Between a rock and a dry place: land snails in arid Australia

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ABSTRACT

The present composition of the arid-zone terrestrial mollusc fauna reflects the post Pliocene aridity with a mix of highly adapted and relictual taxa. A database of 8,200 pulmonate gastropod records derived from museum collections was compiled for continental Australia and interrogated for the purposes of examining distributional trends for inland arid and semi-arid Australia. Endemism and species richness were examined at species, genus and family level. A potentially high correlation was found between species richness, endemism and sharp topographic relief, highlighting the desert ranges – particularly the West MacDonnell and Flinders Ranges as of national significance for conservation. The implications of the use of land snail data for conservation assessment, particularly for the identification of terrestrial refugia, are discussed.

Key words: arid zone, endemism, species richness, biodiversity, refugia, Red Centre, limestone; invertebrate, museum records

Introduction

Australian land molluscs are a significant element of the Australian fauna, with high levels of regional endemism. There were 504 named species listed by Smith (1992) while Stanisic and Ponder (2004) argued for at least 1220 in eastern Australia alone. In the current data base there are about 2,300 taxa listed and while there are probably still some synonyms remaining in the dataset, the more realistic estimate of national taxa is probably at least 2000 named and unnamed taxa. Despite these numbers, land molluscs are taxonomically tractable, with low numbers of species regionally or locally and, because nearly all bear shells, they can be sampled well after death. Their presence is highly dependent on available moisture, even if only seasonal (Ponder 1997, 1998; Stanisic and Ponder 2004). The combination of high local endemism, low numbers of species and sensitivity to moisture make land molluscs important environmental indicators (Stanisic and Ponder 2004). Studies in eastern Australia have demonstrated their excellent potential as indicators for other invertebrate taxa, primarily because, with their durable shells, they are comparatively easy to collect even when living specimens are difficult to find, and most are comparatively easy to identify (Stanisic and Ponder 2004). Biogeographically, land molluscs include both a relict Gondwanan element as well as more recent radiations (Smith and Stanisic 1998). Their distribution across the continent includes significant relictual faunas in arid regions as well as rich coastal faunas in eastern, northern and south-western Australia (Stanisic 1990; Smith and Stanisic 1998).

There have been no recent national reviews of land molluscs in Australia other than the synopses in Beesley *et al.* (1998) and a catalogue of the fauna (Smith 1992; Smith *et al.* 2002). A number of regional revisions focus mainly on eastern (e.g., Stanisic 1990, 1997a, b, c; Hyman and Stanisic 2005) or north-western Australia (e.g., Solem 1979, 1981a,b, 1984, 1985, 1988a, 1989, 1991, 1997) with one on taxa from the 'Red Centre' (Solem 1993) and another on the southern parts of the arid zone including the Flinders Ranges (Solem 1992a,b). More recent reviews have overviewed the fauna, outlined conservation status and identified major areas of significance (e.g., Ponder 1995, 1997, 1998; Smith and Stanisic 1998; Stanisic and Ponder 2004).

The present composition of the arid-zone terrestrial mollusc fauna reflects the post Pliocene aridity with a mix of highly adapted and relictual taxa. Strategies adopted by these taxa are largely to avoid desiccation and to take advantage of the brief periods during and immediately following rain (e.g., Solem 1992).

Work on arid zone snails has been patchy. A few central Australian species were named from material collected on early expeditions to the interior but the great majority of arid zone taxa were not named until the second half of the 1900s. By far the most significant contribution has been the work of Alan Solem which largely focused on Western Australian camaenids but also included work on the southern arid and semiarid areas and the Red Centre (see references above). Apart from Solem's work, no similar revisions have been conducted in other areas or on the northern and eastern parts of the arid zone where significant numbers of new taxa are known to occur. There have not been any published major reviews of the arid zone land snail fauna although the (currently unpublished) work of Hugall and Stanisic on the camaenid radiation (Stanisic pers. com. 2005) is covering significant elements within this fauna and Cameron (1992) made comments on aspects of the camaenid radiation in the Kimberley.

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Of the land snail groups present in the arid zone, by far the most significant is the Camaenidae, a family of medium-sized snails found on mainland Australia and in Asia. The main arid-zone camaenid genera (with number of described, valid species in brackets – data from Smith *et al.* 2002) are:

NW Australia (excluding Kimberley) *Amplirhagada* (25), *Caperantrum* (1), *Falspleuroxia* (1), *Plectorhagada* (6), *Promonturconchum* (1), *Quistrachia* (9), *Rhagada* (26), *Strepsitaurus* (5), *Westraltrachia* (20 – some in Kimberley).

Kimberley – NT – *Cristilabrum* (13), *Exiligada* (2), *Kendrickia* (1), *Mesodontrachia* (3), *Mouldingia* (2), *Ningbingia* (6), *Ordtrachia* (5), *Prototrachia* (1), *Prymnbriareus* (1), *Setobaudinia* (8), *Torresitrachia* (11) (fig. 1a and d), *Turgenitubulus* (8).

Southern South Australia, including Flinders Ranges – *Cooperconcha* (3), *Cupedora* (16 + one from NSW), *Glyptorhagada* (9), *Micromelon* (1), *Pseudcupedora* (1).

Primarily central Australian genera include *Basedowena* (9), *Contramelon* (1), *Divellomelon* (1), *Eximiorhagada* (1), *Granulomelon* (4), *Minimelon* (1), *Montanomelon* (2), *Pleuroxia* (also in NWA) (13), *Semotrachia* (25) (fig. 1b), *Sinumelon* (also Flinders Ranges and Murray-Darling Basin) (32) (fig, 1c), *Tatemelon* (4), *Vidumelon* (1).

A few other families contain taxa that have endemic arid-zone species but these are, with one exception, small in size. The exception is Bulimulidae, with several species of the genus *Bothriembryon* living in arid habitats in coastal and near coastal areas in the west and south of the continent and one (*B. spenceri* Tate, 1894) with a very restricted distribution in central Australia (Solem 1989). Other species in this diverse but poorly studied genus occupy woodland habitats in south Western Australia and one in Tasmania. The other terrestrial families found in Australia's arid zone and included in our analysis are Succineidae, Pupillidae, Helicarionidae and Punctidae. The later families are all represented by only a few species.

The analysis presented below is based on verifiable museum records. While these data have some intrinsic problems (see below) they are generally acknowledged to be the most reliable data for broad-scale mapping for groups that have been moderately to well collected (e.g., Ponder *et al.* 2001; Graham *et al.* 2004).

