generating rather than predictive, since they are limited by the small number of cases available ($N = 22$). This may result in artificially high r^2 values. Since it is the relative importance of these variables to each group of frogs that is used here to generate hypotheses on the determinants of the patterns of species richness, the actual magnitude of the r^2 values is of limited importance. It should also be remembered that the data is the total number of species in each sub-region and not a highly-variable sample. R^2 values are adjusted for sample size and variables that were strongly collinear were not included in the subset of environmental variables examined here. Additionally, a number of alternative modelling procedures were examined to test the consistency of the observed patterns, including (1) using more conservative α levels for variable inclusion in the model and (2) using all the variables in the model and ranking the importance of the variables using their contribution to the variance. None of the alternative methods that were tested produced different general patterns or biological interpretations of the results from the models presented here.

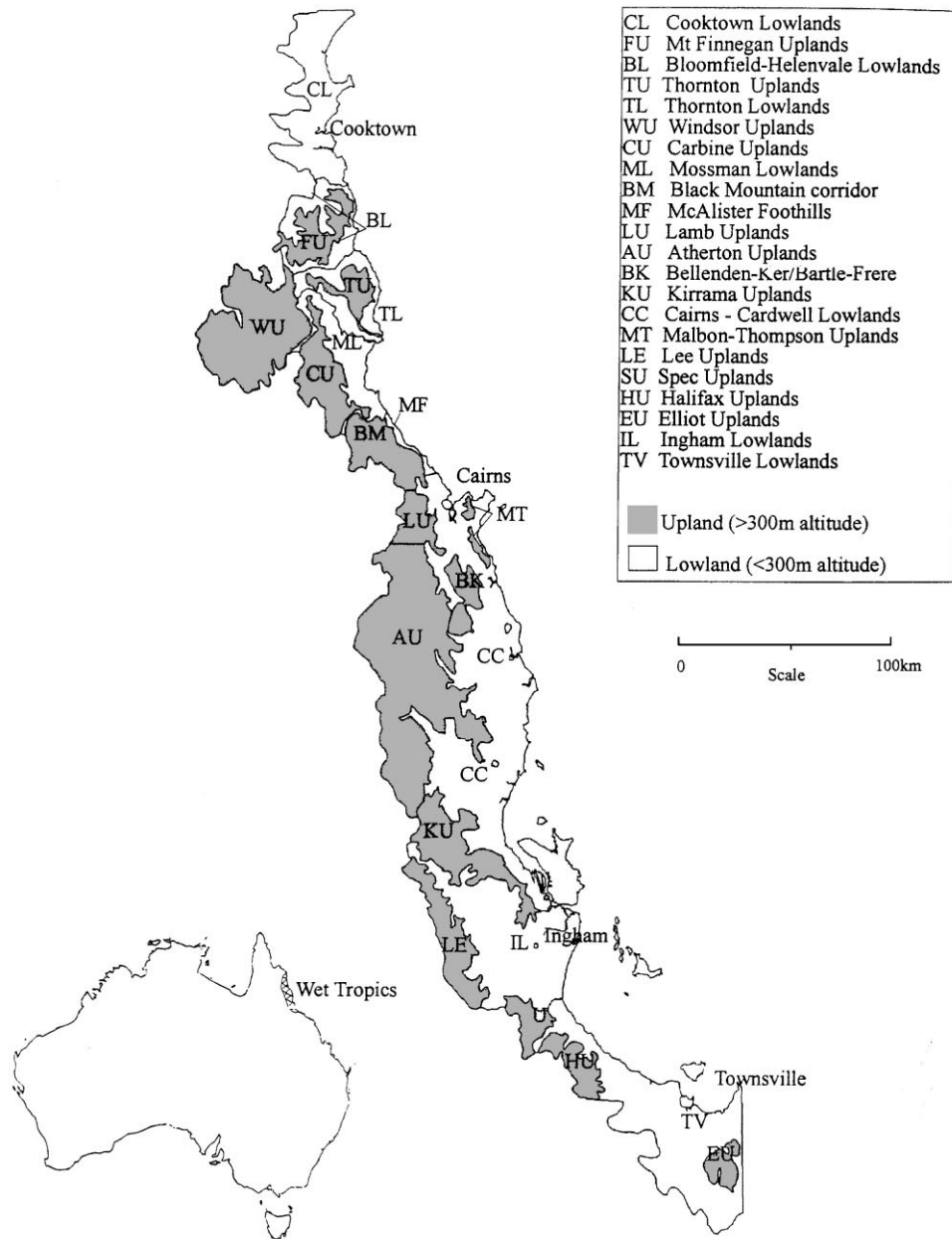


Fig. 1. Faunal sub-regions within the Australian Wet Tropics biogeographic region (modified from Winter et al., 1984; Williams et al., 1996).

