

Determinants of species richness and similarity of species composition of land snail communities on Kimberley islands

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ABSTRACT – We investigated patterns in species richness and similarity in species composition of land snail communities in relation to biogeographic and environmental gradients on continental islands along the Kimberley coastline of Western Australia. The camaenid land snails demonstrated high overall species richness, restricted geographical ranges (mostly to a single island) and almost complete turnover of species among islands. In comparison, the overall number of the smaller non-camaenid land snail species was much lower. They also had much wider distributions and a lower level of species turnover among islands. These results are consistent with the differing dispersal abilities of the two groups, one fostering *in situ* speciation and the other inter-island colonisation. We also show that dispersal ability was not the only driver of species richness and composition of land snail species on islands, but that rainfall, island area and availability of habitat also played a role. Rainfall was the major environmental driver of richness and composition for both groups of land snails. Rainfall was also highly correlated with extent of rainforest cover, habitat that provides a suitable micro-climate for snails and additional ecological niches compared to more open habitats.

KEYWORDS: Pulmonata, island biogeography, land snail diversity, Camaenidae, gastropod richness

INTRODUCTION

The Kimberley region of north-western Australia is recognised as a national biodiversity hotspot, due largely to the number of endemic plant and animal species it supports (<http://www.environment.gov.au/biodiversity/hotspots/national-hotspots.htm>). A relatively little-known, yet significant, component of this diversity and high endemism, are the terrestrial gastropods (or land snails) of the region. Surveys conducted between 1987 and 1989 in the rainforests of the Kimberley (McKenzie et al. 1991a) uncovered a large diversity of land snail species (Solem 1991). Earlier work in the Kimberley also showed that the snail fauna in the Kimberley is dominated by one family, the Camaenidae (Solem 1981a, 1981b, 1984, 1985, 1988a, 1991). The remaining species, which represent various families of non-marine gastropods, are here referred to as ‘non-camaenids’. They account for only a comparatively small proportion of the overall diversity of land snail species in the region (Solem 1988b, 1991). A further striking difference between the two groups of land snails is that most of the camaenids are

narrow-range endemics, with an average range size of approximately 20 km (Solem 1991), while the non-camaenids generally have expansive ranges with geographic distributions extending well outside the Kimberley region (Solem 1988b, 1991). The narrow range endemism observed in the camaenids has been attributed to their poor dispersal capability (Solem and McKenzie 1991).

Highly fragmented and isolated environments, such as island archipelagos, often display high levels of endemism and species diversity (Losos and Ricklefs 2010). One of the factors believed to contribute to the high diversity of camaenid land snails in the Kimberley is the multiplicity of refugia distributed across the region in the form of rainforest patches (Solem 1991). Created by climate fluctuations throughout the Quaternary and Mid to Late Tertiary (Bowler 1982), these patches essentially have been acting as habitat islands whereby gene flow is restricted by intervening unsuitable habitat, resulting in allopatric patterns of speciation and endemism in the isolated refuges (Cameron 1992). The high levels of endemism of land snails in the limestone karsts of Malaysia has

been similarly explained (Clements et al. 2008), as well as land snails occurring on islands or within island archipelagos (e.g. Cowie 1995; Welter-Schultes and Williams 1999; Chiba 2007; Cook 2008; Overton et al. 2009).

Centres of high land snail diversity in the Kimberley region largely correspond with the wetter coastal areas of the north (Solem 1991). Also within this area are extensive island archipelagos which, created by the flooding of an ancient coastline, represent much of the adjacent mainland's geological surfaces and vegetation communities (May and McKenzie 2002). The rainforest survey of the late 1980s included a small number of these islands, but aside from a few opportunistic collections, the diversity of land snails on the majority of islands has remained largely unknown until recently.

From 2007 to 2010, the Kimberley Island Survey (KIS) of biodiversity was conducted on a selection of the largest islands in order to test assumptions of islands acting as natural refuges, particularly for those species susceptible to escalating threatening processes on the Kimberley mainland. Land snails were selected as one of the target groups, because they are considered to be indicators for other restricted range invertebrate groups. Their disjunct distributions on the mainland make them particularly sensitive to processes that alter their optimal habitat, such as changed fire regimes, grazing and introduction of weeds. Descriptions and distributions of each camaenid and non-camaenid land snail species encountered during this survey have been published elsewhere (Köhler 2010a, 2010b, 2011a, 2011b, 2011c; Köhler et al. 2012). Briefly, a total of 104 camaenid species (83 new) in 15 genera (5 new) were recorded from the islands (including a number of additional islands outside of the survey area) with most species found to be island endemics (Köhler 2011b). Additionally, 21 non-camaenid land snails were recorded from the islands, with four of these being freshwater species (Köhler et al. 2012).

Here, we investigated patterns in species richness and similarity in species composition of land snails recorded during the above survey in relation to biogeographic and environmental gradients. We were interested in examining if the species-area relationship held for the Kimberley island snail fauna as has been found on other island archipelagos (e.g. Cowie 1995; Welter-Schultes and Williams 1999; Triantis et al. 2005; Chiba 2007), as well as the effect of island isolation on snail richness and composition. We expected that the high levels of local endemism of camaenid land snails observed on the adjacent mainland (Solem 1991) would be reflected in the island fauna with a high turnover of species among islands. In

contrast, we anticipated a much lower level of turnover in the more widespread non-camaenid species. The conservation implications of the results are discussed, particularly with regard to issues involving short-range endemism.

METHODS

STUDY AREA

We selected 24 of the largest islands for sampling, targeting those with a variety of geological surfaces, as well as ensuring geographic coverage from north to south (see Gibson and McKenzie 2012). These islands extend from Sir Graham Moore Island off the Anjo Peninsula in the north to Sunday Island off Cape Leveque in the south, and to Adolphus Island in the Cambridge Gulf in the east. They include islands from the Bonaparte and Buccaneer Archipelagos, as well as several other island groups (Figure 1).

Geological and detailed vegetation descriptions of the islands are given in Gibson and McKenzie (2012). Briefly, sandstone and volcanic strata structure the island landscapes. The sandstones tend to give rise to rugged, dissected terrains, while the volcanics usually produce a more rounded and gently undulating topography. Tertiary duricrusts occur as mesas and dissected tablelands on some islands, capping volcanic, sandstone or doleritic strata. Broad vegetation communities on the islands include tropical savannas, hummock grassland, rainforest, coastal tussock grassland, riparian paperbark woodlands and mangroves.

The Kimberley experiences a tropical monsoon climate with two distinct seasons: a dry season extending from around April to October, and a wet season from November to March when almost all rainfall occurs. Cyclonic activity is also a feature of the climate. Average annual rainfall ranges from >1,500 mm at Mitchell Plateau to <800 mm at Cape Leveque (<http://www.bom.gov.au>). Daily temperatures range from 23–38°C throughout the year, with high relative humidity peaking during the wet season.