Methods

We used a database compiled by the Department of the Environment and Heritage from available digital specimen records of land snails from all of the major

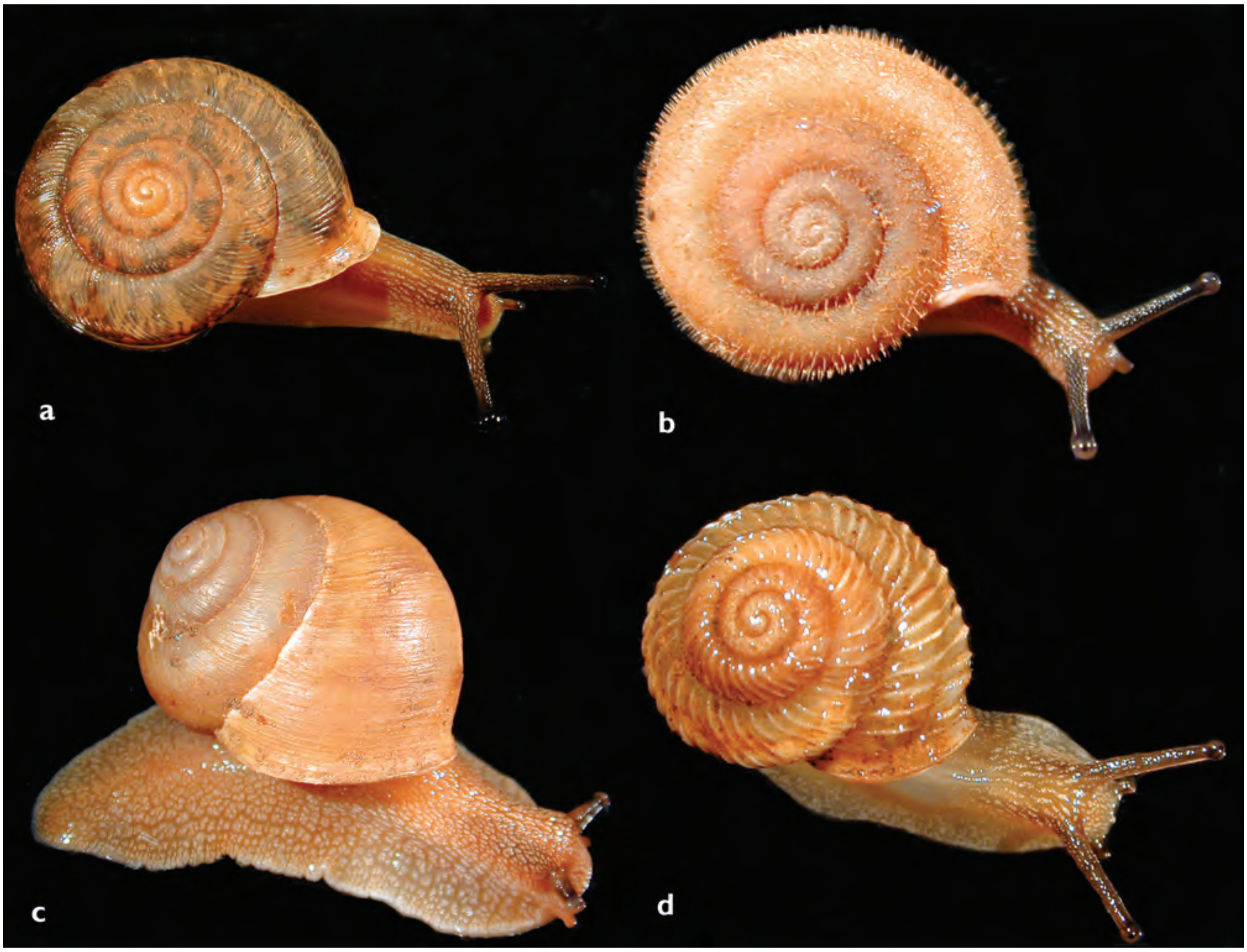

Figure 1. Living specimens of arid zone camaenid snails. A, *Torresitrachia* sp. 12km NNW of Timber Creek, NT, C.437626; B, *Semotrachia* sp., 67km W of Alice Springs, Chewings Range, NT, C.437186; C, *Sinumelon expositum* Iredale, 1937, 52km N of Alice Springs, NT, C.437194; D, *Torresitrachia* sp., 17km NNW of Victoria River Downs HS, NT, C.437659. Photos: A.C.Miller, copyright and specimens Australian Museum.

state museums around Australia with the exception of the Tasmanian Museum and Art Gallery. These data are presence only data and are strongly oriented towards the road systems, particularly in the remote areas of Australia. We acknowledge these limitations but, because studies of richness and endemism in other groups, whether generated from specimen data or expert opinion, suffer from the same problem (Crisp *et al.* 2001), the data presented here provide a fair basis for comparison.

The available datasets were updated to minimise taxonomic and spatial errors. Records dated pre-1950 were excluded from the analyses, as previous experience indicates that early historical records rarely have sufficient spatial accuracy for this type of analysis. Records with a spatial error range >20km were also excluded. All records in the database were corrected to a standard taxonomy (Smith *et al.* 2002) supplemented by expert opinion and any clear anomalies were removed. The result of this is a dataset of 62,419 snail records, of which 8,200 fall within the ambit of the current study, by far the most comprehensive yet compiled for Australia.

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 in a geographic information system (ArcGIS) as a simple shaded map of Australia where each grid cell represents a 1:100,000 map sheet that corresponds approximately to a 50 kilometre square.

Observational data were transferred to 10 x 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 analysis was run on these 10 x 10 km grids, but generalised to 1:100,000 map sheets, i.e. 50 x 50 km grids, for reporting, referred to as planning units in this paper. The number of records, by planning unit, is shown in Fig. 2.

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, providing an estimate of the number of species present within a 30 km x 30 km area. This method, known as a neighbourhood analysis (Prendergast and Eversham 1997; ESRI 1999) minimises the effect of arbitrary boundaries caused by grid analysis. The richness score for each map sheet was the score of the highest scoring 10 km grid cell within it.

Endemism

We calculated weighted endemism following Williams and Humphries (1994), Crisp *et al.* (2001) and others. Weighted endemism (WE) seeks to avoid the traditional problem in endemism studies, where an arbitrary region or range-size threshold is used to define what constitutes an