Nestedness statistics were calculated using the nestedness calculator (Atmar and Patterson, 1995). Nestedness is a measure of the degree to which the assemblages in sub-regions with low species richness are simply a subset of the more diverse sub-regions. A high degree of nestedness in the faunal assemblages of archipelago systems implies non-random patterns of extinction/colonisation related to the specific extinction proneness of each species (Atmar and Patterson, 1993). The index of nestedness (T), which is independent of matrix size, was developed based on thermodynamic theories of order and disorder (Atmar and Patterson 1995). The degree to which nestedness (T) departs from random can be tested statistically using Monte-Carlo simulations.

3. Results

3.1. Environmental correlates of species richness

Total species richness of rainforest frogs in each sub-region increased with the area of rainforest, decreased with latitude and increased with a greater altitudinal diversity ($r^2 = 0.825$) (Table 1). Over 90% of the variance in endemic species richness was explained by positive relationships with rainforest area, altitudinal diversity, vegetation diversity and rainfall consistency, and a negative relationship with habitat shape (SI) ($r^2 = 0.902$).

There are large differences between the biology of microhylid and non-microhylid frogs (Williams and

Table 1
Environmental correlates of the species richness of rainforest frogs in each subregion^a

Environ. variable	All rainforest frogs (30 species)	All endemics (21 species)	Microhylids (12 species)	All non-microhylids (18 species)	Non-microhylid endemics (9 species)	Guild 2 (3 species)	Guild 4 (4 species)	Guild 5 (5 species)	Guild 6 (4 species)	Guild 7 (8 species)
Rainforest Area	0.0000 63.0	0.0030 45.3		0.0003 57.7	0.0003 52.3	0.013 46.7		0.003 52.6		
Rainforest Shape		(–) 0.0070 3.94		(–) 0.0781 18.1	(–) 0.0012 45.1	(–) 0.0201 27.9		(–) 0.0533 19.2		
Vegetation Diversity		0.0325 27.0	0.0006 49.4		0.0175 27.6		0.0188 25.8	0.0571 18.7		0.0005 51.4
Altitudinal Diversity	0.0051 37.8	0.0304 27.6		0.0546 21.2					0.0314 45.2	
Temperature			(–) 0.0366	0.0129 32.8			0.0033 37.3			(–) 0.018 43.7
Rainfall Consistency		0.0373 25.8	0.045 37.0			0.0119 31.8			0.0370 27.4	0.0005 51.8
Annual rainfall									(–) 0.0448 21.1	
Latitude	(–) 0.0036 40.1								(–) 0.0535 19.4	
Total <i>p</i>	0.0000	0.0000	0.0000	0.0002	0.0000	0.0000	0.0006	0.0000	0.0088	0.0000
Total <i>r</i> ²	82.5	90.2	73.2	72.1	82.0	79.1	53.9	78.1	59.8	74.7

^a Multiple regression models (backward removal) were used to select the environmental variables that best explain the spatial patterns of species richness in each subset of the frog fauna. Guild classification follows Williams and Hero (1998). Guilds 1, 3, 8 and 9 had insufficient species to enable regression modelling. Numbers in bold are the significance probability values and the partial *r*² values (%) (adjusted for sample size) are given below the probability. “(–)” indicates a negative relationship. Temperature, mean minimum temperature of the coldest month (Nix 1991); Rainfall consistency, mean rainfall of the driest quarter (Nix, 1991).