SAMPLING AND IDENTIFICATION

A comprehensive description of the survey implementation is given in Gibson and McKenzie (2012). In summary, campsites on the islands were selected using information on geology and vegetation from maps, local knowledge, satellite imagery and a reconnaissance flight. Survey teams (see Gibson and McKenzie 2012) needed to be placed within walking distance of as many habitat/vegetation types as possible. Two campsites were needed to access the environmental variation of

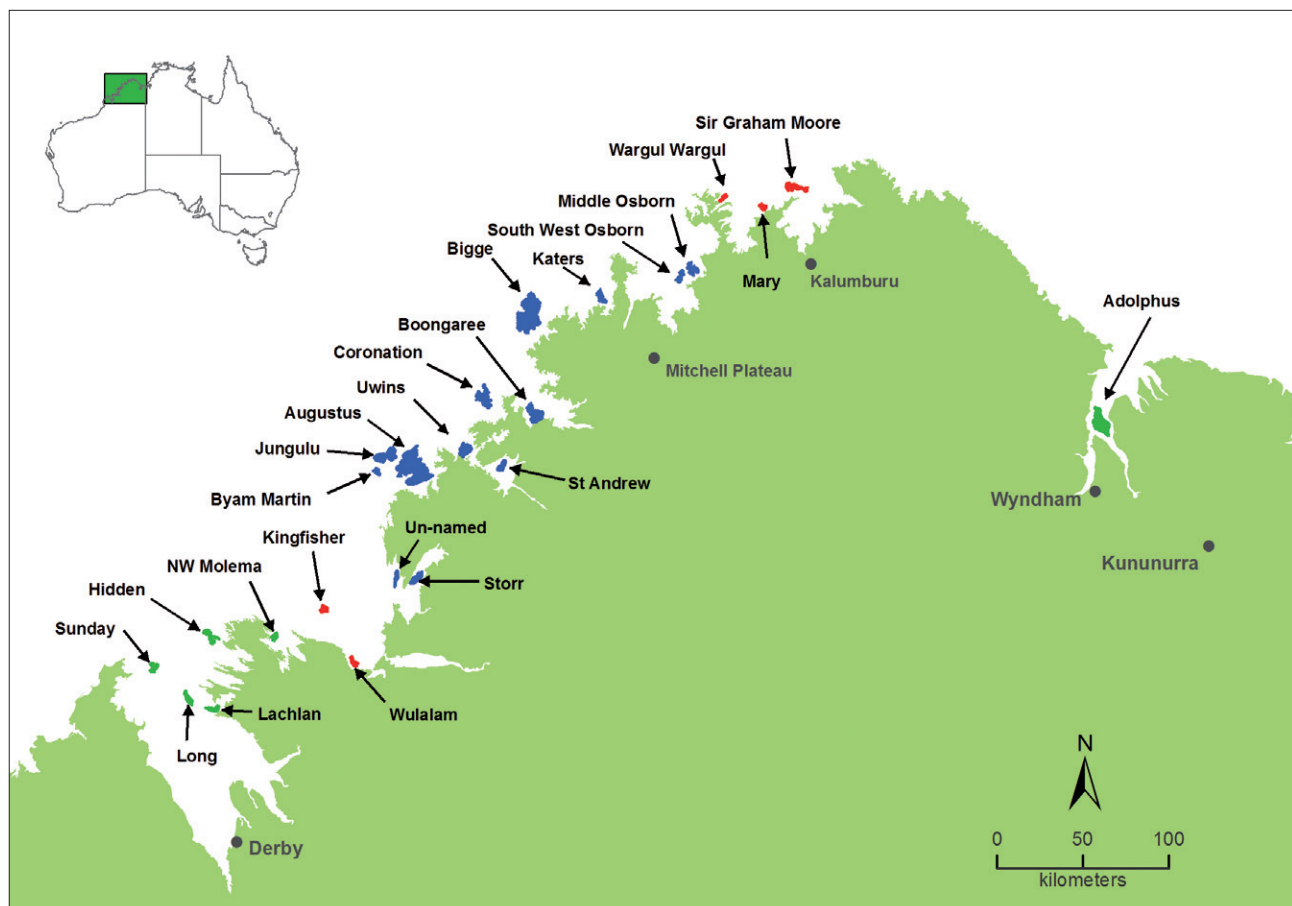


FIGURE 1 Location of Kimberley islands selected for a survey of their biodiversity assets along the north-west coast of Australia. Island colour indicates its average annual rainfall (green <900 mm, red 900 to 1,000 mm, and blue >1,000 mm).

the largest islands. All sites were presented to the Traditional Owners for their approval. In the dry season, campsites were accessed by helicopter and sampled over a six-day period. Sites were then revisited in the wet season using a combination of charter boat and helicopter, and sampled over a single day and night. In total, 31 campsites were sampled over four dry and three wet seasons from 2007 to 2010.

During the dry season, aestivating snails were collected by raking leaf litter, lifting rocks, digging, searching under logs and examining tree crevices. Litter samples were also collected for subsequent sorting in the laboratory. Usually, several locations were searched for land snails within walking distance of the campsite. Search emphasis was placed on rainforest vegetation, including vine thickets, and in gullies and gorges, i.e. areas of high humidity where snails tend to frequently occur. During the wet season, snails were more active, particularly during and following rain, and could be collected directly from the substrate.

All material was sorted, labeled, given preliminary identifications, photographed and catalogued by V. Kessner and sent on to the Australian Museum for formal description by F. Köhler. Details on the methods of identification are given in Köhler (2011b), but basically involved initial comparisons with type specimens, followed by measurement of shell parameters, description of the genital anatomy (following dissection) and radula, and molecular analyses via DNA extraction. Voucher specimens are lodged at the Western Australian Museum in Perth and at the Australian Museum in Sydney.

ISLAND ATTRIBUTES

We selected a number of attributes that have been shown to influence species richness and assemblage composition of land snails (e.g. Solem and McKenzie 1991; Cowie 1995; Welter-Schultes and Williams 1999; Triantis et al. 2005; Clements et al. 2008; Overton et al. 2009) (Table 1). These include island area, distance to a larger landmass, average

TABLE 1

Values of the island attributes selected for the analysis of species richness of land snails sampled along the Kimberley coast. Key: Distance – distance to nearest larger landmass, Area – area of island, Elevation – maximum elevation, Boulder – extent of rock scree (0 = flat; 1 = rounded, soil-mantled hill slopes and plateaux, narrow scree; 2 = shallow joints, wide ledges, moderate scree; 3 = massive scree, deep joints and scarp country), Rainfall – average annual rainfall, Rainforest – extent of rainforest (0 = none present; 1 = rainforest present on island but not sampled; 2 = patchy rainforest sampled; 3 = well developed rainforest sampled), Sites – number of locations sampled on an island.