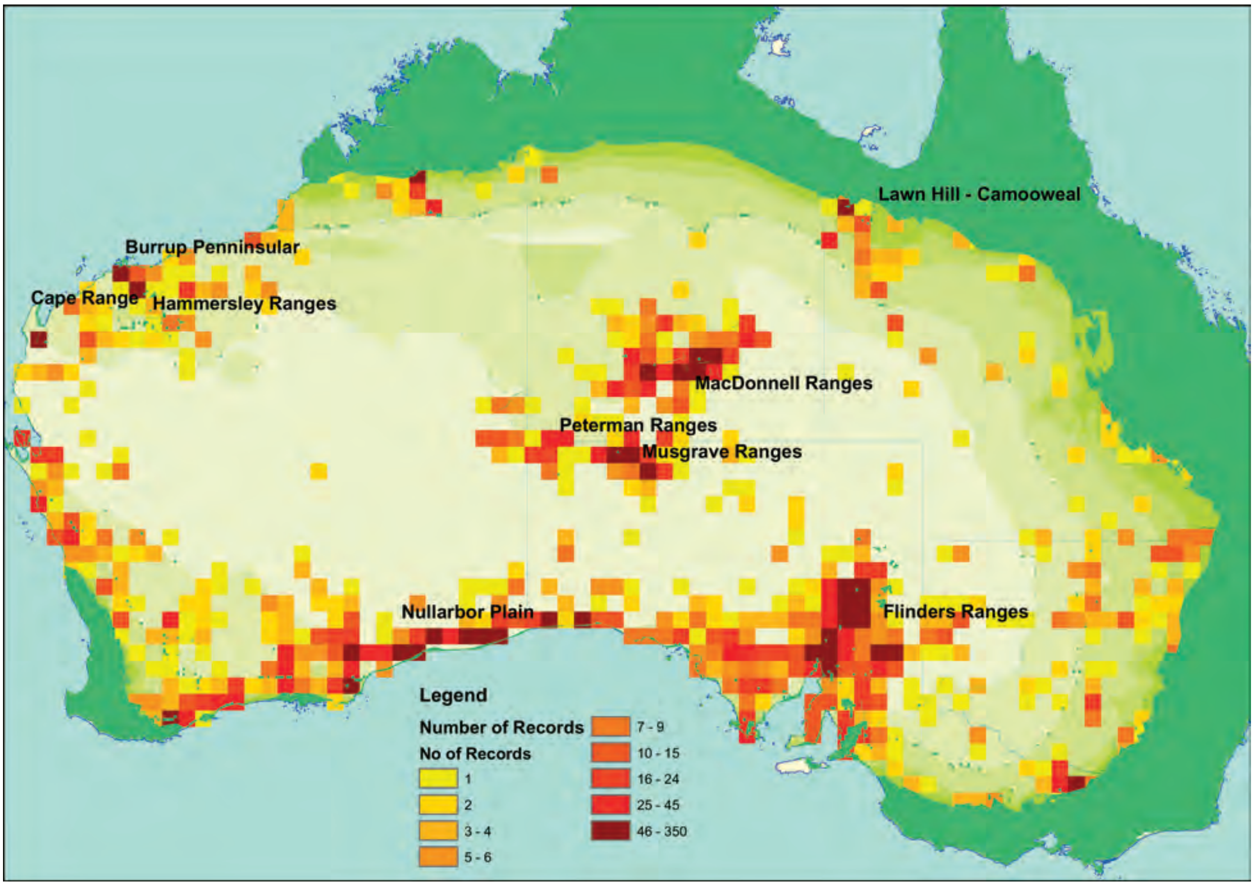

Figure 2. Number of records used in study presented by planning unit.

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 (Laffan and Crisp 2003). We calculated WE by counting all species in each 30 km x 30 km area of 9 adjacent cells, but weighting each by the inverse of its range-size. In the current study, species ranges were estimated by summing the number of 10 kilometre 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.

There are a range of definitions for the arid and semi-arid zone of Australia. We have broadly followed the definition given in Morton *et al.* (1995), being the 250mm rainfall zone in southern Australia and in northern Australia, where evaporation is higher, the 500mm rainfall zone. For the purposes of display, we have used the approximate line of the 550mm rainfall zone. Although this falls well outside the arid and semi-arid zone proper, it helps to provide a context for analysis.

Taxa analysed

The analyses described above were performed for all land snail species together and also collectively at family and genus levels. There were 434 species, 110 genera and 16 families included in the analysis, comprising a total of 8,200 records.

Results

The result of the species richness analysis is shown in Fig. 3. In terms of the arid and semi-arid zone, the most significant areas are the West MacDonnell Ranges, the Peterman Ranges and the Musgrave Ranges in Central Australia, the Flinders Ranges to the south and in the west, Cape Range and Burrup Peninsula. There is a strong relationship between the number of records and general species richness. Major named localities mentioned in the text are included in the map for context.

The result of the endemism analysis is shown in Fig. 4. The increased intensity in colour is a reflection of the high level of endemism exhibited by many of the species present in the arid zone. The Western MacDonnell Ranges, Musgrave Ranges, Peterman Ranges, Flinders Ranges, and the Burrup Peninsula are all of significance at continental scale for the level of endemism exhibited based on a weighted index. Other significance regions of endemism are the Lawn Hill-Camooweal area in far western Queensland, and Shark Bay, Cape Range and Hamersley Ranges in Western Australia. Most of these latter areas have low numbers of records, although, unfortunately, this does not reflect unsuccessful sampling attempts where no snails were obtained at all. Low species numbers are more likely to reflect reality in areas where a reasonable amount of sampling has taken place. In such situations, tests can be applied using background sampling to give an estimate of the reliability of the observed result, whether it be diversity or range size (Ponder *et al.* 2001).