Hero, 1998), and this is reflected in quite different environmental correlates with species richness (Table 1). The number of microhylid species was not correlated with rainforest area or shape; however, 73% of the variation was explained by the combination of vegetation diversity, rainfall consistency and lower temperatures (Table 1). In contrast, the species richness of non-microhylids was related to rainforest area and shape, with shape having a greater influence on the number of endemic non-microhylid species than on total species richness (Table 1). The addition of temperature and altitudinal diversity to the regression model increased the amount of variance explained for non-microhylid species richness (model includes area, shape, temperature and altitudinal diversity; *r*² = 0.721), and vegetation diversity contributed to the model for non-microhylid endemics (model included area, shape and vegetation diversity; *r*² = 0.820).

3.2. Which guilds had the greatest influence on patterns of species richness?

Multiple regression (stepwise) showed that 95% of the variance in the pattern of species richness of rainforest frogs in the Wet Tropics (cumulative *r*² values in Table 2) was explained by variation in within-guild species richness of just three guilds (guilds. 5, stream hylids; 7, large microhylids; and 4, generalists). The correlation

Table 2
Guilds that make the most significant contribution to overall patterns of species richness in rainforest frogs^a

	Individual <i>p/r</i> ² values	Cumulative <i>r</i> ² values
Declining hylids (guild 5)	0.0000/0.7551	0.7551
Large microhylids (guild 7)	0.0000/0.6811	0.8514
Generalists (guild 4)	0.0480/0.1897	0.9464
Total <i>F</i> = 127.6208	Total <i>p</i> = 0.0000	Total <i>r</i> ² = 0.9464

^a Guilds are defined in Williams and Hero (1998) and described in the appendix. Individual probability (*p*) and *r*² values show the results of separate correlations between within-guild species richness and total species richness. Cumulative *r*² values indicate the contribution each guild makes to the total as it is added to the regression model (stepwise). Totals give the statistics for the final regression model with all three guilds included.

between within-guild species richness and total species richness for each significant guild is given in Table 2, with the cumulative *r*² values resulting from their addition to the regression model. This analysis simply determines which specific guilds are driving the observed patterns. Obviously, the addition of all nine guilds would explain 100% of the variation.

3.3. Species richness within guilds

Which environmental variables related to the spatial patterns of species richness within each of the important guilds? The most influential guild on geographic patterns of species richness of rainforest frogs was guild 5 (stream hylids) ($r^2 = 0.755$, Table 2). The species richness within this guild in each subregion correlated with rainforest area, shape and vegetation diversity (total $r^2 = 0.781$, Table 1). Large microhylids (guild 7) also made an important contribution to overall patterns of rainforest species richness (Table 2) and the species richness within this guild correlated with consistent rainfall, vegetation diversity and lower temperatures (Total $r^2 = 0.747$, Table 1). Guilds 4 (widespread, common, generalist, stream/swamp dwellers) and 6 (small microhylids) made significant contributions to overall species richness, although much less so than guilds 5 and 7 (Table 2). Geographic patterns of species richness in guild 4 (widespread, common, generalists, stream/swamp dwellers) were best explained by higher temperatures (at lower altitudes) and vegetation diversity (total $r^2 = 0.539$).

3.4. Sub-regional assemblage nestedness

The subregional assemblages of non-microhylid rainforest frogs had the highest degree of assemblage nestedness of any of the vertebrate groups examined (Table 3; $T = 5.9$). This pattern implies that the species in each subregion belonging to this guild are a non-random subset of the guild and that a region-wide process has produced a high degree of non-random spatial structure

in species composition within this guild. In contrast, although the microhylids (which are all regional endemics) and the habitat generalists both showed significant levels of nestedness ($T = 21.6$ and 22.6 , respectively), it was to a much lesser degree than the non-microhylid rainforest frogs.

4. Discussion

4.1. General patterns

Not unexpectedly, the total species richness of rainforest frogs in each subregion was related to rainforest area, altitudinal diversity and latitude (Table 1). However, the correlates of species richness within subsets of the frog assemblage show that these patterns of total species richness are confounded by contrasting and inconsistent patterns between the various subsets analysed.

The latitudinal decline in frog species richness within the Wet Tropics probably has little in common with classical latitudinal declines in diversity. The observed latitudinal decline is probably due to the combination of a decrease to the south in rainforest area, annual rainfall (as noted by McDonald, 1992), rainfall consistency and the more convoluted and fragmented shape of rainforest blocks in the southern uplands (higher levels of extinctions during rainforest contraction episodes). The area of rainforest present in each sub-region has a strong influence on total species richness of the non-microhylid frogs; however, it is not significantly correlated with microhylid species richness, species richness within either of the separate microhylid guilds (guilds 6 and 7) or the more generalist species (guild 4) (Table 1).

