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ORIGINAL ARTICLE

An assessment of endemism and species richness patterns in the Australian Anura

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ABSTRACT

Aim To assemble a continental-scale data set of all available anuran records and investigate trends in endemism and species richness for the Anura.

Location Continental Australia.

Methods 97,338 records were assembled, covering 75% of the continent. A neighbourhood analysis was applied to recorded locations for each species to measure richness and endemism for each half-degree grid square (*c*. 50 km) in the continent. This analysis was performed for all anurans, and also for each of the three main anuran families found in Australia. A Monte Carlo simulation was used to test a null hypothesis that observed centres of endemism could result simply from an unstructured overlapping of species ranges of different sizes.

Results Eleven main centres of anuran endemism were identified, the most important being the Wet Tropics and the south-west near Bunbury-Augusta and near Walpole. With the exception of south-western Australia, all of the identified significant endemic centres are in the northern half of the continent. The regions identified as significant for endemism differed from those identified for species richness and are more localized. Species richness is greatest in the Wet Tropics and the Border Ranges. High species richness also occurs in several areas not previously identified along the east and northern coasts.

Main conclusions Weighted endemism provides a new approach for determining significant areas for anuran conservation in Australia and areas can be identified that could be targeted for beneficial conservation gains. Patterns in endemism were found to vary markedly between the three main anuran families, and south-eastern Australia was found to be far less significant than indicated by previous studies. The need for further survey work in inland Australia is highlighted and several priority areas suggested. Our results for species richness remain broadly consistent with trends previously observed for the Australian Anura.

Keywords
Anura, conservation biogeography, endemism, frogs, Hylidae, Microhylidae, Myobatrachidae, palaeogeography, species richness, weighted endemism.

INTRODUCTION

In recent years there has been increasing recognition of the importance of endemic species in conservation planning. Endemic species are those restricted entirely to a specified region (Anderson, 1994). Centres of endemism, where a significant unit of biological diversity is restricted to a relatively small area, are likely to be of great importance for conservation planning (e.g. Stattersfield *et al.*, 1998; Myers *et al.*, 2000) because the species involved can only be

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conserved *in situ* within that region. Analyses of endemism and the identification of so-called 'biodiversity hotspots' (endemism and threat) have become popular in the international literature (e.g. Myers *et al.*, 2000; Roberts *et al.*, 2002). The value of identifying areas of endemism is twofold. As well as their importance for conservation, a centre of endemism challenges us to identify the factors, historical or current, that can explain the underlying patterns of speciation or range restriction.

In Australia, endemism has only been explored in the published literature in any detail for invertebrates, generally in literature reviews or at regional or state scales (e.g. Horowitz, 1997; Harvey, 2002; Yeates *et al.*, 2002), and for vascular flora (Crisp *et al.*, 2001; Laffan & Crisp, 2003; Hopper & Gioia, 2004; Woinarski *et al.*, 2006), but not for the Anura. The only specific efforts to consider anuran endemism noted low levels of endemism in the myobatrachids of semi-arid and arid Australia (Littlejohn *et al.*, 1993) and high levels of endemism in the Wet Tropics (e.g. Williams & Hero, 2001). Several other papers comment briefly on endemism (Heyer & Liem, 1976; Tyler *et al.*, 1981; Roberts & Watson, 1993; Tyler, 1999), but there has been no systematic spatial analysis of endemism for the Australian Anura at a continental scale.

Two factors strongly influence biogeographical assessments: first, the level of available survey effort and the consequent number of records available for assessment, and secondly the identification of new species. In the first case, previous anuran distribution studies were based on the data obtained before the mid to late 1980s, but substantial additional survey effort has occurred over the subsequent years, adding significantly to the records available for analysis and providing information on previously unsurveyed or poorly surveyed lands. The number of species recognized has increased substantially in recent years. Cogger (1983) recorded only 174 species whereas we now recognize 216 species. Both changes could significantly alter our understanding of the distribution of anuran fauna.

Biogeographic studies of Australia's anurans have historically concentrated on understanding patterns of species richness across the continent, particularly looking to identify areas of high richness that may represent places where the greatest degree of faunal conservation can be achieved. Several studies during the 1980s and early 1990s assessed these patterns of distribution (Brook, 1979a,b, 1981, 1982, 1983; Cogger, 1980; Tyler *et al.*, 1980, 1981; Watson, 1980; Littlejohn *et al.*, 1993; Roberts, 1993; Tyler & Davies, 1993; Tyler, 1999) and are best summarized by Roberts (1993) and Roberts & Watson (1993). They found the greatest species richness along the eastern seaboard, with major foci centred within the Wet Tropics region and in the coastal region near the New South Wales–Queensland border (see Fig. 1a for place names). Less significant centres were the New South Wales–Victorian border, the greater Sydney region, Cape York, Darwin, the Kimberleys and south-west Western Australia. In contrast, low richness was found in a broad region extending from the Nullarbor into central Australia, although this may have been a consequence of historically low survey effort. Watson (1980) and Tyler *et al.* (1981) also identified areas of low species richness in southern central Western Australia, the Gulf country and central Queensland.

In this paper we present the first systematic analysis of endemism in the Australian Anura, and reanalyse the Australian species richness patterns using an updated and more comprehensive data set than previous studies. We compare the latter to the observed richness patterns of Roberts (1993), to highlight if and how increased survey effort and taxonomic complexity have altered our understanding of anuran richness patterns in Australia. These issues are also important in the conservation of all other Australian faunal and floral groups.

METHODS

Data base

We used data sets available through the Australian Government's Department of the Environment and Heritage as the basis of the current study. These data comprise specimen and observation records held in state agency wildlife atlases, museum collections and the work of individual researchers (hereafter called observational data). These are presence only data and are strongly oriented towards the road system, particularly in the remote areas of Australia (Crisp *et al.*, 2001). We acknowledge these limitations, but obtaining true presence/absence data is very difficult for almost any study. Previous Australian studies of richness and endemism, whether generated from specimen data or expert opinion, suffer from the same problem, and therefore, are comparable.

The available data sets were updated to minimise taxonomic and spatial errors. Records dated pre-1950 were excluded from the analyses, as examination of the data indicated a low degree of spatial accuracy among early records. Records with a spatial error range > 20 km were also excluded. All records in the data base were carefully corrected to a standard taxonomy (Cogger *et al.*, 2002) and any clear anomalies removed. The result of this is a data set of 97,338 frog records. Of these, 51% were collected since Brook's studies (i.e. post-1983) and 35% since Roberts (1993).

These records were loaded into the Australian Natural Heritage Assessment Tool (ANHAT), a custom-designed analysis tool built on Microsoft Access (Microsoft, 2000) and ArcGIS geographic information system (ESRI, 1999). ANHAT is designed to perform basic comparative analyses on the presence or absence of taxa across multiple genera, families or orders. It displays the result as a map of Australia where each grid cell represents a 1 : 100,000 map sheet, a 1/2 degree square. This varies with latitude, but corresponds approximately to a 50-km square.

Observational data were allocated to 10×10 km grid cells, generating species lists for every cell within Australia within ANHAT. Use of a grid measured in kilometres rather than degrees ensured a consistent sample area across the continent. The results were generalized to the 1 : 100,000 map sheets for reporting.