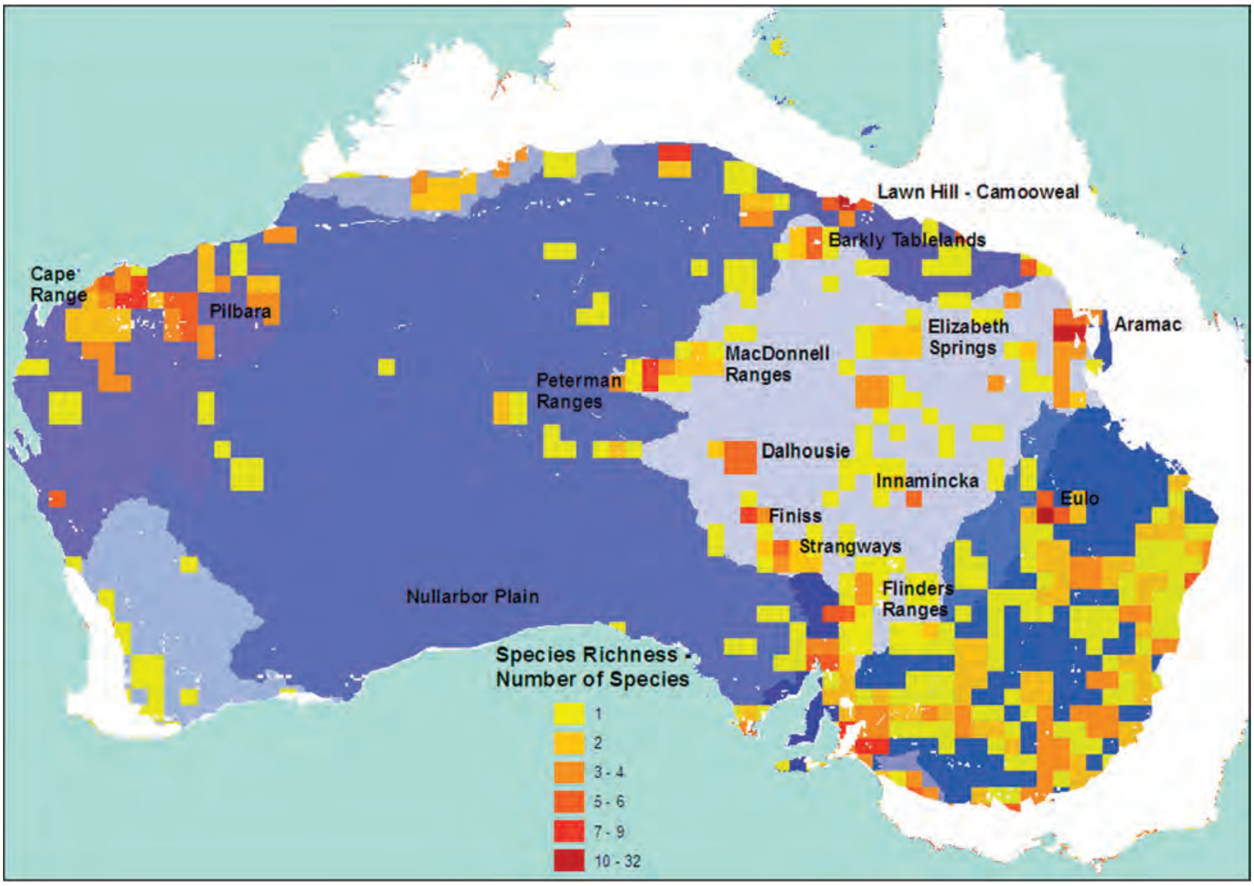

Figure 3. Map of overall species richness.

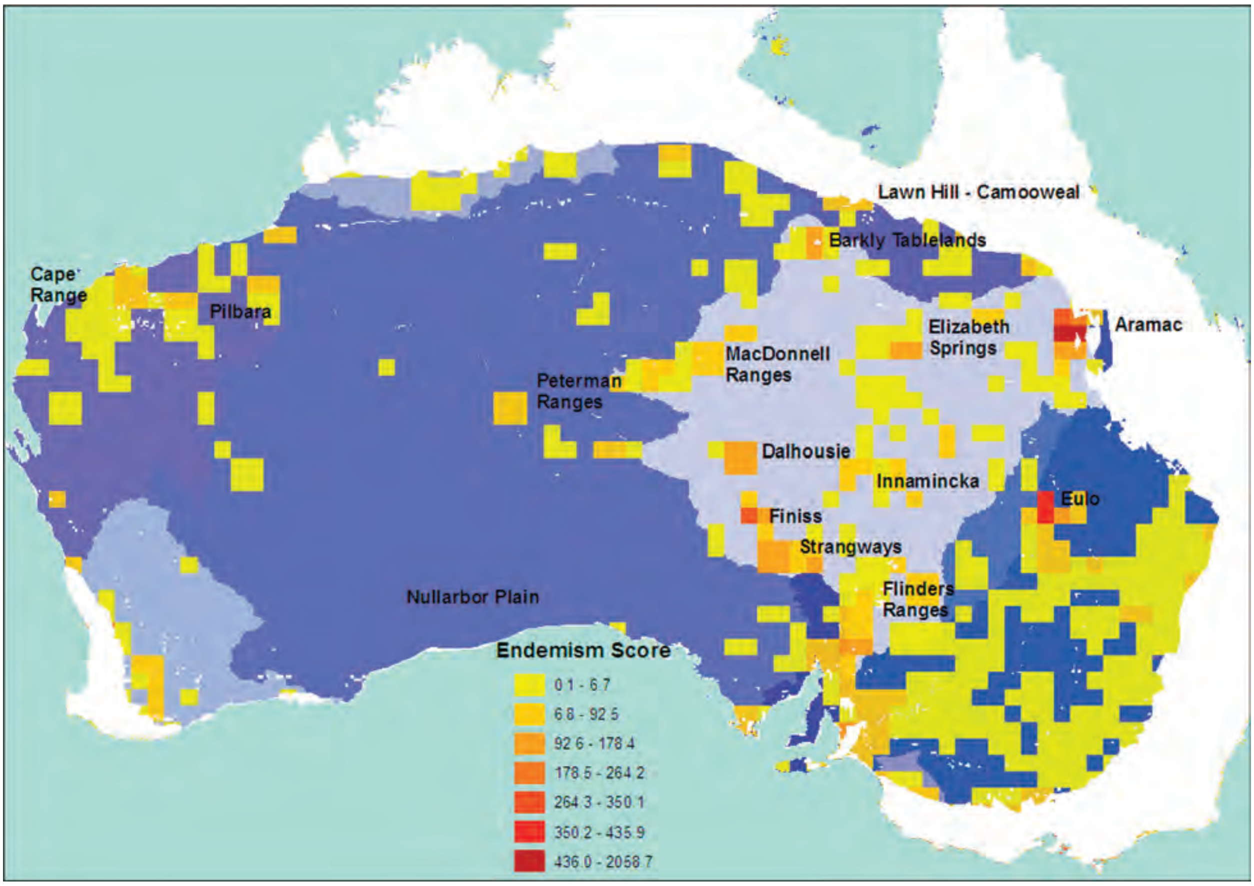

Figure 4. Map of overall species endemism.

The result of intersecting species richness with the approximate area of outcropping limestone is shown in Fig. 5a. The absence of collection records for many areas that may have outcropping limestone is problematic. There is a surprisingly low level of correlation between species richness and limestone outcrops with the exception of Flinders Range, Cape Range and the Lawn Hill-Camooweal area in far western Queensland. This may be explained, in part by the poor quality of mapping available for limestone outcrops. The high species richness across the southern part of the Nullarbor Plain is also certainly attributable to limestone outcropping or calcium-rich soils.

There is a higher degree of correlation between limestone and endemism (Fig. 5b), primarily the areas previously identified above. There is also a comparatively high degree of correlation between snail endemism and limestone in the Pilbara and the area south of Fitzroy Crossing in Western Australia, though it is obvious that low collecting effort may be misrepresenting this.

Fig. 6 shows the result of overlapping all records on a genus by genus (Fig. 6a) and then family by family basis (Fig. 6b), providing a map of genus- and family-level richness. The analysis at genus level shows two major concentrations, the West MacDonnell Ranges and the Flinders Ranges and two secondary concentrations, Fitzroy Crossing in Western Australia and the Lawn Hill-Camooweal area. The analysis at family level shows the same major concentrations, with the Western MacDonnell Ranges clearly the richest.

Fig. 7 shows the high level of correlation between species richness and topographic relief. Areas indicated by black arrows show particularly strong correlations including most of the richest concentrations of species richness and endemism in the arid zone.

Discussion

Richness and Endemism

The arid and semi-arid zones of Australia are marginal habitat for land snails. More mesic temperate and tropical regions to the south, north and east all possess higher diversity in terms of both species and family-level richness. Given the recognition of the strong correlation between land snails and soil moisture, this is hardly surprising. Nevertheless, the arid and semi-arid zones possess regions of high land snail species richness and very high levels of endemism, particularly when compared to most non-molluscan taxa occurring in the arid zone. For example, reptiles have a maximum endemism index of 157 with only 16 planning units with an index of 125 or above in the arid and semi-arid zone (Slatyer and Rosauer, unpublished data 2005). By comparison, land snails have a maximum index of 416 and have 50 planning units with an index above 125.