Island	Distance (km)	Area (ha)	Elevation (m)	Boulder	Rainfall (mm)	Rainforest	Sites
Adolphus	1.96	4157	244	2	827	1	9
Augustus	1.79	18992	181	3	1170	3	16
Bigge	2.97	17096	138	3	1103	3	23
Boongaree	0.24	4215	235	3	1138	3	16
Coronation	5.94	3817	153	2	1141	3	28
Hidden	1.48	1901	127	3	839	0	4
Jungulu	3.23	4841	95	3	1148	2	18
Katers	1.4	1718	101	3	1069	3	14
Kingfisher	15.47	367	82	1	943	1	9
Lachlan	0.17	1181	93	2	787	1	6
Long	9.36	1136	65	2	768	1	3
Mary	0.68	810	11	0	968	1	2
Middle Osborn	2.34	2361	240	2	1051	3	17
NW Molema	1.06	610	154	2	881	1	6
Sir Graham Moore	2.84	2746	61	1	979	1	34
St Andrew	1.6	1470	284	2	1127	3	8
Storr	0.26	1896	165	3	1007	3	11
Sunday	8.06	1198	59	2	778	1	6
South West Osborn	2.67	1339	134	3	1041	3	18
Un-named	0.69	911	83	2	1000	2	13
Uwins	0.23	3247	134	3	1155	2	11
Wargul Wargul	0.25	634	87	1	946	3	7
Wulalam	0.86	418	77	1	901	1	6

annual rainfall, maximum elevation of an island and sampling effort. We also included two habitat descriptors: 'boulder' which represents the extent of rock scree on each island (i.e. refuge habitat) and 'rainforest' representing the extent of rainforest patches on each island. We defined island size as the area of land mass (ha) that was unlikely to be inundated (i.e. tidal mudflats and mangroves were excluded), and was determined from digitised 1:100,000 topographic maps. Maximum elevation (m) was extracted from the 1:100,000 topographic maps. Distance to the nearest larger landmass (km) was estimated using Google Earth™ imagery. Average annual rainfall (mm) was derived using the BIOCLIM module of ANUCLIM (Houlder et al. 2000). Using ArcMap GIS (ESRI Inc., Redlands, California, USA), rainfall values were extracted for each site sampled on an island as well as either four (one-site islands) or six (two-site islands) additional random sites across the islands and averaged for each island. Pairwise Pearson correlations between all candidate variables revealed a strong inter-correlation between rainforest and rainfall ($P = 0.80$); the latter was retained in the analysis as rainforest was largely subjective and rainfall was considered more informative.

DATA ANALYSIS

SPECIES RICHNESS

The total number of camaenid species and genera, and non-camaenid species was calculated for each island and investigated for overall sampling adequacy by examining the observed (sample-based) species accumulation curves generated in the package PRIMER version 6 (Clarke and Gorley 2006).

The association between species/genus richness and all possible subsets of the six predictor variables (described above) was modelled using a generalised linear model (GLM), assuming a *Poisson* distribution. Island size and distance to the nearest larger landmass was log-transformed prior to analysis. Possible curvilinear relationships were first examined by preliminary inspection of response curves after fitting univariate generalised additive models (GAM) (see Wintle et al. 2005). As near-linear relationships were observed, the use of GLM was considered appropriate compared to techniques that fit more complex relationships. However, polynomial terms were included where required (i.e. according to inspection of the GAMs). Model selection was based on the second-order Akaike Information Criterion (AIC_c) (Burnham and Anderson 2002). There was no evidence of overdispersion (i.e. $\hat{c} > 1$). We included models in a final candidate set for model averaging, where

inference is based on a set of plausible models to estimate parameters. We also calculated AIC_c weights (w_i) and used these to weight model coefficients. The relative importance of covariates was examined by summing the AIC_c weights for each covariate across all models in which it occurred (w_i ; Burnham and Anderson 2002). Data analyses were run in the R statistical computing language (R Development Core Team 2009) and the 'AICcmodavg' package to calculate the AIC_c values and standard errors. We evaluated the performance of the model-averaged model by regressing the fitted values against observed species richness values.

PATTERNS IN SPECIES COMPOSITION

Compositional patterns of land snail communities across the islands were investigated using PRIMER version 6 (Clarke and Gorley 2006). Compositional similarity among all pairs of sites (based on presence/absence data) was computed using the zero-adjusted (Clarke et al. 2006) Sørensen association measure. Hierarchical clustering on the resulting similarity matrix was used to derive classification groups, coupled with a similarity profiled permutation test (SIMPROF) to identify genuine clusters in samples which are *a priori* unstructured (using default settings). The dimensionality of the similarity matrix was reduced using non-metric multi-dimensional scaling (nMDS; minimum stress of 0.005 and 100 restarts) and displayed as a scatter plot. To explore the relationship between compositional similarity and island attributes (explained above), we used the BEST/BIOENV procedure where the distances in the similarity matrix are rank-order matched with the Euclidean distances among each of the island attributes using Spearman's rank correlation and 99 permutations. This procedure calculates the Spearman's rank correlation coefficient (ρ) using every possible combination of the predictor variables (island attributes here) until it finds the combination whose Euclidean distance matrix yields the highest value of ρ (Geffen et al. 2004).

The degree of spatial structure (or distance decay) in the composition of the snail faunas was examined using Mantel's tests. A Euclidean distance matrix was calculated for geographical distance based on the geographical coordinates of the mid-points of the islands. The significance of the relationship between this matrix and the compositional similarity matrices (described above) were examined using 999 permutations. Partial Mantel tests were used to examine the relationship between compositional similarity and each of the environmental attributes (after calculating Euclidean distance matrices for each attribute), while holding the geographic distance matrix

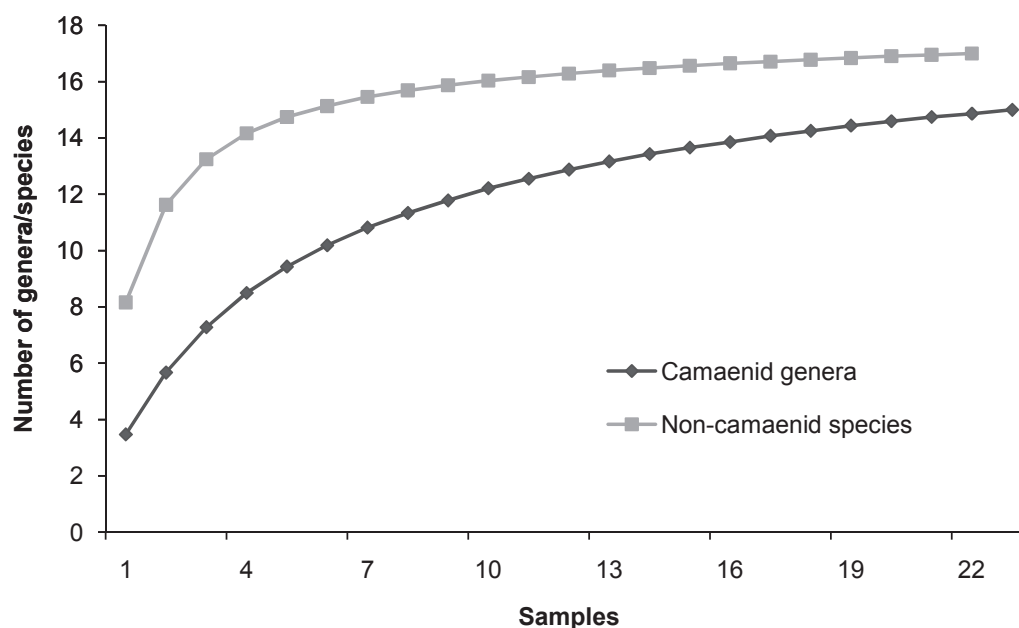


FIGURE 2 Observed (sample-based) species accumulation curves for the richness of camaenid land snail genera and non-camaenid species across the Kimberley islands sampled.

constant. All Mantel tests were performed using the program PASSaGE 2.0.11.6 (Rosenberg and Anderson 2011).