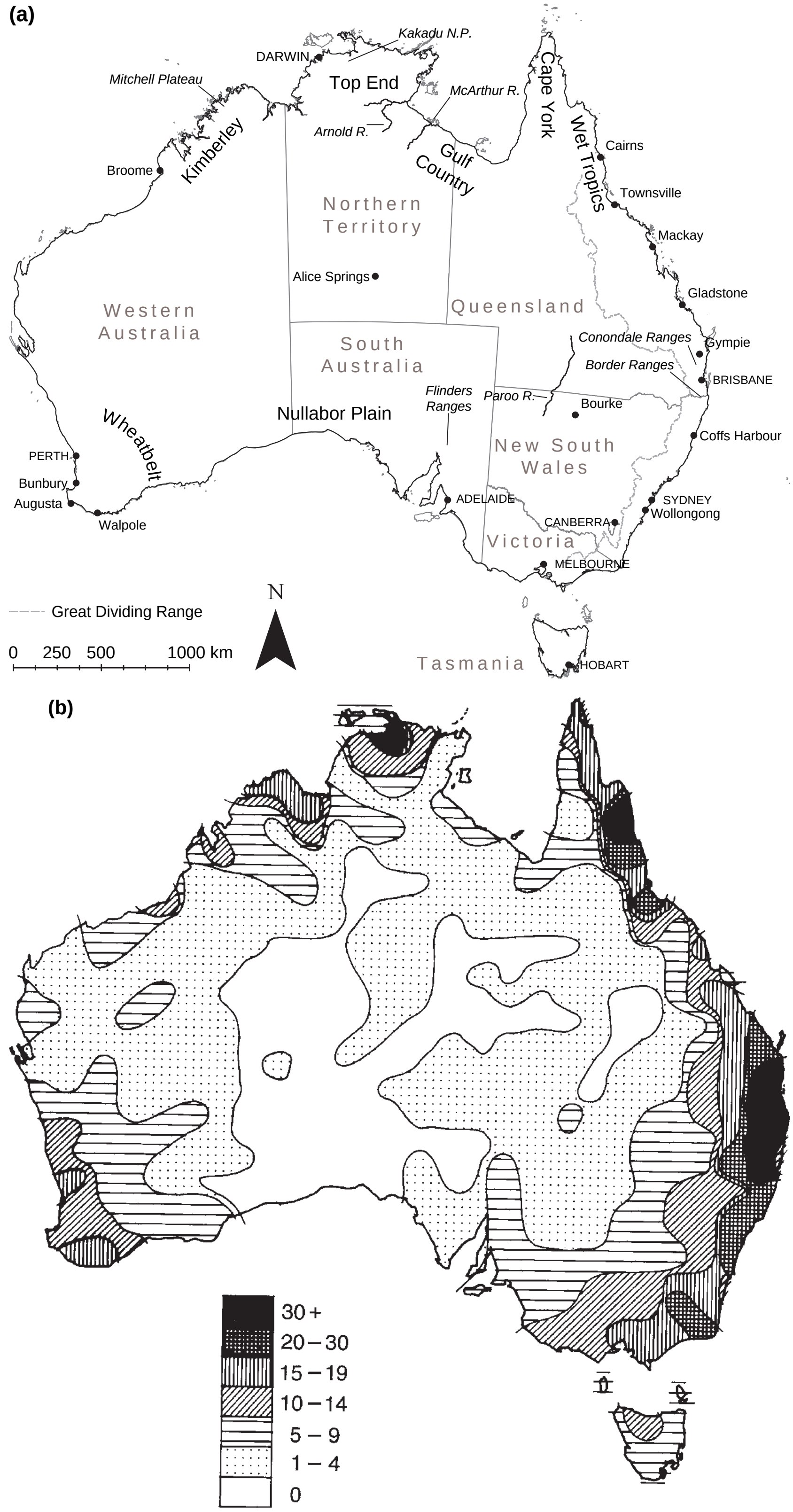

Figure 1 (a) Map of Australia showing geographic localities referred to in the text. (b) Map of anuran species richness reproduced from Roberts (1993).

Species richness

A score was allocated to each 10-km grid cell representing the total number of species recorded in that cell and the eight surrounding grid cells (a 3 × 3 cell moving window) which is a 30-km square. This neighbourhood analysis (Prendergast & Eversham, 1997) ensures that species are counted over a constant area, while minimizing the effect of arbitrary boundaries between areas used for counting. Richness for each map sheet was the score of the highest scoring 10-km grid cell within it. By plotting those map sheets with no records, this methodology also provides an analysis of areas potentially requiring further survey effort (see below).

Endemism

We calculated weighted endemism (WE) following Williams & Humphries (1994), Crisp *et al.* (2001) and others. Weighted endemism seeks to avoid the traditional problem in endemism studies, where an arbitrary region or range-size threshold is used to define what constitutes an endemic species. WE avoids a threshold for endemism by applying a simple continuous weighting function, assigning high weights to species with small ranges, and progressively smaller weights to species with larger ranges. We calculated WE by counting all species in each 30×30 km area of nine adjacent cells, but weighting each by the inverse of its range-size. Species ranges were estimated by summing the number of 10-km grid cells that contained observation records. A species recorded in only one grid cell would thus contribute to the cell's endemism score 1000 times as much as a widespread species recorded in 1000 cells, but widespread species still contribute to the score.

Crisp *et al.* (2001) proposed an alternative measure, corrected weighted endemism (CWE), to reduce the correlation between richness and endemism. CWE is calculated as the weighted endemism score for each cell divided by the richness score and represents the average degree of endemism of the species recorded in an area.

This method was tested for the current project, but was not pursued for two reasons. First, it changes the meaning of the endemism measure. Under CWE, for example, if two areas are both home to several highly localized species, but one area also has a number of widespread species, that area will receive a far lower score. We thus preferred WE, which is primarily sensitive to the presence of localized species, over CWE, which measures the mean endemism of all the species present. Secondly, CWE significantly magnified the effects of uneven sampling, generating very high endemism scores in some poorly sampled areas where the widespread species were undersampled. We note that correlation between weighted endemism and richness in our study ($r^2 = 0.30$) was far lower than observed by Crisp *et al.* ($r^2 = 0.76$), who cited this correlation as a reason to use CWE.

While the study area was restricted to Australia, a small proportion of species have ranges beyond Australia – generally to New Guinea. It is possible that the degree of endemism could be over-estimated for these species, as our method includes only the Australian part of the range. We examined a list of species native to both Australia and New Guinea (IUCN, Conservation International & Nature Serve, 2004; A. Allison, personal communication), and assessed the extent to which their range outside Australia could affect the endemism scores.

A Monte Carlo simulation was used to test a null hypothesis that observed WE scores in a particular area could result simply from an unstructured overlapping of species ranges of different sizes (Jetz *et al.*, 2004). While some areas host more species than others, including those with narrow ranges, rejection of this hypothesis for a given area implies that there is a significant, non-random structure to the distribution of range sizes creating this centre of endemism.

Following methods used by Laffan & Crisp (2003) and similar to Jetz *et al.* (2004), we randomly reallocated the species in the study to different grid cells. The two constraints on allocation of species were: (1) richness in each cell was held constant by allocating the same number of species to each cell as were actually recorded there, and (2) the estimated range of each species was held constant by allocating it to as many cells as it was actually recorded in. WE was calculated based on the randomized species distributions. The randomization was repeated 500 times and the frequency that the observed score for each map sheet was above the random score was calculated.

Taxa analysed

The analyses described above were performed for all anuran species together, and also for each of the families Hylidae, Myobatrachidae and Microhylidae. No analysis was conducted for the family Ranidae as it contains just one Australian species.