Previous workers have noted that land snails are not distributed uniformly across the landscape and "hotspots" of species richness are well known in eastern Australia such as the Wet Tropics and Brigalow Lands Bioregions and the Macleay valley (Stanisic 1997a; Smith and

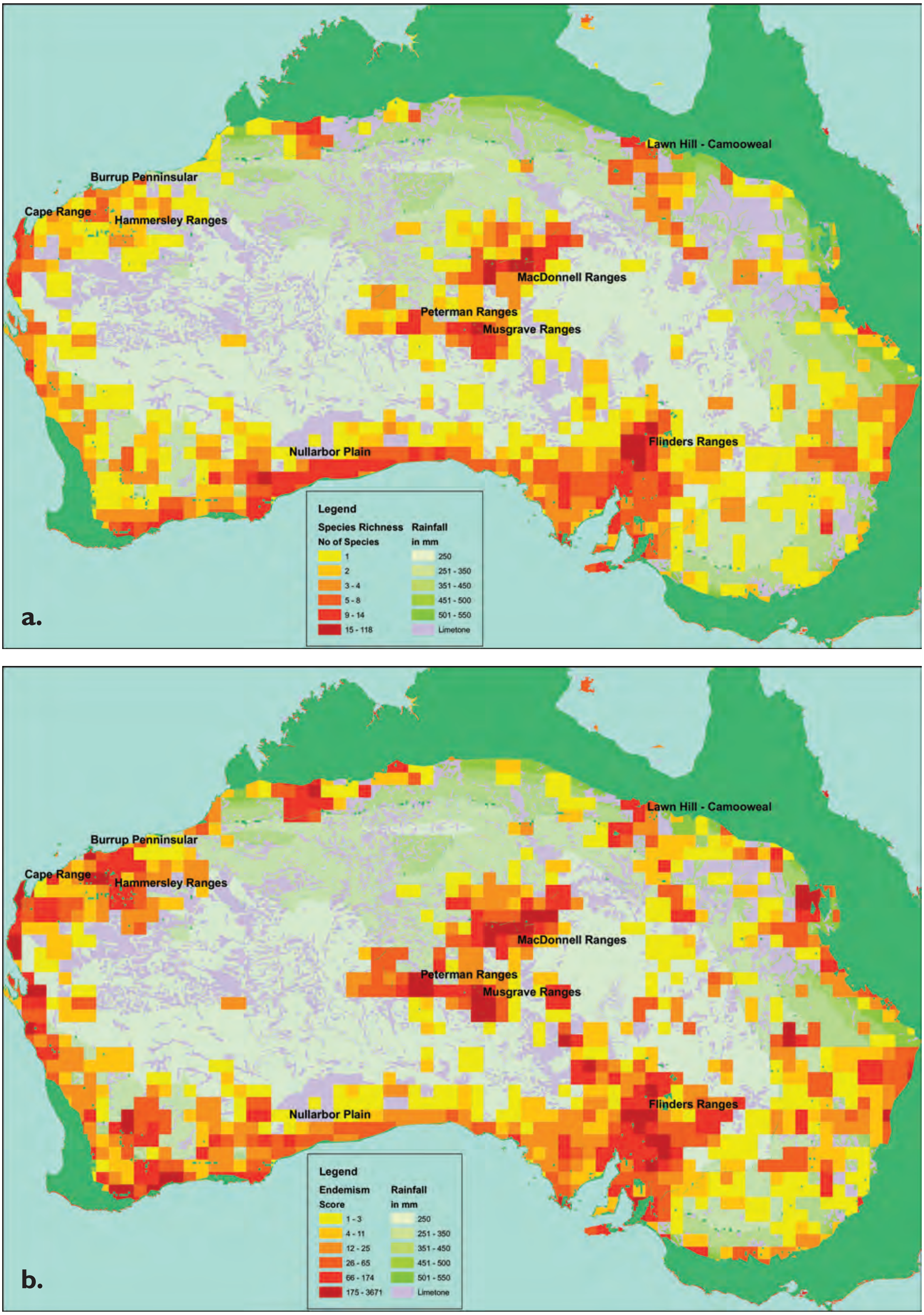

Figure 5. Map of approximate area of outcropping limestone and a. (above) species richness and b. (below) species endemism in land snails.