To examine co-occurrences of camaenid genera and non-camaenid species on the same islands we used the association measure 'Two-step' (Belbin 1980) in the analysis package PATN (Belbin 1995). Flexible UPGMA (unweighted pair-group mean averaging) (Sneath and Sokal 1973), with the clustering parameter (Beta) set to -0.1, was used to derive classification groups. The resulting association matrix was imported into PRIMER and displayed as nMDS ordination.

RESULTS

CAMAENID LAND SNAILS

On average 4.0 ± 0.3 (mean \pm standard error; range: 1–13) camaenid species and 3.4 ± 0.4 (range: 1–8) camaenid genera were recorded per island (Appendix 1, Table 2). The average number of islands where an individual species was recorded was 1.07 ± 0.03 . In only four cases, the same species was recorded on two islands (*Globorhagada wurroolgu*, *G. yoowadan*, *Rhagada cygna* and *Setabaudinia umbadayi*) and one case where the same species (*Xanthomelon obliquirugosa*) was recorded

on the three northern-most islands (Mary, Sir Graham Moore and Wargul Wargul). Islands with duplications were in close proximity to each other. In all other cases each species was unique to a single island. On large islands with two sampling sites, some species were recorded at only one of these localities, indicating that these species' ranges were actually smaller than the island. This almost complete turnover among islands resulted in a steeply rising species accumulation curve (SAC), indicating that each new island sampled is likely to contain unique species. We recorded a total of 89 camaenid species on the islands sampled, with 73 endemic to the islands. At the level of genus, the SAC reached an asymptote (Figure 2), indicating that all existing genera were well represented on the suite of islands sampled. We removed Byam Martin from the analysis as it was under-sampled in the dry season and was not sampled in the wet season.

An examination of the factors potentially influencing species richness of the camaenids on the islands revealed no clear best approximating model (i.e. $w_{\min} \geq 0.9$), and therefore the model-averaging approach we used was appropriate (Burnham and Anderson 2002). In Table 3, the top eight models are ranked according to their AIC_c differences (Δ_i), from best to worst. Model-averaged coefficients, unconditional standard errors and

TABLE 2 Camaenid land snail genera recorded on the islands sampled along the Kimberley coast. Total number of genera recorded on each island is also shown.

Abbreviations: AM – *Amplirhagada*, AU – *Australocosmica*, BA – *Baudinella*, CA – *Carinotrachia*, GL – *Globorhagada*, KD – *Kimberleydiscus*, KM – *Kimberlymelon*, KT – *Kimberleytrachia*, KB – *Kimboraga*, MO – *Molema*, RE – *Retroterra*, RG – *Rhagada*, SB – *Setobaudinia*, TI – *Torresitrachia*, XM – *Xanthomelon*.

Island	AM	AU	BA	CA	GL	KD	KM	KT	KB	MO	RE	RG	SB	TI	XM	Total
Adolphus	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Augustus	X	X	X	-	X	-	-	X	-	-	-	X	X	X	-	8
Bigge	X	-	-	-	X	X	-	X	-	-	-	X	X	X	-	7
Boongaree	X	-	X	-	X	-	-	X	-	-	X	X	X	X	-	8
Byam Martin	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	2
Coronation	X	X	-	-	X	-	-	-	X	-	-	-	X	-	-	5
Hidden	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	2
Jungulu	-	X	X	-	X	-	-	X	-	-	-	-	-	X	-	5
Katers	X	-	-	-	X	-	-	-	-	-	-	-	-	X	-	3
Kingfisher	X	-	-	-	-	-	-	-	-	-	-	-	-	X	-	2
Lachlan	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	1
Long	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	1
Mary	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	1
Middle Osborn	X	-	-	X	-	-	X	-	-	-	-	-	X	-	-	4
NW Molema	X	-	-	-	-	-	-	-	-	X	-	-	X	X	-	4
Sir Graham Moore	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	2
St Andrew	X	-	-	-	-	-	-	-	X	-	-	-	X	-	-	3
Storr	X	-	-	-	X	-	-	X	-	-	-	X	X	X	-	6
Sunday	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	1
South West Osborn	X	-	-	X	-	-	-	-	-	-	-	-	X	-	-	3
Un-named	X	-	-	-	X	-	-	-	-	-	-	-	-	X	-	3
Uwins	X	-	-	-	X	-	-	X	-	-	X	-	-	-	-	4
Wargul Wargul	X	-	-	-	-	-	-	-	-	-	-	-	X	-	X	3
Wulalam	-	-	-	-	-	-	-	-	X	-	-	-	X	-	-	2

TABLE 3 Results of AIC_c -based model selection for the species richness of camaenid land snails on Kimberley islands (top eight most-supported models are shown; also shows maximised log-likelihood function ($\log(L)$), number of model parameters (K), AIC_c differences (Δ_i), Akaike weights (w_i) and percent of deviance explained by each model (%Dev).

* Model includes variables: rain – average annual rainfall; area – area of island; distance – distance from nearest larger land mass; elevation – maximum elevation; boulder – extent of rock scree.

Model*	$\log(L)$	K	AIC_c	Δ_i	w_i	%DEV
rain + log(area)	-42.39	3	92.04	0.00	0.108	68.7
rain + boulder	-42.52	3	92.31	0.27	0.095	68.2
rain + log(area) + elevation	-41.22	4	92.66	0.62	0.079	73.6
rain	-44.14	2	92.88	0.83	0.071	61.4
rain + elevation	-42.84	3	92.94	0.90	0.069	66.9
rain + boulder + elevation	-41.45	4	93.12	1.08	0.063	72.7
rain + log(area) + log(distance)	-41.59	4	93.39	1.35	0.055	72.1
rain + log(area) + boulder	-41.76	4	93.75	1.71	0.046	71.4

the sum of weights for models containing each candidate variable are shown in Table 4. In terms of explaining variation in species richness across all the islands sampled, the model-averaged model performed well (Adjusted R -square = 0.70, $P < 0.0001$). Species richness increased with

rainfall, island area, maximum elevation and the extent of rock scree on an island. Rainfall was clearly the most strongly supported ($w_+ = 0.92$) followed by area ($w_+ = 0.49$), maximum elevation ($w_+ = 0.43$) and boulder ($w_+ = 0.40$). A positive relationship with the number of sites sampled on

TABLE 4 Model-averaged coefficients and unconditional standard errors for each variable in the camaenid analysis. Sum of weights for models containing each coefficient w_+ are also shown.

Key: rain – average annual rainfall; area – area of island; elevation – maximum elevation; boulder – extent of rock scree; distance – distance from nearest larger landmass; sites – number of sites sampled on an island.