To enable a useful comparison between the different families, summary statistics for each richness and endemism analysis were generated only from map sheets with a result above zero. For example, the Microhylidae are restricted to a small area of the continent and including areas where the family does not occur would considerably reduce the mean and median values for this family.

RESULTS

Endemism

We identified eleven areas of very high anuran endemism (Fig. 2a), the most important being the Wet Tropics region and parts of the south-west region between Bunbury and Augusta and near Walpole (Table 2). The others are the Mitchell Plateau in the Kimberley, Cape York, Kakadu in the Top End, Eungella National Park near Mackay, near Gladstone and areas between Gympie and Coffs Harbour including the Conondale and Border Ranges. The maximum score for WE was 161.5 in eastern Cape York, with a mean score of 5.95 and a median score of 2.18 (Table 1). The randomization supported these areas with > 95% confidence, except those between Gympie and Coffs Harbour on the east coast.

With the exception of south-western Australia, all of the identified significant endemic centres are in the northern half of the continent. The regions identified as significant for WE are more localized than those for richness. There is a broad region of high richness from Gympie to Wollongong, but only two small isolated centres of endemism in the same region: the Conondale ranges in the north and the Border Ranges in the centre. Many of the identified peaks of endemism

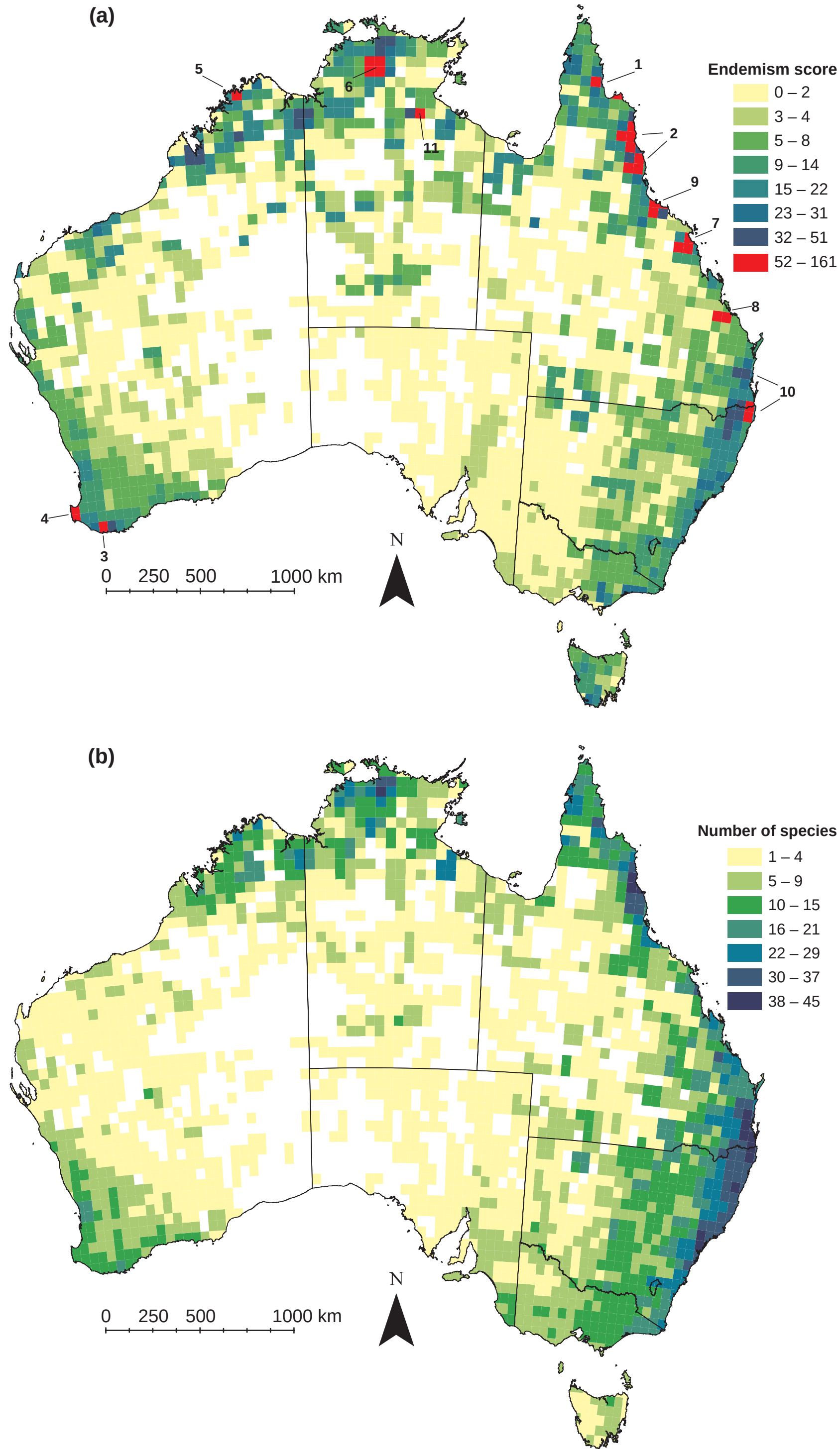

Figure 2 Patterns of (a) weighted endemism and (b) species richness for Australian anurans. The numbers 1–11 in Figure part (a) refer to centres of endemism listed in Table 2.

were not revealed by simple species richness, including areas between Gympie and the Wet Tropics on the east coast and the areas near Bunbury-Augusta and Walpole in south-western Australia.

Although 16 species were native to both Australia and New Guinea, they had very little effect on endemism scores of the centres of endemism described above. The largest impact of species occurring outside Australia was for a small part of Cape York where 9% of the endemism score was due to species also occurring in New Guinea. This was not enough to significantly change the rankings.

Species richness

Anuran species richness across Australia is presented in Fig. 2b. The highest species richness score for a 30-km square was 45 species in the Wet Tropics, with a mean of 7.11 and a median of four species (Table 1). The most significant areas

Table 1 Comparison of richness and weighted endemism scores for all Anura and major families. Richness is the number of species and weighted endemism is an index score

			All map sheets		Map sheets > 0	
Type of analysis	Taxon	Maximum	Mean	Median	Mean	Median
Richness	Anura	45	5.31	3	7.11	4
	Hylidae	26	2.71	1	4.46	3
	Myobatrachidae	22	2.70	1	4.08	3
	Microhylidae	9	0.06	0	2.22	2
Endemism	Anura	161.5	4.44	1.02	5.95	2.18
	Hylidae	53.7	1.59	0.26	2.61	0.87
	Myobatrachidae	145.3	2.68	0.62	4.05	1.58
	Microhylidae	129.8	0.37	0	14.71	2.89

Table 2 Centres of endemism and richness. WE = weighted endemism. R = species richness. Results of randomization for endemism: $^{**}P > 99.5\%$, $^{*}P > 95\%$. Area place names are shown in Fig. 1a and identified by endemism rank in Fig. 2a.

		All Anura		Hylidae		Myobatrachidae		Microhylidae	
Endemism rank	Area	WE	R	WE	R	WE	R	WE	R
1	Cape York	161**		54**	21			161	
2	Wet Tropics	153*	45	41*	26	125**		86	9
3	Walpole	147**				145**			
4	Bunbury-Augusta	120*				118**			
5	Mitchell Plateau	104*		32		72**			
6	Kakadu	76**	31		26	67**			
7	Mackay/Eungella N. P.	62*			22	56*			
8	Gladstone	60				55*			
9	Townsville	58**						50	
10	Gympie–Coffs Harbour	56	43	37	25		21		
11	Arnold River	52**							
–	Coffs Harbour–Wollongong		42		21		22		

for species richness, listed in Table 2, were the Wet Tropics (45 species) and the central East Coast (30–43 species) with the latter extending almost 1000 km from Gympie in the north to near Wollongong in the south. Kakadu National Park in the Top End has 39 species, and areas of the Kimberley up to 27 species, making both areas significantly richer than identified by previous overview studies. Our analysis indicates that 15–20 species have been recorded along the Paroo River, which is the equivalent of much wetter areas far to the east. These records considerably raise the expected species richness of areas west of the Great Dividing Range. The Gulf Country around McArthur River (26 species) is another significant new area previously defined as species poor.