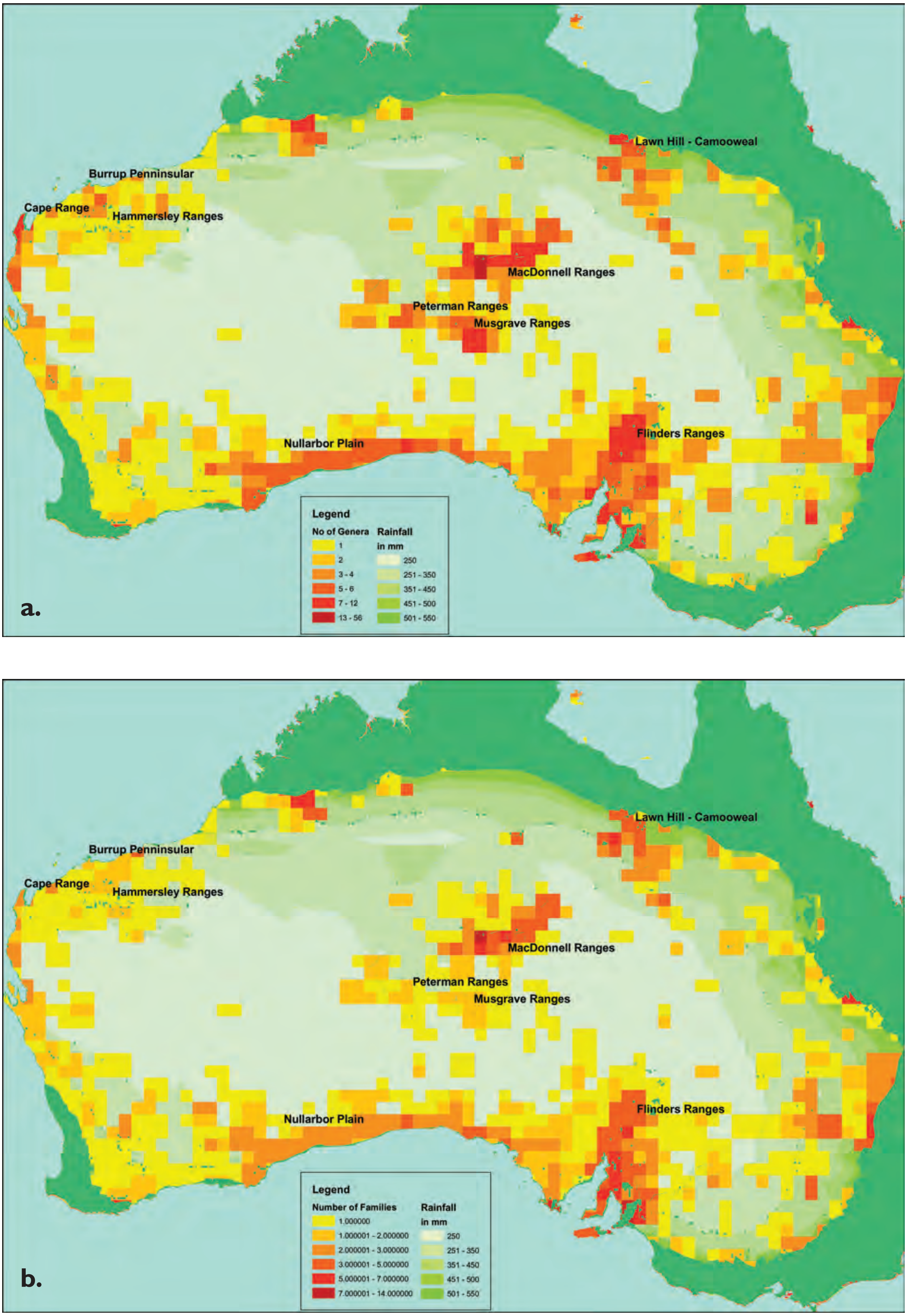

Figure 6. Map of ANHAT output for a. (above) genus and b. (below) family-level richness.

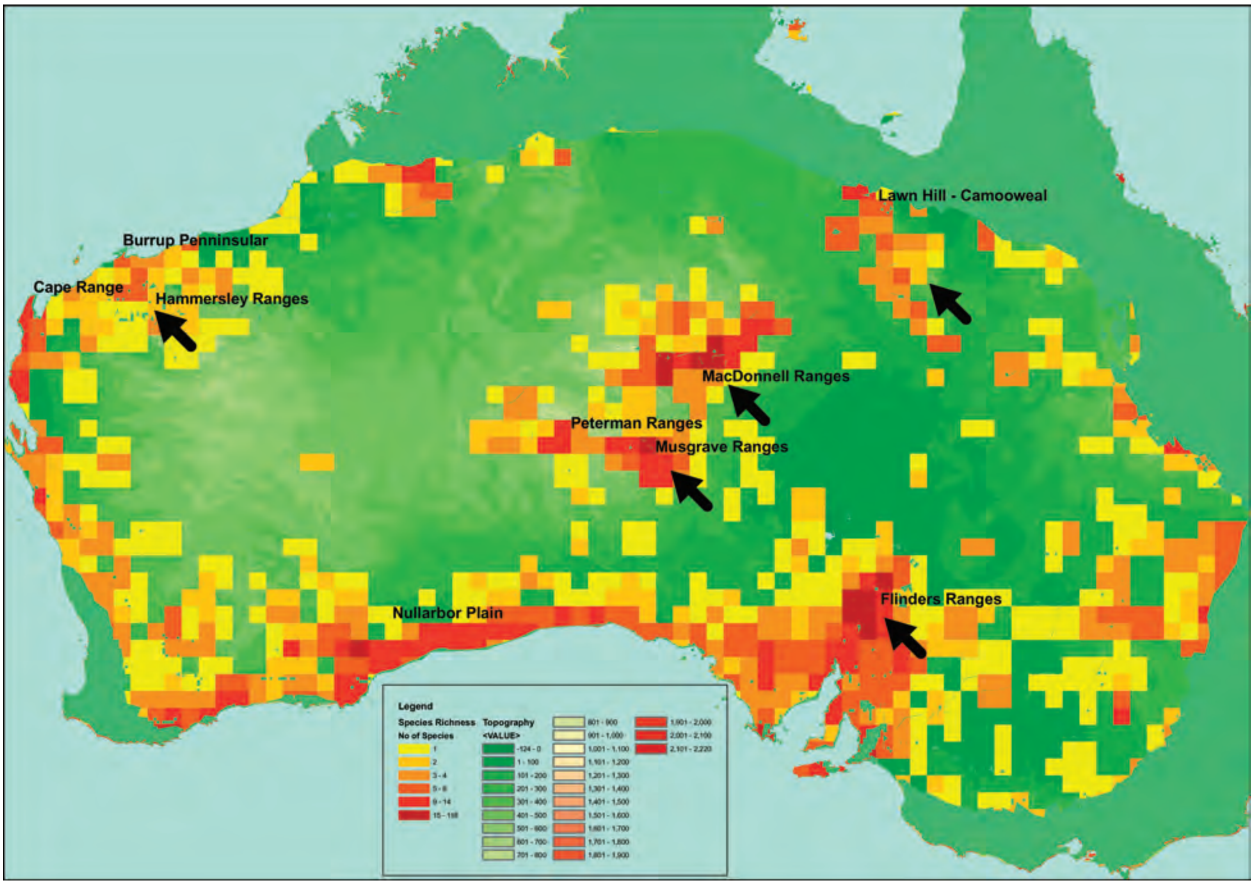

Figure 7. Altitudinal variation and land snail species richness.

Stanisic 1998; Stanisic and Ponder 2004). Similarly, land snails in the arid and semi-arid zone are not distributed uniformly across the continent. Previous authors have noted that much of the patterning observed in species richness can be accounted for by rare or endemic species (e.g., Summerville *et al.* 2002; Gering *et al.* 2003).

Narrow range or short range endemics can be defined as species with a distribution range of less than 10,000 km^2 (Harvey 2002). It is noteworthy that few vertebrate groups possess significant levels of endemism in the arid zone and there are comparatively few narrow-range endemic vertebrates generally (Harvey 2002). For example, birds have an average distribution range (based on available observational data) of 174,900 km^2 (Slatyer and Rosauer unpublished data 2005). In contrast, some land snails have very small ranges. Solem (1988b) examined ranges of 28 restricted range camaenid snails in the Ningbing region of the Kimberley and found their area ranges were 0.01 to 7.45 km^2 (median 0.825 km^2). Mobility and body size are likely to play key roles in this observed difference, with vertebrates having a distinct advantage in dispersal ability over land snails. This study has found few of the arid and semi-arid zone snail species possess distributions that exceed 10,000 km^2. In fact the mean distribution for land snails was only 1,200 km^2.

Our results clearly indicate that there are significant concentrations in terms of both species richness and endemism across the arid and semi-arid zone of the continent and that the most important of these appear consistently in a range of different analyses. We contend that the patterns of species richness exhibited in this study are largely being driven by the underlying distribution patterns of narrow-range endemic species. These taxa are dependent on suitable habitats, many of which are small in extent (some examples are illustrated in figure 8, although some of these fall outside the study area).

Significance of Topographic Relief

Our study has identified a clear correlation between sharp topographic relief in the drier part of the continent and land snail diversity, in terms of both richness and endemism (Fig. 6). The Western MacDonnell Ranges, Musgrave Ranges, and Flinders Ranges are all of outstanding significance at continental scale for the level of richness and endemism exhibited. Other significant regions of richness and or endemism are the Lawn Hill-Camooweal area in far western Queensland, the Barrier Range north of Broken Hill in New South Wales and the Cape Range and Hammersley Ranges in the Pilbara in Western Australia.