Habitat heterogeneity was consistently related to species richness in all subsets examined. The diversity of structural vegetation types was significantly correlated with species richness in most of the groups of frogs (Table 1). The amount of variance explained by vegetation diversity increased markedly when area is removed from the regression model, and much of this variation is related to the increased significance of altitudinal and rainfall diversity in larger subregions. All of the measures of environmental heterogeneity (vegetation, rainfall, topography, etc.) increase with area. This relationship suggests that area may be primarily indexing the combined expression of various forms of habitat heterogeneity. In similar analyses on mammal diversity, Williams (1997) found that either area or the sum of several measures of habitat heterogeneity could explain a similar amount of the variance in patterns of mammalian species richness. It is difficult to determine which of these gradients, if any, give rise to this pattern; however, it is clear that areas of greater habitat diversity support more species of frogs.

About 95% of the variance in overall patterns of species richness of rainforest frogs can be explained by variation in

Table 3
Nestedness statistics for various subsets of the vertebrate fauna^a

Taxon	<i>T</i>	<i>p</i>
Frogs, non-microhylid	5.4	4.09×10^{-8}
Frogs, non-microhylid rainforest	5.9	21.3×10^{-9}
Birds, endemic	7.1	1.34×10^{-11}
Mammals, non-endemic rainforest	9.9	5.04×10^{-12}
All vertebrates, endemic	15.1	3.81×10^{-64}
Mammals, rainforest	15.5	2.77×10^{-35}
Reptiles endemic	16.3	3.53×10^{-14}
Birds, rainforest	16.8	2.58×10^{-39}
Frogs, all rainforest	20.1	3.12×10^{-31}
Frogs, microhylids	21.6	4.72×10^{-5}
Mammals, endemic	22.5	6.24×10^{-4}
Frogs, habitat generalists (guilds 1,3,4)	22.6	5.48×10^{-3}
All non-endemic vertebrates	25.1	1.09×10^{-72}
Reptiles, rainforest	28.9	3.01×10^{-39}

^a Endemics are defined as those species restricted to the Wet Tropics biogeographic region. Rainforest simply indicates those species that are found in rainforest. T = nestedness statistic, p = probability that T is significantly more nested than expected from random sub-regional species distributions.

the species richness of three, biologically different guilds (Table 3): stream-dwelling hylids (guild 5), larger microhylids (guild 7) and habitat generalists (guild 4). The species richness of these three guilds within each subregion exhibit contrasting relationships with the environmental variables (Table 1), suggesting that the determinants of frog species richness varies and can be separated into at least three different pattern types.

4.2. Three types of diversity patterns

There were three broad types of diversity patterns exhibited by the frogs of the Wet Tropics, including: (i) a diverse group of generalist species that did not show any strong correlation with rainforest variables; (ii) a group of non-microhylid rainforest specialists, where the results suggested a strong influence of habitat diversity and historical biogeography (subregional extinctions and subsequent recolonisations during the fluctuations in rainforest area during the Pleistocene); and (iii) the microhylid frogs, where the observed patterns of species richness suggest very old *in situ* speciation (with limited dispersal between subregions in most species), especially in subregions that have a high and consistent rainfall pattern. We will discuss each of these diversity patterns separately.

4.2.1. Habitat generalists

All of the species in guilds 1, 3 and 4 are not strictly rainforest species. Although guild 4 makes a significant contribution to subregional species richness within rainforests (Table 2), the species richness of this group is unrelated to all of the rainforest variables. Additionally, the fact that the subregional assemblages of generalists exhibit a much lower degree of nestedness (Table 3) than most other groups implies a more random regional distribution pattern. Most species are habitat generalists that breed in still ponds or swamps and it is likely that they are independent of rainforest *per se* and are simply dependent on the presence of specific habitat features within the landscape, such as swamps.

4.2.2. Historical biogeography: subregional sifting by non-random extinctions and recolonisation

There are four lines of evidence that strongly suggest that contractions and expansions in rainforest area during the Quaternary climate fluctuations have been the most significant factor in determining the spatial patterns of species richness in the non-microhylid rainforest frogs.