Family level analysis

Summary

The most striking observation at family level is the difference in the nature of endemism between the two largest families (Table 2, Figs 3a & 4a). A strong northern Australian bias of hylid distribution is exemplified in the results for both richness and endemism, which are strongly correlated ($r^2 = 0.54$). In contrast, endemism in the Myobatrachidae is not only far higher than for Hylidae (Table 1) but is almost completely decoupled from myobatrachid richness ($r^2 = 0.16$). The richest area for Myobatrachidae on the central east coast is distant from the family's centres of endemism in the Wet Tropics region, the Kimberley and south-western Australia. The difference between families is emphasized by the randomization test, which strongly supported all the peaks of myobatrachid endemism ($P > 99.5\%$) but failed to support most peaks of hylid endemism at even the 95% level (Table 2).

Hylidae

The hylids have a near continent-wide distribution (Fig. 3a,b) with richness and endemism strongly associated with the north and east of the continent. There are few narrow-range endemic hylids in continental Australia (Table 1), with WE scores generally well below 30. The maximum score for endemism across the continent was 53.7 with a mean of 2.61. The main centres of endemism are Cape York, the Wet Tropics, the Border Ranges between Brisbane and Coffs Harbour, and the Mitchell Plateau. Of these, the randomization test supported only Cape York, and part of the Wet Tropics region with > 95% confidence.

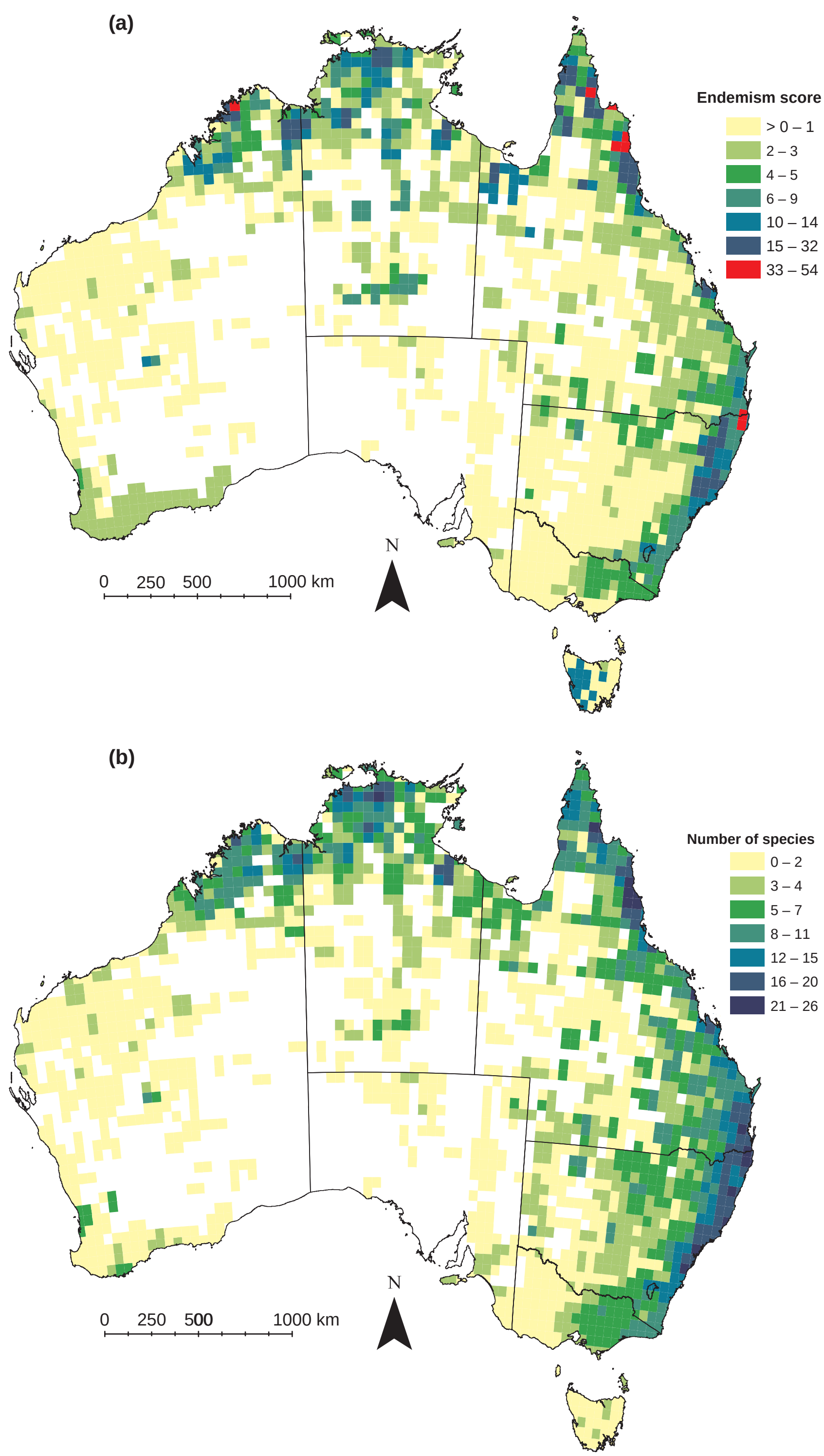

Figure 3 Patterns of (a) weighted endemism and (b) species richness for Australian Hylidae.

Hylid richness generally follows the patterns of overall anuran species richness. The richest areas, holding 22–26 species, are found in the Wet Tropics area, Kakadu in the Top End, the Queensland–New South Wales border, and Coffs Harbour. A noteworthy area of secondary significance is the Kimberley. The Macarthur River region in the Gulf Country is of particular interest as a peak of species richness in a region previously regarded as species poor. The richest areas in the continent contained 26 species, with a mean of 4.46 species (Table 1).