These arid and semi-arid mountain ranges and isolated mesas represent the most complex habitats and best niche for moisture conservation in the arid zone. Arid zone snails avoid desiccation by using various strategies – burrowing deep in the soil, sealing their aperture with an epiphragm (free sealing – Solem 1991) or sealing with hardened mucus to rocks (Smith and Stanisic 1998). It is

Figure 8. Some land snail habitats in the arid zone. **a.** Limestone outcrops, Chillagoe, N Qld. Such outcrops are amongst the richest habitats for arid-zone land snails. Photo C. Slatyer. **b.** dry gorge, Flinders Ranges. Rocks, vegetation and shade combine to provide suitable habitat for several endemic species. Photo C. Slatyer. **c.** sandstone outcrop, Shark Bay, WA. The scree provides suitable habitat for a couple of species in this very dry location. Photo J. Ponder. **d.** outcrop in the southern Northern Territory. Rocks and a few bushes provide some suitable habitat. Photo W. Ponder. **e.** Palm Valley, Central Australia. Oases such as this provide good habitat for land snails. Photo W. Ponder. **f.** Spinifex in Central Australia. Some species of *Sinumelon* live in the soil beneath such Spinifex clumps. Photo J. Ponder.

not therefore surprising that topographic features should be highly correlated with land snail distributions.

Significance of Limestone Outcrops

Solem (1988b) described a spectacular concentration of limestone endemic camaenid land snails from the Ningbing and Jeremiah Hills (both in the Kimberleys) with further studies by Cameron (1992) and biological studies by Solem and Christensen (1984), although these areas fall outside our study area. Other workers have similar reported the significance of limestone outcrops in arid and semi-arid Australia (e.g. Smith and Stanisic 1998; Stanisic and Ponder 2004). One of the difficulties of demonstrating this correlation is the absence of a reliable continental scale map of limestone outcrops. Nevertheless, major outcrops of limestone are of identifiable significance across the arid and semi-arid zone for land snails, reflected in our results, with Flinders Range, Cape Range and the Lawn Hill-Camooweal area in far western Queensland clearly being important both for endemic species and species richness.

Relict Species and Refugia

Some of the major centres of richness and endemism identified in our study clearly exhibit comparatively high diversity at the genus (up to 14 genera) and family (up to 6 families) level. The Western MacDonnell Ranges is clearly the most significant region, followed by the Flinders Ranges and two secondary concentrations, Fitzroy Crossing in Western Australia and the Lawn Hill-Camooweal area.

Various authors (e.g., Andersen 1995; Gaston and Williams 1993) have debated the use of higher-level taxon richness categories as a surrogate for species-level richness. We found that richness at genus or family level was an inconsistent predictor of species-level richness, with some areas such as the Western MacDonnell Ranges performing well, and others, such as Cape Range, poorly.

The strong correlation between genus and family level diversity is because families are usually represented by only one or two genus and species level taxa. This is definitely not a case supporting families as surrogates for lower taxonomic levels. Rather than surrogacy, we suggest that use of higher-level taxon richness categories may have more utility in better understanding the phylogenetic diversity of a region but tell us nothing about endemism.

We suggest that this combination of high endemism, high-level taxonomic richness and comparatively low species richness is indicative of accumulated multiple, sometimes relict, lineages in an historical background of high levels of extinction. Previous workers have hypothesised about the multiple northern (i.e., Asian or Papuan) origins of some families such as the Camaenidae (e.g., Solem 1992 a, b). Current work by Stanisic and Hugall certainly supports this, at least in the Camaenidae, with molecular work suggesting that arid zone species are phylogenetically related to geographically disjunct species occurring in the north or east of the continent (Stanisic pers. comm. 2005). Our analysis suggests that two regions, the West MacDonnell Ranges and Flinders Ranges, are significant for such phylogenetic diversity.

There are inadequate data available to test the impact of land management practices and feral animals on land snails, and the extent to which the areas identified as significant in the current study, are indicative of refugia from contemporary perturbations. Colman (1987) observed heavy population losses from burning spinifex in the Kimberley and other authors have cited or theorised impacts from burning critical refugia such as vine thickets (Mckenzie *et al.* 1991; Stanisic and Ponder 2004). It is highly likely that management practices such as clearing, burning or grazing that substantially modify the microclimate in terms of vegetation complexity or the disturbance of micro-shelters such as rocks, fallen litter or wooden debris, will have a significant impact on land snail survival. Land snail surveys in the rangelands between the Flinders Ranges and Musgrave Ranges, shown as a data poor area in this study, produced only one land snail record in ten days of survey in 2006 (Gaut pers. comm. 2006). There was found to be little available habitat because of the open nature of the rangeland, however there was also strong evidence that this was because of habitat simplification from grazing coupled with the impacts of drought. Areas of elevated topography tends to be subjected to less intensive management in terms of clearing and grazing, and rock scree slopes can impede fires (e.g., Stanisic and Ponder 2004). It seems likely that open rangelands provide generally poor habitat for many land snails and this is further exacerbated by contemporary land use and feral species. It is expected, therefore that the areas of significance identified are highly likely to be significant contemporary refugia as well as long term refugia.

A comparison with other taxa is beyond the scope of this paper, but we suggest that the widespread collections of snails through the arid zone, their ease of collection, handling and identification, as well as their endemic, relict nature, make them excellent candidates for indicators of potential refugia for other taxa in the arid and semi-arid zone.

Conclusions

Arid and semi-arid land snails have been found in a wide region of inland Australia. Diversity of land snails in terms of both endemism and richness in such environments were found to be strongly correlated with areas of sharp topographic relief and to a lesser extent, limestone outcrops. It is suggested that the relict nature of land snail species in arid and semi-arid Australia, their dependence on high soil moisture and their relative ease of collection and identification, in combination, make them excellent indicators for arid and semi-arid refugia. A number of important areas for land snail conservation were identified based on species richness, endemism and richness at generic or family level. These were (in order of priority) West MacDonnell Ranges, Flinders Ranges, Musgrave Ranges, Lawn Hill-Camooweal area, Peterman Ranges, Burrup Peninsula, Cape Range, Shark Bay and Fitzroy Crossing (see Fig. 4). Several regions are obvious priorities for further collection or systematic work, notably the Pilbara and Lawn Hill regions. It should be noted that there are a number of highly significant areas that fall in dry parts of the tropical zone outside the boundaries of the current study that should also be regarded as highly significant, notably Katherine, Chillagoe and the Kimberley.

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References

Andersen, A.N., 1995. Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation* **73:** 39-43

Beesley, P.L., Ross, G.J.B. and Wells, A., (eds) 1998. *Mollusca: The southern synthesis. Fauna of Australia Vol 5.* CSIRO Publishing: Melbourne, Part A xvi 563 pp.