Variable	Coefficient	Standard Error	w_+
Intercept	-3.320	1.184	-
rain	0.003	0.002	0.92
log(area)	0.266	0.354	0.49
elevation	0.001	0.002	0.43
boulder	0.105	0.174	0.40
log(distance)	-0.061	0.159	0.26
sites	0.003	0.011	0.22

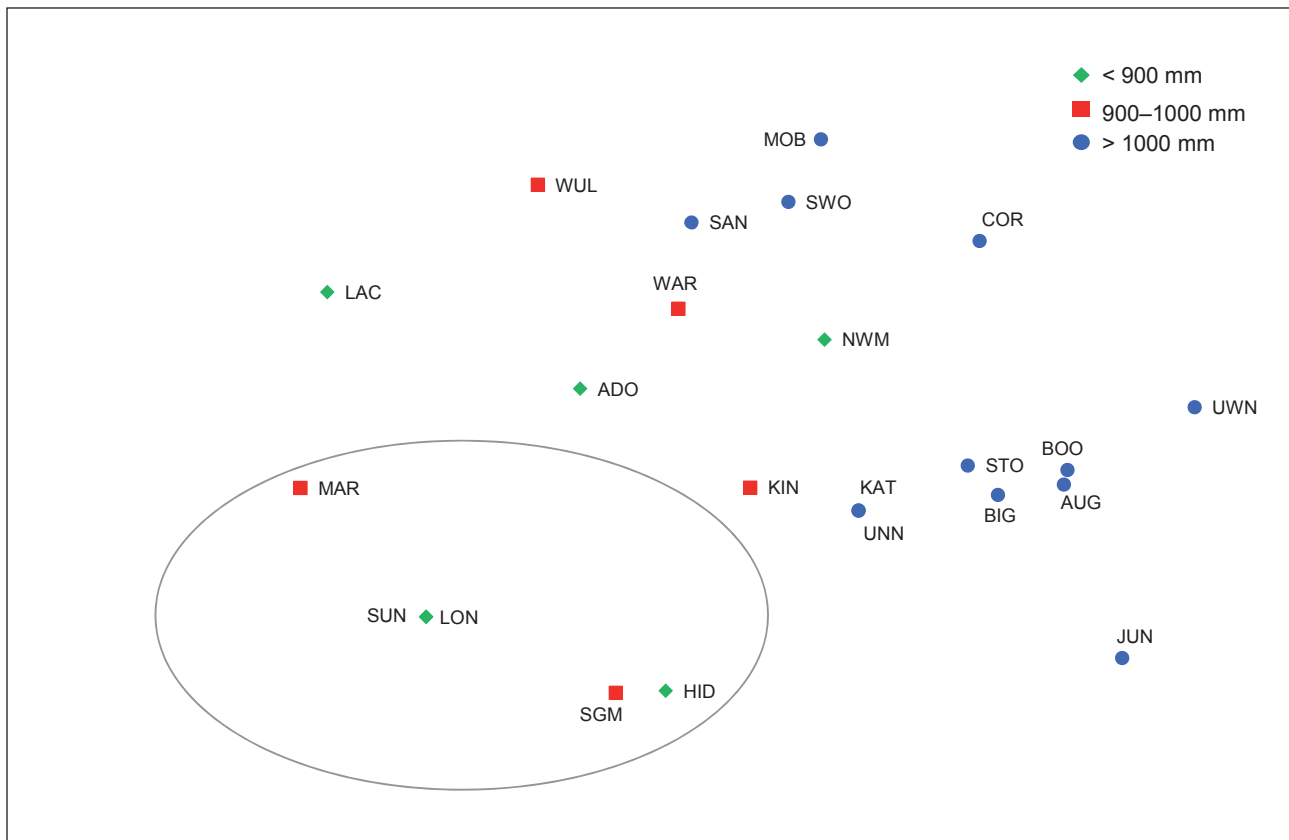


FIGURE 3 Non-metric MDS plot of compositional patterns of camaenid land snail communities (genera) across the Kimberley islands sampled, based on zero-adjusted Sørensen similarity matrix (2D stress = 0.14). Three rainfall bands (low, moderate and high) are indicated by dot shape and colour on the plot. SIMPROF clusters are indicated (i.e. points either within or outside the ellipse).

Key: ADO – Adolphus, AUG – Augustus, BIG – Bigge, BOO – Boongaree, COR – Coronation, JUN – Jungulu, HID – Hidden, KAT – Katers, KIN – Kingfisher, LAC – Lachlan, LON – Long, MAR – Mary, MOB – Middle Osborn, NWM – NW Molema, SGM – Sir Graham Moore, SAN – St Andrew, STO – Storr, SUN – Sunday, SWO – South West Osborn, UNN – Un-named, UWN – Uwins, WAR – Wargul Wargul, WUL – Wulalam. Note that SUN and LON, and KAT and UNN are coincident on the plot.

an island and a negative relationship with distance from the nearest larger land mass was also observed, but these variables had relatively weak support ($w_+ < 0.3$). All of the eight most-supported models explained at least 61% of the deviance (range: 61–74%) with the model that contained rainfall on its own explaining 61.4%.

Due to the exceptionally high turnover of camaenid species among islands, we examined the compositional patterns at the level of the genus (Köhler 2011b). The most widespread genus was *Amplirhagada*, detected on over half of the islands sampled (15), closely followed by *Torresitrachia* (12 islands) and *Setobaudinia* (11 islands) (Table 2). When the islands were re-ordered according to similarities in their composition of genera, two main groups became apparent (Figure 3). Hidden,

Long, Sunday, Mary and Sir Graham Moore were clustered into one group and the remaining islands into another. All the islands in the first group have a relatively low annual rainfall (<1,000 mm) and, with the exception of Hidden, they were devoid of extensive rock scree and were amongst the lowest of the islands in terms of elevation. The maximum number of genera on any one of these islands was two. The majority of islands in the remaining group received an annual rainfall of greater than 1,000 mm, and includes islands with extensive rock scree and high in maximum altitude. With a few exceptions (e.g. Katers and St Andrew), the diversity of genera on these islands was much higher with a maximum of eight. Examining the role of individual genera in contributing to the separation between the two groups (using SIMPER