Firstly, the spatial patterns of species richness within all subgroups of non-microhylid rainforest specialists were correlated with rainforest area and shape (Table 1). Williams and Pearson (1997) suggested that the combination of current area and shape may be an index of the relative effect of historical rainforest contractions on refugial rainforest area, and that current species

assemblages have been strongly affected by differential patterns of localised extinctions in these refugial areas. The effect of the areographic shape of rainforest within each sub-region is most pronounced on non-microhylid endemics (Table 1). Shape makes a significant contribution to the regression model explaining the species richness within guilds 2 and 5, both of which make significant contributions to overall patterns of rainforest frog species richness.

Secondly, the ecological guild that was responsible for most of the regional variance in species richness (guild 5, Table 2) consists of species that have undergone severe population declines in recent years (Richards et al., 1993). We showed previously that the species in this guild have similar ecological characteristics that make them more extinction-prone (Williams and Hero, 1998). We suggest that these extinction-prone species were the most severely affected guild during rainforest contractions, which explains their large contribution to the variance in regional patterns of species richness. This hypothesis is consistent with the idea that recent declines could have been caused by an epidemic disease (Laurance et al., 1996; Berger et al., 1998). However, although these results do not contradict the disease hypothesis, it does not differentiate between alternative hypotheses. The species that have undergone the recent declines are simply those species that are most susceptible to localised extinction.

The third analysis to suggest historical biogeography as a primary process determining these patterns is the high degree of assemblage nestedness exhibited by these groups (Table 3). In fact, non-microhylid, regionally-endemic frogs show the highest degree of nestedness of any vertebrate group examined in the region. This level of non-random spatial structuring implies that this group of species has been strongly affected by non-random patterns of sub-regional extinctions during contraction episodes, determined by the relative extinction-proneness of each species and/or non-random patterns of recolonisation dependent on relative dispersal ability during phases of rainforest expansion.

The fourth piece of evidence to support the importance of historical biogeography is molecular analyses of within-population genetic structure, which support the hypothesis of sub-regional extinctions and recolonisations in a number of frog species examined to date (Schneider et al., 1998; Schneider and Williams, *in press*; Hoskins and C. Moritz, unpublished data).

4.2.3. Microhylids

Consistent rainfall throughout the year is the most important environmental variable related to the spatial patterns of microhylid species richness. In contrast, the patterns in the species richness of non-microhylids show no consistent relationship with any of the rainfall variables. This is not surprising considering the different biology of these two groups (Williams and Hero, 1998).

Microhylid frogs are small, terrestrial and lay their eggs in leaf litter or other suitably moist microhabitats. This behaviour requires a habitat that is consistently moist to avoid desiccation, especially of larvae and eggs.

Temperature is correlated positively with non-microhylid and negatively with microhylid species richness. This relationship is almost certainly driven by areas of high altitude. There are four species of microhylids that are restricted to high altitudes, thereby producing a positive correlation between colder minimum temperatures and microhylid species richness. High altitude areas are also wetter than indicated by rainfall variables because of the frequent presence of cloud moisture producing a consistently moist environment that is ideal for microhylids.

It is interesting that the species richness of microhylids does not relate to the area or shape of the rainforest blocks (Table 1). The increase in species richness with area has been described as “one of community ecology’s few genuine laws” (Schoener, 1976) and yet the number of microhylid species does not increase with rainforest area. However, the total rainforest area is probably not a good indicator of the area of suitable habitat for microhylids because a number of species are restricted to mountain tops. Species–area relationships of microhylids should be examined at a finer habitat resolution; that is, the area of montane rainforest in each subregion, rather than the total area of rainforest. Alternatively, the lack of a relationship between the species richness of microhylids and the combination of rainforest area and shape may also be indicative of a group that has not been strongly influenced by the Pleistocene contractions. Hopkins et al., (1993) demonstrated that the Wet Tropics rainforest was probably fragmented into many small refugia during the contractions in rainforest of the Pleistocene and that most refugia would have been dissected by sclerophyll forest. Species (or guilds) with the ability to survive in small rainforest refugia during historical contractions in rainforest area may have been less susceptible to local extinction. Localised extinction may be due to minimum viable population size or to the loss of a micro-habitat type or other resource (related to a lower habitat heterogeneity in smaller areas). Ecological groups that can survive in small refugia would therefore not show a strong relationship with shape or area. The small size, microhabitat use and reproductive mode of microhylids may enable them to survive in small remnant patches of moist forest. This would suggest that spatial patterns of localised extinctions and recolonisations during the Pleistocene contractions would not have been the major factor determining patterns of species richness within the microhylids. This hypothesis is supported by the relatively low degree of nestedness exhibited by this group, which again suggests that processes of non-random spatial patterns of extinction and recolonisation have not been as significant for microhylid