Cameron R.A.D., 1992. Land snail faunas of the Napier and Oscar Ranges Western Australia: Diversity, distribution and speciation. *Biological Journal of the Linnean Society* **45**: 271-286.

Colman, P.H., 1987. Blazing snail trails. *Australian Natural History* Summer 1986-87: 119.

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

Environmental Systems Research Institute (ESRI) 1999. *ARCMAP 8.1* Redland United States of America.

Gaston, K.J. and Williams, P.H., 1993. Mapping the world's species – the higher taxon approach. *Biodiversity Letters* **1**: 2-8.

Gaut, A. 2006. Personal Communication on current land snail survey work undertaken by the South Australian Museum in the Woomera region.

Gering, J.C., Crist, T.O. and Veech, J.A., 2003. Additive portioning of species diversity across multiple spatial scales: Implications for regional conservation of biodiversity. *Conservation Biology* **17**: 488-499.

Graham, C.H., Ferrier, S., Huettman, F., Moritz, C. and Peterson, A.T., 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution **19**: 498-502.

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

Hyman, I.T. and Stanisic, J., 2005. New charopid land snails chiefly from limestone outcrops in NSW (Eupulmonata: Charopidae). *Memoirs of the Queensland Museum* **50**: 219-302.

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

Microsoft. 2000. *Microsoft Access.* Microsoft Corporation, United States of America.

McKenzie, N. L., Johnston, R. B. and Kendrick, P. G., 1991. *Kimberley rainforests of Australia.* Surrey Beatty & Sons, Chipping Norton, NSW. xvi + 490 pp.

Morton, S. R., Short, J. and Barker, R. D., 1995. Refugia for Biological Diversity in Arid and Semi-arid Australia. *Biodiversity Paper No. 4, Biodiversity Unit.* Department of Environment, Sport and Territories. CSIRO, Canberra.

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

Ponder, W.F., 1995. The conservation of non-marine molluscs in perspective. Pp 55-67 in *Biodiversity and conservation of the Mollusca,* edited by A. C. Bruggen, S. M. Wells and T. C. M. Kemperman. Backhuys Publishers, Leiden.

Ponder, W.F., 1997. Conservation status, threats and habitat requirements of Australian terrestrial and freshwater Mollusca. *Memoirs of the Museum of Victoria* **56:** 421-430.

Ponder, W.F., 1998. Conservation. Pp. 105-115 in *Mollusca: The Southern Synthesis, Fauna of Australia, Vol 5, Part A,* edited by P. L. Beesley, G. J. B. Ross and A. Wells. CSIRO Publishing, Melbourne.

Ponder, W.F., Carter, G.A., Flemons, P. and Chapman, R.R., 2001. The evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology* **15**: 648-657.

Smith, B.J., 1992. Non-marine Mollusca. *Zoological Catalogue of Australia, vol. 8.* , Australian Government Publishing Service, Canberra. Pp 1-405.

Smith B.J., Reid S. and Ponder W.F., 2002. Pulmonata. *Australian Faunal Directory*. Viewed 9 December 2004. http: //www.deh.gov.au/biodiversity/abrs/online-resources/fauna/afd/index.html

Smith, D.M. and Stanisic, J., 1998. Pulmonata Introduction. Pp. 1037-1061 in *Mollusca: the southern synthesis, Fauna of Australia, Vol 5, Part B*, edited by P. L. Beesley, G. J. B. Ross and A. Wells. CSIRO Publishing, Melbourne.

Solem, A., 1979. Camaenid land snails from western and central Australia (Mollusca : Pulmonata : Camaenidae) I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum, Supplement* **10**: 5–142.

Solem, A., 1981a. Camaenid land snails from Western and central Australia. II. Taxa from the Kimberley, Amplirhagada Iredale, 1933. *Records of the Western Australian Museum, Supplement* **11**: 147–320.

Solem, A., 1981b. Camaenid land snails from Western and Central Australia (Mollusca : Pulmonata : Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. *Records of the Western Australian Museum, Supplement* **11**: 321–425.

Solem, A., 1984. Camaenid land snails from Western and Central Australia (Mollusca : Pulmonata : Camaenidae). IV. Taxa from the Kimberley, Westraltrachia Iredale, 1933 and related genera. *Records of the Western Australian Museum, Supplement* **17**: 427–705.

Solem, A., 1985. Camaenid land snails from Western and central Australia (Mollusca : Pulmonata : Camaenidae). V. Remaining Kimberley genera and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* **20**: 707–981.

Solem, A., 1988a. New camaenid land snails from the northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* **9**: 27–58.

Solem, A., 1988b Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, north-east Kimberley, Western Australia. *Journal of the Malacological Society of Australia* **9**: 59-113.

Solem, A., 1989. Non-camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy* **2**: 455-604.

Solem, A., 1991. Land snails of the Kimberley rainforest patches and biogeography of all Kimberley land snails. *Kimberley rainforests of Australia.* (ed by N.L. McKenzie, R.B. Johnston, and P.G. Kendrick), pp 145-246, Surrey Beatty and Sons, Chipping Norton, NSW.

Solem, A., 1992a. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Pt 1. Systematics, distribution and variation. *Records of the South Australian Museum, Monograph* **2**: 1–338.

Solem, A., 1992b. Camaenid land snails from southern and eastern Australia, excluding Kangaroo Island. Part 2. Biogeography and covariation. *Records of the South Australian Museum, Monograph Series* **2**: 339-424.

Solem, A., 1993. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). VI. Taxa from the Red Centre. *Records of the Western Australian Museum, Supplement* **43**: 983–1459.

Solem, A., 1997. *Camaenid land snails from Western and Central Australia (Mollusc: Pulmonata: Camaenidae)*. *Records of the Western Australian Museum, Supplement* **50**, 1461–1906.

Solem, A. and Christensen, C., 1984. Camaenid land snail reproductive cycle and growth patterns in semi-arid areas of north-western Australia. *Australian Journal of Zoology* **32:** 471–491.

Stanisic, J., 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca: Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* **30:** 1-241.

Stanisic, J., 1997a. An area of exceptional land snail diversity: the Macleay valley, northern New South Wales. *Memoirs of the Queensland Museum* **39:** 343-354.

Stanisic, J., 1997b. Land snail diversity in Queensland: An overview. Part 1. *Australasian Shell News* **94**: 6.

Stanisic, J., 1997c. Land snail diversity in Queensland: An overview. Part 2. *Australasian Shell News* **95**: 6.

Stanisic, J. and Ponder, W.F., 2004. Forest snails in eastern Australia – one aspect of the other 99%. Pp127-149, in *The Conservation of Australia's forest fauna (second edition)* edited by D. Lunney. Royal Zoological Society of New South Wales, Mosman.

Stanisic, J., 2005. Personal Communication on current research with Andrew Hugall on Camaenid Snails.

Summerville, K.S., Boulware, M.J., Veech, J.A. and Crist, T.O., 2002. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* **17**: 1045-1057.

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