Myobatrachidae

The narrower distribution ranges and higher proportion of narrow range endemics within the family are reflected in higher endemism scores (23 areas with a score ≥ 40 vs. 4 areas

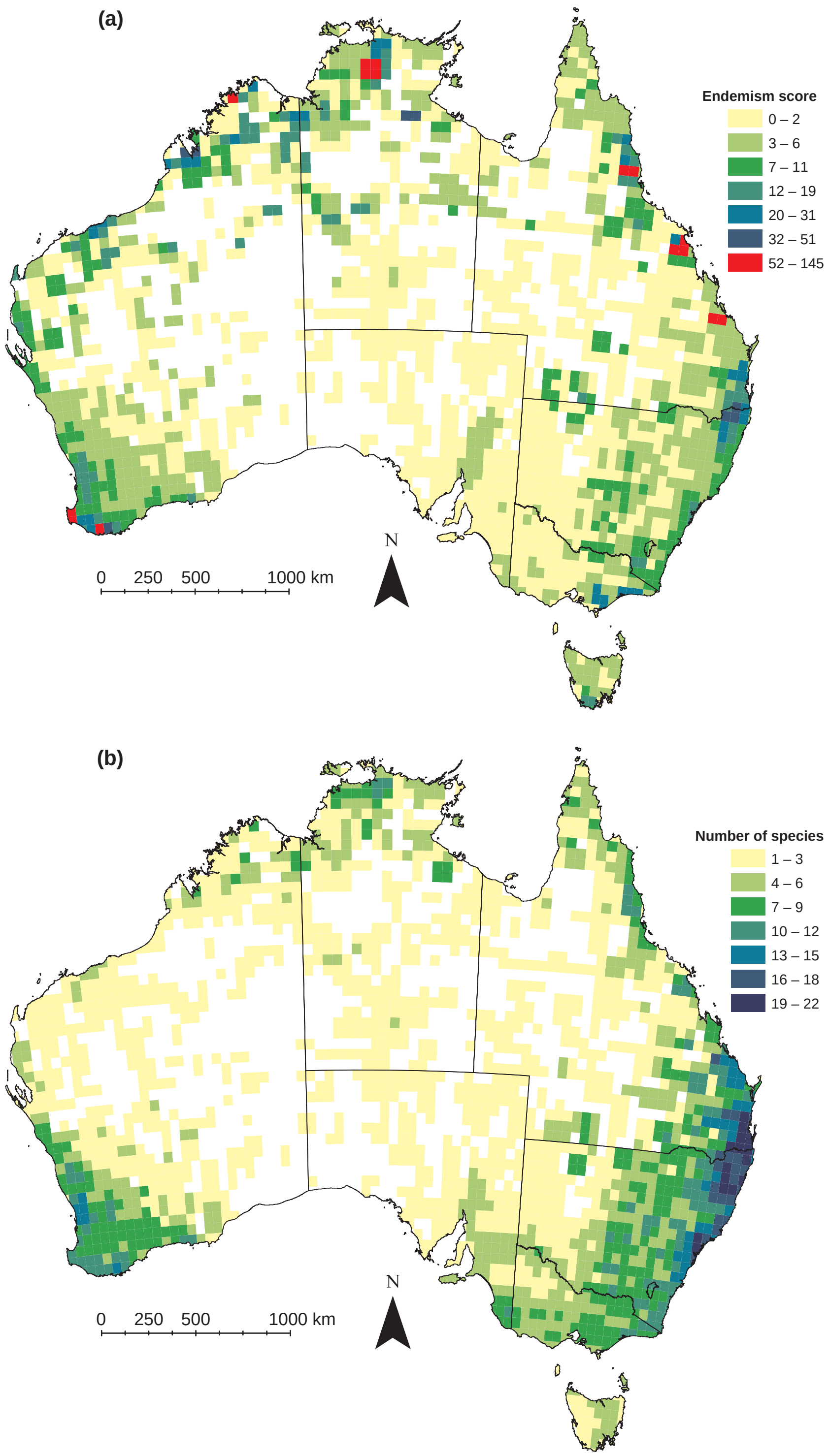

Figure 4 Patterns of (a) weighted endemism and (b) species richness for Australian Myobatrachidae.

for hylids). The maximum score was 145.3, with a mean score of 4.0, and a median of 1.58 (Table 1). The map of WE in Myobatrachidae (Fig. 4a), differs notably from the northern Australian emphasis exhibited by Hylidae, with the major areas of significance being near Bunbury-Augusta and Walpole in south-western Australia, followed by the Wet Tropics in north-eastern Australia. These areas are all supported by the randomization test with > 99.5% confidence. Scattered regions through the Kimberley and Top End and down the east coast also scored highly.

The Myobatrachidae also show a near continental distribution, with major areas of species richness in two separate districts along the east coast: Gympie to Coffs Harbour and the central coast of New South Wales north of Sydney (Fig. 4b). These districts mark the northern and southern extents of a major zone of nearly continuous high species richness in the

Myobatrachidae that is significantly richer than the rest of the continent and in marked contrast to the pattern shown in Hylidae. The richest 30-km square for the Myobatrachidae, just north of Sydney, had 22 species and the mean was 4.09 species (Table 1).

Microhylidae

The Microhylidae have a narrow northern Australian distribution with major richness and endemism in Cape York and the Wet Tropics (Fig. 5a,b). The endemism analysis reflects the comparatively high number of narrow range endemics in Microhylidae in Australia, with a maximum endemism score of 129.78 and a mean score of 14.71 (Table 1). The area with the highest endemism score is the southern part of the Cape York Peninsula (randomization support > 95%), followed by the Wet Tropics region which was not supported by the randomization. The richest area had nine species and the mean was 2.22 species (Table 1).

Data coverage and survey effort

Anurans are a comparatively well surveyed taxon in Australia. Overall, the observational data base had species records across 75% of the continent. There are some notable shortcomings in the coverage of species location records across much of inland Australia. This reflects the difficulty in surveying inland areas because of wet-weather access and the infrequency of conducive environmental conditions. There are clearly areas that should have records but do not, and a roading artefact is obvious within arid Australia. Figure 6 provides a map of areas potentially requiring further work.

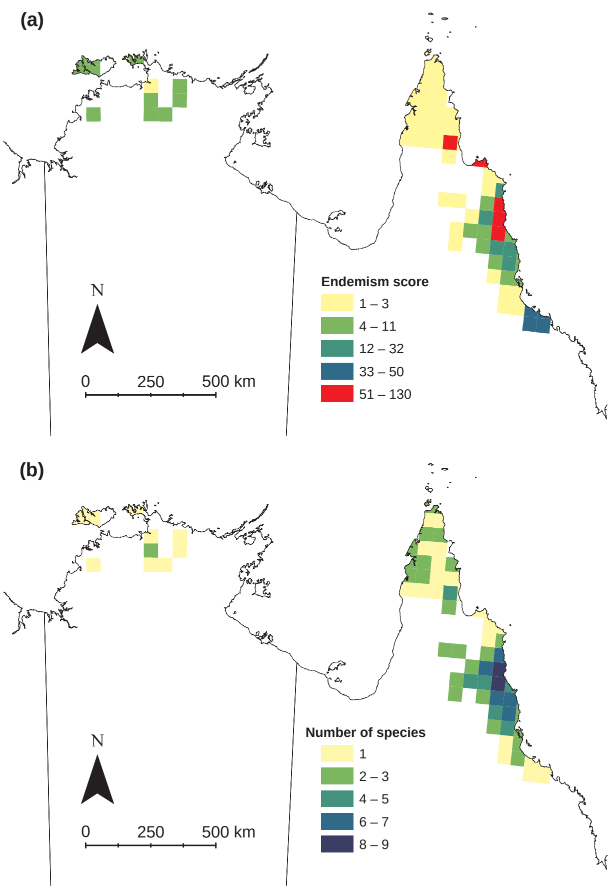

Figure 5 Patterns of (a) weighted endemism and (b) species richness for Australian Microhylidae.

DISCUSSION

Species richness

Spatial analysis of species richness and endemism based on observational and specimen data has become a popular methodology globally (e.g. Myers *et al.*, 2000; Crisp *et al.*, 2001; Hijmans & Spooner, 2001; Hopper & Gioia, 2004). These methods have proved useful in displaying species richness and endemism in a more systematic way than has been possible in the past and provide an opportunity for examining previous work and comparing patterns in different taxa (Williams & Gaston, 1998). They have also been used to map centres of endemism and theorize about likely influences on their development (e.g. Manrique *et al.*, 2003).