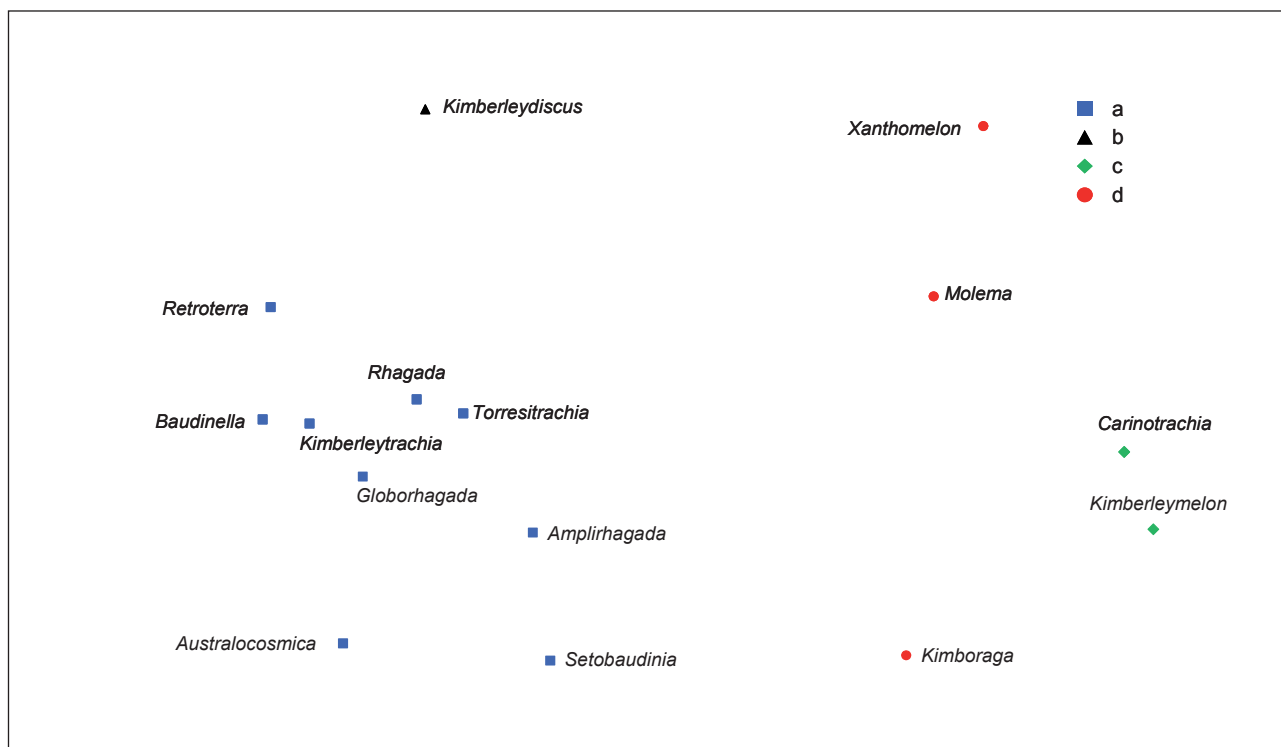


FIGURE 4 Non-metric MDS plot of camaenid genera according to their co-occurrences on the Kimberley islands, based on the Two-step association measure (2D stress = 0.06). UPGMA classification clusters (a, b, c, d) are indicated by dot shape and colour on the plot.

in PRIMER) showed that *Amplirhagada*, *Rhagada*, *Setobaudinia* and *Torresitrachia* contributed to over half (56.7%) of the average dissimilarity between groups. In coastal areas, species of *Amplirhagada* and *Setobaudinia* are restricted to rainforest habitats, whereas *Rhagada* are known to occur in a variety of habitats including semi-arid areas (Solem and McKenzie 1991; Köhler 2010a). The BIOENV procedure indicated that of the six attributes considered, a combination of average annual rainfall and the extent of rock scree on an island had the strongest association with compositional similarity (Spearman's $\rho = 0.52$). The strongest relationship between compositional similarity and any single variable was rainfall (Spearman's $\rho = 0.41$), indicating that the added influence of rock scree was marginal. Overlaying three rainfall bands (<900, 900–1,000 and >1,000 mm) on the nMDS plot also revealed an overt rainfall gradient (Figure 3). The remaining variables such as island area, distance to a larger landmass and sampling effort contributed little to explaining the compositional patterns observed.

Species similarity among islands did not decrease significantly with geographical distance (Mantel $r = 0.234$, $P = 0.05$), genus similarity among islands however did (Mantel $r = -0.262$, $P < 0.01$). When we corrected for the effect of geographical distance, the

correlation of genus similarity with both rainfall and extent of rock scree (expressed as distance matrices) remained significant (Mantel $r = -0.371$, $P < 0.01$ and Mantel $r = -0.300$, $P < 0.01$, respectively).

When we examined genera according to their co-occurrences on the same island, four groups emerged (Figure 4). Group 'a' comprises nine genera, which includes the widespread *Amplirhagada*, *Torresitrachia*, *Setobaudinia*, *Rhagada* and *Globorhagada* that are known to occur through high to medium rainfall areas of the Kimberley region (Solem 1981a, 1985, 1991, 1997; Köhler 2011b). At least two of the remaining genera (*Baudinella* and *Retroterra*) in this group are known to be confined to the high rainfall area of the Kimberley (Solem 1985, 1991; Köhler 2011b). The other two are new genera (*Australocosmica* and *Kimberleytrachia*) (Köhler 2011a, 2011b) but also appear to be restricted to higher rainfall areas (islands where they occurred have an annual rainfall greater than 1000 mm). Group 'b' consists of *Kimberleydiscus*, a newly described monotypic genus recorded only from Bigge. Group 'c' contains two genera *Carinotrachia* and *Kimberleymelon* confined to Middle Osborn and South West Osborn. *Carinotrachia* has a highly restricted distribution occurring only in the wettest parts of the Kimberley region (Solem 1985; Köhler 2011b). *Kimberleymelon* is a new monotypic genus

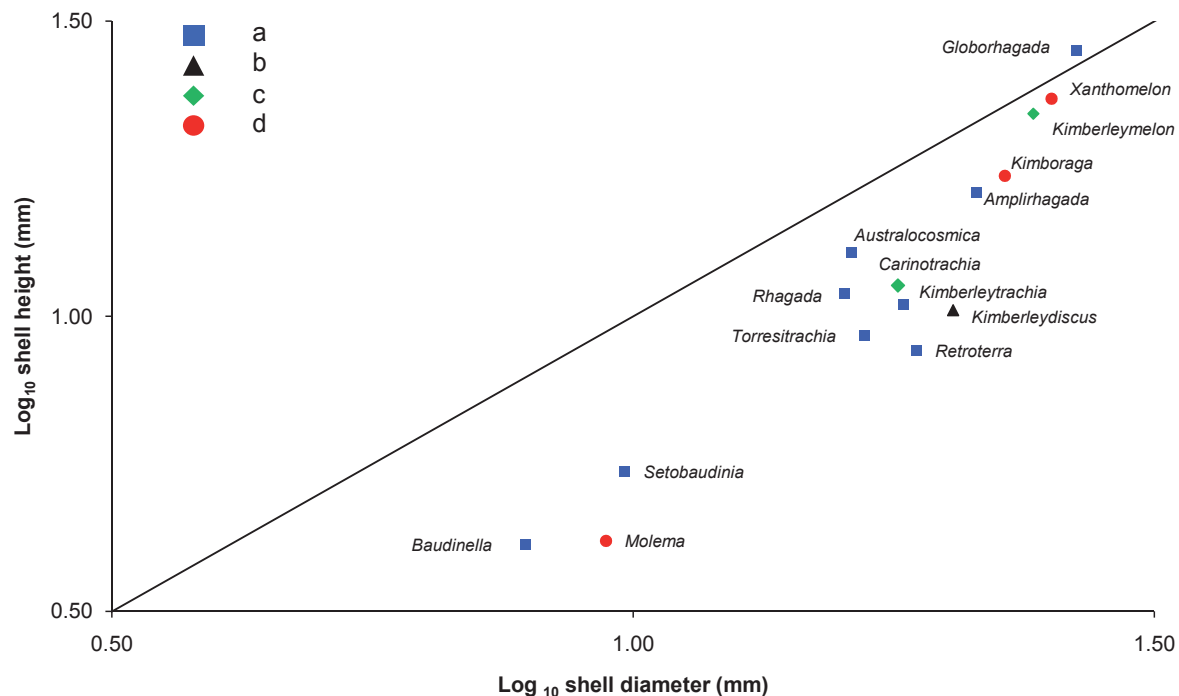


FIGURE 5 Average shell spire dimensions (height/diameter) of each of the camaenid genera across all of the islands sampled. UPGMA classification clusters (a, b, c, d) are indicated by dot shape and colour on the plot. Diagonal line indicates where height equals diameter.

known only from Middle Osborn (Köhler 2011b). *Molema*, *Kimboraga* and *Xanthomelon* form group 'd'. The latter two are known to extend into the driest parts of the Kimberley (Solem 1985; Köhler 2011b). *Molema* is a new genus (Köhler 2011b), which was recorded on NW Molema only (an island with an average rainfall of less than 900 mm). *Xanthomelon* was recorded only on the three northern-most islands.