frogs as they have for most of the other frog species in the Wet Tropics. Vicariant speciation and limited dispersal ability may have been the most important processes determining spatial patterns of microhylid diversity. However, recent molecular analyses have shown that microhylid species, like all of the vertebrates examined thus far, are much older than the Pleistocene (C. Hoskins and C. Moritz, unpublished data). Therefore, even if the patterns of diversity of microhylid frogs are due to in situ speciation it must have been at a time pre-dating the climatic fluctuations of the Pleistocene.

5. Conclusions

We have described three very different types of regional patterns of diversity within the frog assemblages of the Australian Wet Tropics. Although most groups showed relationships with the current environment, particularly with habitat heterogeneity and rainfall variables, many species appear to have been profoundly affected by processes related to the historical biogeography of the region. Our results show that it is imperative to examine diversity using objective and ecologically meaningful groups within any broad taxonomic class. The analyses show that different subsets of the frog fauna had different and contrasting patterns of species richness that, when combined, can confound each other to prevent the detection of important patterns and processes. Therefore, it is simply not adequate to examine total species richness in order to understand the determinants of diversity, even within a taxonomic group such as frogs.

It is especially significant to the conservation and management of the frogs of the Wet Tropics region that the single guild that explains most of the regional variance in frog species richness is also the guild that has undergone recent declines. Williams and Hero (1998) emphasised that these declines are particularly worrying for two reasons: firstly, the declines may be indicative of a general decline in global health and these species are simply the first to exhibit the effects; and secondly, it represents a significant loss of biodiversity, because we show here that it is this guild that produces the majority of regional variability in frog diversity and assemblage structure throughout the rainforests of the Australian Wet Tropics.

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Appendix. Guilds and their ecological characteristics (from Williams and Hero, 1998).

Guild	Species	Guild Description
1	<i>Litoria bicolor</i> <i>Lit. fallax</i>	Small (< 30 mm) tree frogs; high fecundity; non-endemic habitat generalists; larval development in swamps and ponds.
2	<i>Litoria genimaculata</i> <i>Lit. revelata</i> <i>Lit. xanthomera</i>	Moderate sized (25–55 mm) tree frogs; high fecundity; non-endemic and endemics; associated with wet forest; larval development in streams, swamps and ponds.
3	<i>Litoria infrafrenata</i>	Largest treefrog in Australia (90–120 mm); high fecundity; non-endemic; habitat generalist; larval development in swamps.
4	<i>Limnodynastes ornatus</i> <i>Lim. peronii</i> <i>Rana daemeli</i> <i>Litoria lesueurii</i>	Small and large (33–70 mm) terrestrial species; high fecundity; non-endemic habitat generalists; larval development in streams, swamps and ponds.
5	<i>Litoria lorica</i> <i>Lit. namotis</i> <i>Lit. nyakalensis</i> <i>Lit. rheocola</i> <i>Nyctimystes dayi</i>	Moderate sized (25–55 mm) tree frogs; low fecundity; endemic rainforest specialists; larval development in streams.
6	<i>Cophixalus</i> spp.	Small (< 20 mm) microhylids; low fecundity; endemic rainforest specialists; terrestrial larval development in the leaf litter.
7	<i>Cophixalus</i> spp. <i>Sphenophryne</i> spp.	Large (> 20 mm) microhylids; low fecundity; endemic rainforest specialists; terrestrial larval development in the leaf litter.

8	<i>Mixophyes schevilli</i>	Largest (65–80 mm) terrestrial frog in the wet tropics; high fecundity; endemic rainforest specialist; larval development in streams.
9	<i>Taudactylus acutirostris</i> <i>T. rheophilus</i>	Small (25–30 mm) tinker frogs; low fecundity; endemic rainforest specialists; larval development in streams.

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