While trends in anuran species richness in the current study are similar to the findings of earlier researchers (Heyer & Liem, 1976; Watson, 1980; Tyler *et al.*, 1981; Brook, 1983; Littlejohn *et al.*, 1993; Roberts, 1993), this study has indicated new centres of richness and extended the boundaries of previously known ones. New findings include localized areas of species richness in Queensland between Gympie and the Wet Tropics region, an area of high species richness in the Gulf Country around McArthur River, and the extension of areas of species richness in the Top End generally. Another interesting increase in species richness occurs along the inland rivers west, north and south of Bourke. We attribute most of these changes from Roberts (1993) to the major survey effort that has been put into some regions of Australia since the early 1990s. The appearance of an area of high species richness in the Gulf country almost certainly reflects the previous absence of a comprehensive survey through this region and we suggest that high anuran species richness is probably much more continuous through this region than our results or the work of previous authors have found. The result is not unexpected, as this region has many permanent or semi-permanent rivers, refugia in the form of rain forests and vine thickets, high seasonal rainfall and regions of topographic complexity, consistent with known centres of anuran endemism elsewhere in northern Australia. Again, in the Bourke region, particularly along the Paroo, environmental complexity in the form of the frequency of permanent and semi-permanent rivers and waterholes in comparison to surrounding regions may be important, although further work is needed to prove this.

Our analysis did not find an area of higher species richness down the west coast of Australia, south of the Kimberley, as suggested by Roberts (1993) (Fig. 1b). Nor did we find support

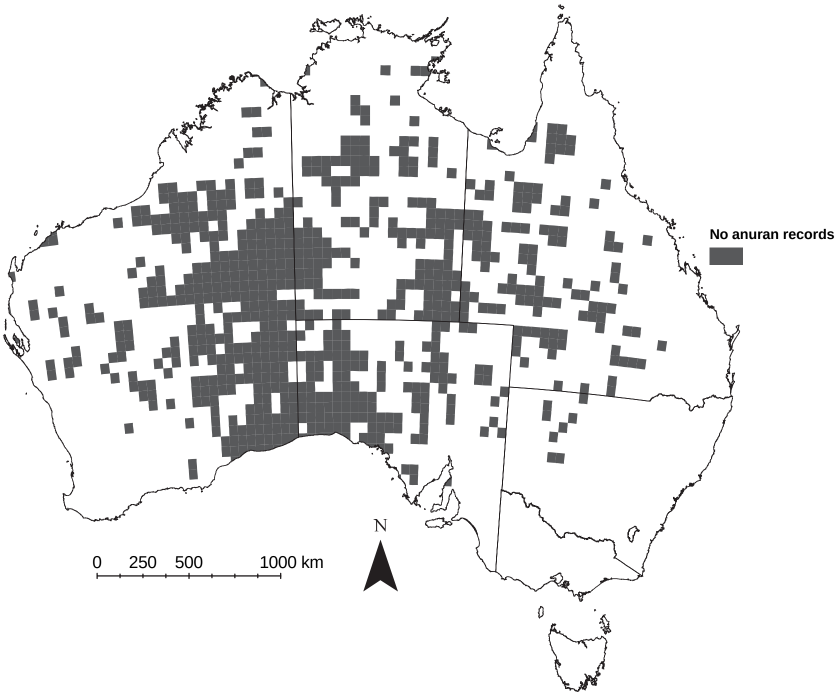

Figure 6 Map sheets without observational data in this study.

for the identification of Victoria and Tasmania as cool temperate centres of species richness, areas identified by Tyler *et al.* (1981), Roberts (1993) and Tyler (1999).

Our results also do not support Tyler's (1999) identification of a broad region of south-eastern Australia as an important zone of species richness. The significant region in the south-east is a much smaller area covering the coast and escarpment of New South Wales north from Wollongong and excludes the Flinders Ranges, Victoria and Tasmania. Nor do we define the high rainfall zone of south-western Australia between Bunbury and Albany as an area of high species richness at a national scale as has been suggested by a number of previous authors (e.g. Littlejohn *et al.*, 1993; Roberts, 1993; Tyler, 1999). These differences are entirely due to methods and we strongly advocate the use of equal area grids or other non-subjective systematic approaches rather than species count by region.

Sources of error

Two types of errors noted in this study should be considered in interpreting the results, particularly for endemism. First, for species that are regarded as widespread in the literature but with few observational records (e.g. some *Cyclorana* species), there is an underestimation of species range, and hence an over-weighting of the species in endemism calculations. Accounting for such species is difficult as we remain uncertain about their true distributions and therefore we cannot correct for false negatives. Targeting these areas with surveys is probably the only means of correcting this bias, however this is extremely difficult due to cost and access issues.

The second type of error is for species with a narrow recorded range. Because such species make a large contribution to weighted endemism scores, records with an erroneous location create comparatively high endemism scores in wrong places. This type of error was obvious in many cases and could be fixed by excluding the erroneous records. A third type of error (taxonomic and naming errors), which was carefully excluded from the current study, was presumed to be random by Crisp *et al.* (2001). Despite these issues, we believe that WE remains a good index for endemism calculations.

There are, of course, alternative methodologies for generating distribution maps and range sizes for endemism calculations, such as using predictive spatial modelling (Nix, 1986; Stockwell & Peters, 1999). Modelling would reduce the problem of an undersampled species range, described above, but is also likely to generate errors – albeit different ones – in predicted species ranges, particularly for species represented by only a small number of records.

A quarter of map sheets still contained no records in our data base, although most and probably all map sheets contain anurans. In most instances the areas have not been surveyed, although there may still be survey data that we have not captured. Despite this, we believe that ANHAT produced a usable characterization of anuran species richness and endemism in Australia. Furthermore, the analysis has produced a map of areas for which we have no observational data (Fig. 6). This provides a useful guide to where further fieldwork (or access to existing data) would most benefit our understanding of anuran distributions.

Endemism

This paper provides a first attempt at a systematic broad scale analysis of anuran endemism across the Australian continent and provides new insights into anuran endemism at a continental scale.

There are few published maps of endemism in either the Australian fauna or flora, making comparisons with other taxa groups problematic. There is some overlap with the endemic bird areas identified by Stattersfield *et al.* (1998), which is scarcely surprising given the large areas they delineated. Our major centres of endemism are broadly consistent with centres of plant endemism identified in the national analysis of Crisp *et al.* (2001) and Myers *et al.* (2000) and in the Northern Territory by Woirnarski *et al.* (2006). There is no correlation with the centres of endemism identified by Hopper & Gioia (2004) in the south-western Australian flora. There are also many areas documented as important for endemic invertebrates and endemic flora, such as the sand plains north of Perth, viney-scrub thickets and mound springs, that have no relevance for frogs at all (e.g. Horowitz, 1997; Harvey, 2002; Yeates *et al.*, 2002; Hopper & Gioia, 2004; Stanisic & Ponder, 2004).

The limitation in assuming corresponding endemic patterns between taxa is illustrated effectively by the sole Australian hotspot identified by Myers *et al.* (2000) in south-west Australia on the basis of high plant endemism intersected with threat. A conservation strategy focused on this florally biodiverse region would include the major centres of anuran endemism in the south-west but conserve less than 10% of the Australian anuran fauna, albeit including some highly restricted and phylogenetically interesting species.