We superimposed the groups above on a plot showing average shell height v. shell diameter for each genus (Figure 5). Co-occurring genera tended to be well separated along the height/width gradient indicating clear differences in shell shape. Five genera within the first group are similar in shape, but with the exception of *Torresitrachia* and *Rhagada*, they are from different sub-groups within the main cluster, implying less frequent co-occurrences.

NON-CAMAENID LAND SNAILS

The non-camaenid land snail fauna detected on the islands consisted of terrestrial and aquatic species. Freshwater snails were more restricted in their occurrence due to the scarcity of permanent freshwater on the islands, with only four species detected (Köhler et al. 2012). Consequently, we

consider only the terrestrial non-camaenid species in further analyses. The 17 species detected during the survey represent 75% of all terrestrial, non-camaenid gastropods known from the entire Kimberley region (Solem 1991). We again removed Byam Martin from the analysis due to under-sampling.

The mean number of non-camaenid land snail species recorded per island was twice as high as the camaenids at 8.23 ± 0.91 (range: 1–15) (Table 5). The average number of islands where an individual species was recorded was 10.65 ± 1.15 (range: 1–19). The most widespread species were *Gastrocopta macdonnelli* and *Westracystis lissus* which were detected on 19 and 18 islands, respectively. One species was endemic to the islands, the new 'Assimineid n. gen. n. sp.', found on Middle Osborn only. The SAC curve reached an asymptote (Figure 2) indicating that, overall, non-camaenid species were sufficiently sampled across the islands surveyed.

As for the camaenids, there was no clear best approximating model (i.e. $w_{\min} \geq 0.9$) in terms of explaining variation in species richness across all the islands sampled. However, only two models were strongly supported (i.e. Akaike differences < 2) and both had in common the attribute of rainfall. The number of locations sampled on

TABLE 5 Terrestrial non-camaenid land snail species recorded on islands sampled along the Kimberley coast. Total number of species recorded on each island is also shown.

Abbreviations: Am – *Amimopina macleayi*, As – Assimineid n. gen., n. sp.,
 Cm – *Coneuplecta microconus*, Da – *Discocharopa aperta*, Ei – *Eremopeas interioris*,
 Gk – *Gastrocopta kessneri*, Gm – *Gastrocopta macdonnelli*, Gp – *Gastrocopta pediculus*,
 Gs – *Gastrocopta stupefacians*, Nm – *Nesopupa mooreana*, Pw – *Pleuropoma walkeri*,
 Pc – *Pupisoma circumlitum*, Po – *Pupisoma orcula*, Pp – *Pupoides pacificus*,
 Sc – *Stenopylis coarctata*, Wl – *Westracystis lissus*, Wm – *Wilhelminaia mathildae*.

Island	Am	As	Cm	Da	Ei	Gk	Gm	Gp	Gs	Nm	Pw	Pc	Po	Pp	Sc	Wl	Wm	Total
Adolphus	-	-	-	-	-	-	-	X	-	-	-	-	-	X	-	X	-	3
Augustus	X	-	-	X	X	X	X	-	X	X	X	X	-	-	X	X	-	11
Bigge	X	-	-	-	X	X	X	X	X	X	X	-	X	X	X	X	-	12
Boongaree	X	-	X	X	X	X	X	-	X	X	X	X	X	X	X	X	X	15
Byam Martin	-	-	-	-	X	-	-	-	X	-	-	-	-	-	X	X	-	4
Coronation	X	-	-	X	X	X	X	X	X	X	X	X	X	X	X	X	X	15
Hidden	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	1
Jungulu	X	-	-	-	-	X	X	-	X	X	X	X	X	X	X	X	-	11
Katers	-	-	-	-	-	X	X	-	X	X	X	-	X	X	X	X	-	9
Kingfisher	-	-	-	X	X	-	X	-	-	X	X	-	-	-	X	X	-	7
Lachlan	-	-	-	-	X	-	X	-	-	X	-	-	-	X	-	-	-	4
Long	-	-	-	-	X	-	X	-	-	-	-	-	-	-	X	-	-	3
Mary	-	-	-	-	-	-	X	X	-	X	-	-	-	X	-	-	-	4
Middle Osborn	X	X	X	-	X	X	X	-	X	X	X	X	X	X	X	X	-	14
NW Molema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Sir Graham Moore	-	-	-	-	-	X	X	X	X	X	-	X	-	X	-	X	-	8
St Andrew	X	-	-	X	X	X	X	-	X	X	X	-	X	-	X	X	-	11
Storr	X	-	-	X	X	X	X	-	-	-	X	X	-	X	X	X	X	11
Sunday	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	X	-	3
South West Osborn	X	-	-	X	X	X	X	-	X	X	X	X	X	X	X	X	-	13
Un-named	-	-	-	-	X	-	X	-	-	X	-	-	-	-	X	X	-	5
Uwins	X	-	-	-	X	X	X	-	X	X	X	-	X	-	X	X	-	10
Wargul Wargul	X	-	-	-	X	X	-	-	X	-	X	-	-	-	X	X	-	7
Wulalam	-	-	-	-	-	-	-	-	X	X	-	-	X	-	-	X	-	4

TABLE 6 Results of AIC_c-based model selection for the species richness of non-camaenid land snails on Kimberley islands (the 10 most-supported models are shown). Also shown are maximised log-likelihood function (log[L]), number of model parameters (*K*), AIC_c differences (Δ_i), Akaike weights (w_i) and percent of deviance explained by each model (%Dev).

*Model includes variables: rain – average annual rainfall (mm); sites – number of sites sampled; sites2 – sites squared; area – area of island (ha); boulder – extent of rock scree; distance – distance from nearest larger landmass (km); elevation – maximum elevation (m).