Our study suggests that anuran endemism is dispersed in pockets across the continent, with a strong focus on the north and east coasts, and strongly supports the Wet Tropics region and the south-west of Western Australia between Bunbury-Augusta and Walpole as the major centres of frog endemism in Australia. Others are the Mitchell Plateau in the Kimberley, Cape York, Kakadu in the Top End, Eungella National Park near Mackay, near Gladstone and areas between Gympie and Coffs Harbour including the Conondale and Border Ranges. The congruence of some of the major centres of endemism with centres of species richness is consistent with the findings of other recent international work on endemism (e.g. Myers *et al.*, 2000; Crisp *et al.*, 2001; Hijmans & Spooner, 2001; Hopper & Gioia, 2004). Collectively, the defined centres contain more than 80% of Australia's anuran fauna, individually they average between 10% and 21%. This mirrors the findings of other international studies, e.g. Hijmans & Spooner (2001), that in some taxa, endemism is dispersed across the landscape and while a single area does not contain a large number of endemics, and therefore a high percentage of biodiversity, a small number of sites can be selected that do. The identified centres of endemism are of great significance for conservation planning as defined regions that collectively contain both a large percentage of anuran biodiversity and have species not likely to be located in many other areas.

Our systematic analysis challenges previously held assumptions about the great significance of south-eastern Australia as a centre of endemism (see Littlejohn *et al.*, 1993; Tyler, 1999). Our data support the high species richness of this region; they suggest that it has at best only moderate significance for endemism. This is because the endemic species in the south-east occur widely scattered down the Great Dividing Range rather than clustered together as they are in the south-west and north-east of Australia. Whereas previous studies have counted endemics within pre-defined regions of various sizes, and have treated the south-eastern species as a single spatial cluster, our equal-area comparison does not reveal a high degree of endemism.

Most of the identified areas in northern and eastern Australia are typified by tropical or sub-tropical climates, high rainfall, topographic complexity and often habitat complexity with a wide range of habitats from wetlands and heaths, through dry forests to tall forests and rain forests. We consider it highly likely that these areas represent major, long-term evolutionary refugia. At least one of these areas, the Wet Tropics, has been studied in detail for herpetofauna (Schneider *et al.*, 1998; Moritz *et al.*, 2005). These phylogeographic studies suggest that rain forest remnants in the Wet Tropics acted as multiple small refugia for herpetofauna populations during aridification associated with Quaternary glacial maximums and that this explains much of the observed endemism and phylogenetic diversity. We theorize that the environmental complexity exhibited by other centres in northern and eastern Australia may have acted in a fashion and that similar processes have been in operation.

By contrast, the centres in south-western Australia, Bunbury-Augusta and Walpole are notably different. Both of these areas fall in the high rainfall zone of a mediterranean climate with subdued topography, and in comparison with eastern and northern Australia show little habitat complexity. Clearly, different influences are playing a role in the south-west than in other parts of Australia. *In situ* speciation and subtle barriers such as edaphic features have been used to explain the local endemism exhibited by *Geocrinia* species in the south-west (Wardell-Johnson & Roberts, 1996) and these species contribute much of the endemism exhibited in the south-west. Similar fine-scale environmental changes have been invoked to explain high endemism in other taxa such as the vascular plants (Hopper & Gioia, 2004). It seems likely that the south-west represents an area of recent or active speciation and that anurans may be responding to fine-scale environmental changes in a fashion similar to other groups, such as vascular plants, although the resulting patterns vary.

The Monte Carlo randomization confirmed the significance of many of the centres of endemism identified in this study, and also highlighted a distinction in what is meant by endemism based on the explanation for the observed endemism score. We argue that areas where endemism passes this test (> 95%) are not an accidental consequence of independent, overlapping species ranges. These areas have an interesting biogeographic story to tell. In areas that fail the test, the presence of restricted range species is just as real and demands the same attention for conservation, even though the cause may be dismissed as random. It is thus useful to distinguish centres of endemism of both evolutionary and conservation significance, from those that are primarily important for conservation. A good example of the latter is the east coast between Gympie and Coffs Harbour where a number of areas rank highly for anuran endemism (WE > 40) but are far below significance by the randomization test.

Comparison of families

The two largest families have species adapted to live in nearly all parts of Australia, but display markedly different patterns of richness and endemism. Richness in the Hylidae is predominantly northern, and Myobatrachidae strongly orientated towards the central East Coast. The endemism patterns also differ. These patterns suggest a long history on the continent and this is supported by the nearest relatives of both these groups occurring in South America (Frost *et al.*, 2006). The results also show markedly different responses to presumably similar historical pressures. The localized endemism of the Myobatrachidae is arguably strongly rooted in its evolutionary history, whereas endemism in the Hylidae could be dismissed as a by-product of the patterns of richness. One interpretation is that the Myobtrachidae have a long evolutionary history centred on the Australian mainland, whereas the Hylidae have a more diverse northern dominated pattern resulting from more recent and multiple interactions between New Guinea and Australia. We believe that phylogenetic work currently underway for both groups will provide a better understanding of these relationships.

By contrast, the microhylids are restricted to northern Australia, possibly indicating recent arrival in Australia from New Guinea (Tyler, 1999), or tropical niche conservatism (Wiens & Donoghue, 2004).

Future priorities

The major centres of species richness and endemism that we have identified (Table 1) are of use in informing conservation priorities for the future. Collectively, these centres contain a large proportion of Australia's anuran biodiversity and are of great conservation significance for aiding our evolutionary understanding of the Anura. While a number of centres occur in regions well represented in conservation reserves, a number do not. Even within regions that are well conserved, the threat posed by exotic species and diseases does not guarantee anuran conservation.

Our results suggest that the major field survey effort of the past 10 years has made a substantial contribution to an understanding of anuran distributions in Australia. Given this, we can expect that future detailed surveys of poorly surveyed areas will change further the observed patterns of richness and endemism. Clearly, further survey work is needed across inland Australia. Because of the access and timing issues, such work is expensive; however, two areas, the inland rivers of the Bourke region and the rivers of the Gulf Country in the vicinity of the Macarthur River, merit further investigation. Both regions appear to be conservation significance for anuran richness and survey work is the principal means of testing this.

The availability of spatial data and the phylogenetic work currently being completed offers the opportunity to further explore the significance of endemic centres using phylogenetic diversity-endemism calculations (Faith *et al.*, 2004) and other methodologies to resolve more finely conservation priorities.

Looking beyond the Anura, there is an opportunity with the increasing digitization and availability of specimen data to extend the systematic analysis of endemism to document and compare the patterns of endemism in Australia's vertebrates.

CONCLUSION

Our study indicates previously unidentified areas of species richness down the east coast and across northern Australia, most attributable to greater survey coverage in these regions over the past 10–15 years.

There is strong support for the Wet Tropics Region and areas of the south-west of Western Australia near Bunbury-Augusta and Walpole as the major centres of frog endemism in Australia. We found that the centres of endemism derived from weighted endemism correlated broadly with species richness in Hylidae and Microhylidae but less so in Myobatrachidae, where more complex underlying patterns were revealed. The weighted endemism measure provides an objective, meaningful index of endemism.

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REFERENCES

Anderson, S. (1994) Area and endemism. *Quarterly Review of Biology*, **69,** 451–471.

Brook, A.J. (1979a) *The atlas of frogs of Victoria*. University of Melbourne, Melbourne.

Brook, A.J. (1979b) *The atlas of frogs of Tasmania*. University of Melbourne, Melbourne.

Brook, A.J. (1981) *The atlas of frogs of South Australia*. University of Melbourne, Melbourne.

Brook, A.J. (1982) *The atlas of frogs of Victoria*, 2nd edn. University of Melbourne, Melbourne.

Brook, A.J. (1983) *Atlas of Australian Anura: progress report*. University of Melbourne, Melbourne.

Cogger, H.G. (1980) A biogeographic study of the Arnhem Land herpetofauna. *Proceedings of the Melbourne Herpetological Symposium* (ed. by C.B. Banks and A.A. Martin), pp. 148–152. Zoological Board of Victoria, Melbourne.

Cogger, H.G. (1983) *Reptiles and amphibians of Australia*. Revised edition. Reed Books, Sydney.

Cogger, H.G., Cameron, E. & Cogger, H.M. (2002) *Australian faunal directory: Amphibia*. Australian Biological Resources Study, http://www.deh.gov.au/biodiversity/abrs/online-resources/fauna/afd/AMPHIBIA/tree.html.

Crisp, M.D., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28,** 183–198.

ESRI (Environmental Systems Research Institute) (1999) *ArcGIS 8.1*. http://www.esri.com.

Faith, D.P., Reid, C.A.M. & Hunter, J. (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, **16,** 255–261.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297,** 1–371.

Harvey, M.S. (2002) Short-range endemism among the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics*, **16,** 555–570.

Heyer, W.R. & Liem, D.S. (1976) Analysis of the intrageneric relationships of the Australian frog family Myobatrachidae. *Smithsonian Contributions to Zoology*, **233,** 1–29.

Hijmans, R.J. & Spooner, D.M. (2001) Geographic distribution of wild potato species. *American Journal of Botany*, **88,** 2101–2112.

Hopper, S.D. & Gioia, P. (2004) The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Evolutionary Systematics*, **35,** 623–650.

Horowitz, P. (1997) Comparative endemism and richness of the aquatic invertebrate fauna in peatlands and shrublands of far south-western Australia. *Memoirs of the Museum of Victoria*, **56,** 313–321.

IUCN, Conservation International & Nature Serve (2004) *Global Amphibian Assessment*. http://www.globalamphibians.org (Downloaded on 30 January 2006).

Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, **7,** 1180–1191.

Laffan, S.W. & Crisp, M.D. (2003) Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *Journal of Biogeography*, **30,** 511–520.

Littlejohn, M.J., Roberts, J.D., Watson, G.F. & Davies, M. (1993) Family Myobatrachidae. *Fauna of Australia, Vol. 2A: Amphibia and Reptilia* (ed. by C.J. Glasby, G.J.B. Ross and P.L. Beesley), pp. 41–57. Australian Government Printing Service, Canberra.

Manrique, C.E., Duran, R. & Argaez, J. (2003) Phytogeographic analysis of taxa endemic to the Yucatan Peninsula using geographic information systems, the domain heuristic method and parsimony analysis of endemicity. *Diversity and Distributions*, **9,** 313–330.

Microsoft (2000) *Microsoft Access*. Microsoft Corporation, Redmond, WA, USA.

Moritz, C., Hoskin, C., Graham, C.H., Hugall, A. & Moussalli, A. (2005) Historical biogeography, diversity and conservation of Australia's tropical rainforest herpetofauna. *Phylogeny and conservation* (ed. by A. Purvis, J.L. Gittleman and T.M. Brooks), pp. 244–264. Cambridge University Press, London.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403,** 853–858.

Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of Australian elapid snakes* (ed. by R.C. Longmore), pp. 4–15. Australian Flora and Fauna Series, 7. Australian Government Publishing Service, Canberra.

Prendergast, J.R. & Eversham, B.C. (1997) Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. *Ecography*, **20,** 210–216.

Roberts, J.D. (1993) Natural history of the Anura. *Fauna of Australia, Vol. 2A: Amphibia and Reptilia* (ed. by C.J. Glasby, G.J.B. Ross and P.L. Beesley), pp. 28–34. Australian Government Printing Service, Canberra.

Roberts, J.D. & Watson, G.F. (1993) Biogeography and phylogeny of the Anura. *Fauna of Australia, Vol. 2A: Amphibia and Reptilia* (ed. by C.J. Glasby, G.J.B. Ross and P.L. Beesley), pp. 35–40. Australian Government Printing Service, Canberra.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., Mcallister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. & Werner, T.B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295,** 1280–1284.

Schneider, C.J., Cunningham, M. & Moritz, C. (1998) Comparative phylogeography and the history of endemic vertebrates in the Wet Tropics rainforests of Australia. *Molecular Ecology*, **7,** 487–498.

Stanisic, J. & Ponder, W.F. (2004) Forest snails in eastern Australia – one aspect of the other 99%. *Conservation of Australia's forest fauna* (ed. by D. Lunney), pp. 127–149. Royal Zoological Society of New South Wales, Mosman, NSW.

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, M.J. (1998) Endemic bird areas of the world: priorities for biodiversity conservation. *Birdlife Conservation Series 7*, pp. 13–26. Birdlife International, Cambridge, UK.

Stockwell, D. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13,** 143–158.

Tyler, M.J. (1999) Distributional patterns of amphibians in the Australo-Papuan region. *Patterns of distribution of amphibians – a global perspective* (ed. by W. Duellman), pp. 541–560. John Hopkins University Press, Baltimore.

Tyler, M.J. & Davies, M. (1993) Family Hylidae. *Fauna of Australia, Vol. 2A: Amphibia and Reptilia* (ed. by C.J. Glasby, G.J.B. Ross and P.L. Beesley), pp. 58–63. Australian Government Printing Service, Canberra.

Tyler, M.J., Davies, M. & Martin, A.A. (1980) Frogs of the Kimberley. *Proceedings of the Melbourne Herpetological Symposium* (ed. by C.B. Banks and A.A. Martin), pp. 1–2. Zoological Board of Victoria, Melbourne.

Tyler, M.J., Watson, G.F. & Martin, A.A. (1981) The Amphibia: diversity and distribution. *Ecological biogeography of Australia* (ed. by A. Keast), pp. 1277–1301. Junk, The Hague.

Wardell-Johnson, G. & Roberts, J.D. (1996) Morphological variation in the *Geocrinia rosea* (Anura: Myobatrachidae) complex in southwestern Australia. *Gondwanan heritage: past, present and future of the Western Australian biota* (ed. by S.D. Hopper, J.A. Chappill, M.S. Harvey and A.S. George), pp. 172–178. Surrey Beatty & Sons, Chipping Norton, Australia.

Watson, G.F. (1980) Diversity and distribution of Australian amphibians. *Proceedings of the Melbourne Herpetological Symposium* (ed. by C.B. Banks and A.A. Martin), p. 3. Zoological Board of Victoria, Melbourne.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19,** 639–644.

Williams, P.H. & Gaston, K.J. (1998) Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. *Ecography*, **21,** 551–559.

Williams, S.E. & Hero, J.M. (2001) Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation*, **98,** 1–10.

Williams, P.H. & Humphries, C.J. (1994) Biodiversity, taxonomic relatedness, and endemism in conservation. *Systematics and conservation evaluation* (ed. by P.L. Forey, C.J. Humphries and R.I. Vane-Wright), pp. 269–287. Oxford University Press, Oxford.

Woinarski, J.C.Z., Hempel, C., Cowie, I., Brennan, K., Kerrigan, R., Leach, G. & Russell-Smith, J. (2006) Distributional pattern of plant species endemic to the Northern Territory, Australia. *Australian Journal of Botany*, **54,** 627–640.

Yeates, D.K., Bouchard, P. & Monteith, G.B. (2002) Patterns and levels of endemism in the Australian wet tropics rainforest: evidence from flightless insects. *Invertebrate Systematics*, **16,** 605–619.

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