Model*	log(L)	<i>K</i>	AIC _c	Δ_i	w_i	%DEV
rain	-53.72	2	112.03	0.00	0.18	65.3
rain + sites + sites2	-51.00	4	112.21	0.18	0.16	73.2
rain + elevation	-53.41	3	114.08	2.05	0.06	66.2
rain + sites + sites2 + log(area)	-50.31	5	114.15	2.12	0.06	75.2
rain + sites + sites2 + boulder	-50.34	5	114.22	2.18	0.06	75.1
rain + log(distance)	-53.58	3	114.43	2.40	0.05	65.7
rain + log(area)	-53.69	3	114.64	2.61	0.05	65.4
rain + sites + sites2 + elevation	-50.58	5	114.68	2.65	0.05	74.4
rain + boulder	-53.71	3	114.69	2.66	0.05	65.4
rain + sites + sites2 + log(distance)	-50.91	5	115.34	3.31	0.03	73.4

TABLE 7 Model-averaged coefficients and unconditional standard errors for each variable for the non camaenid analysis. Sum of weights for models containing each coefficient w_+ are also shown.

Key: rain – average annual rainfall (mm); sites – number of sites sampled on an island; sites2 – sites squared; elevation – maximum elevation (m); area – area of island (ha); boulder – extent of rock scree; distance – distance from nearest larger landmass (km).

Variable	Coefficient	Standard Error	w_+
Intercept	-1.662	1.050	-
rain	0.003	0.001	0.93
sites	0.061	0.075	0.52
sites2	-0.001	0.002	-
elevation	0.0003	0.0008	0.24
log(area)	-0.035	0.133	0.22
boulder	-0.019	0.079	0.21
log(distance)	-0.0003	0.081	0.19

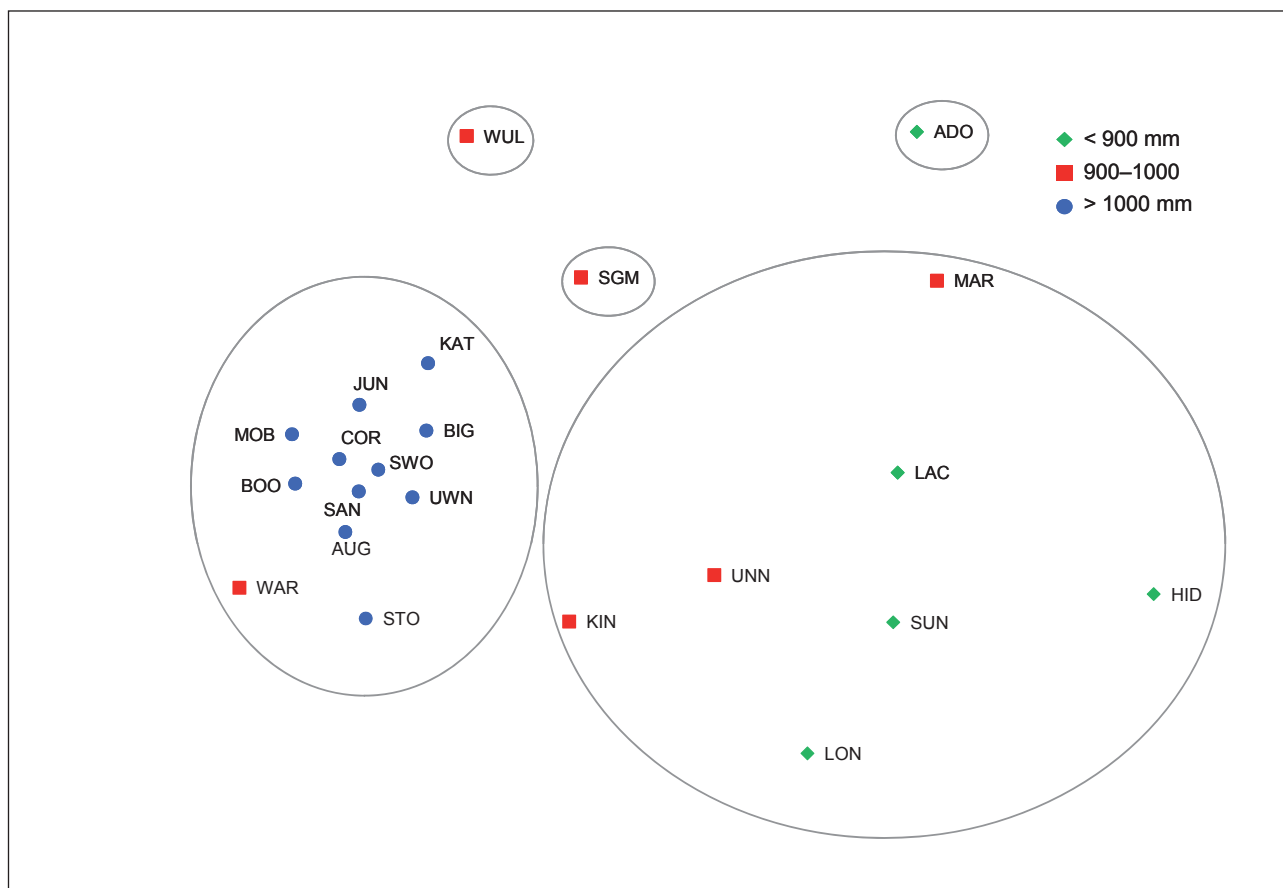


FIGURE 6

Non-metric MDS plot of compositional patterns of non-camaenid land snail communities (species) across the Kimberley islands sampled based on zero-adjusted Sørensen similarity matrix (2D stress = 0.10). Three rainfall bands (low, moderate and high) are indicated by dot shape and colour on the plot. SIMPROF clusters are indicated by the ellipses.

Key: ADO – Adolphus, AUG – Augustus, BIG – Bigge, BOO – Boongaree, COR – Coronation, JUN – Jungulu, HID – Hidden, KAT – Katers, KIN – Kingfisher, LAC – Lachlan, LON – Long, MAR – Mary, MOB – Middle Osborn, SGM – Sir Graham Moore, SAN – St Andrew, STO – Storr, SUN – Sunday, SWO – South West Osborn, UNN – Un-named, UWN – Uwins, WAR – Wargul Wargul, WUL – Wulalam Island.

an island (or sampling effort) was included in the second-ranked model (Table 6). As shown in Table 7, species richness of the non-camaenids was strongly influenced only by rainfall ($w_+ = 0.93$), with moderate support for sampling effort ($w_+ = 0.52$). The importance of all other attributes was relatively weak ($w_+ < 0.3$). Species richness increased with rainfall, sampling effort (to a threshold level) and maximum elevation, and decreased with extent of rock scree, island area and distance from a larger land mass (Table 5). The performance of the model-averaged model was high (Adjusted R -square = 0.78, $P < 0.0001$). All of the 10 most-supported models explained at least 65% of the deviance (range: 65–75%) with the model including only rainfall explaining 65.3%.

As no non-camaenid species were recorded on NW Molema, we removed this island from the compositional analysis. When we examined the islands according to similarities in their species composition, five groups emerged (Figure 6). Three groups consisted of only one island (Adolphus, Wulalam and Sir Graham Moore). The small number of species on both Adolphus and Wulalam may be an artifact of sampling effort. The main distinction between the two remaining groups appeared to be species diversity with one group (blue dots in Figure 6) containing islands with a higher number of co-occurring species. These islands are also located in the high rainfall zone (> 1,000 mm), with the exception of Wargul Wargul (946 mm). Examining the role of individual species in contributing to the separation between these

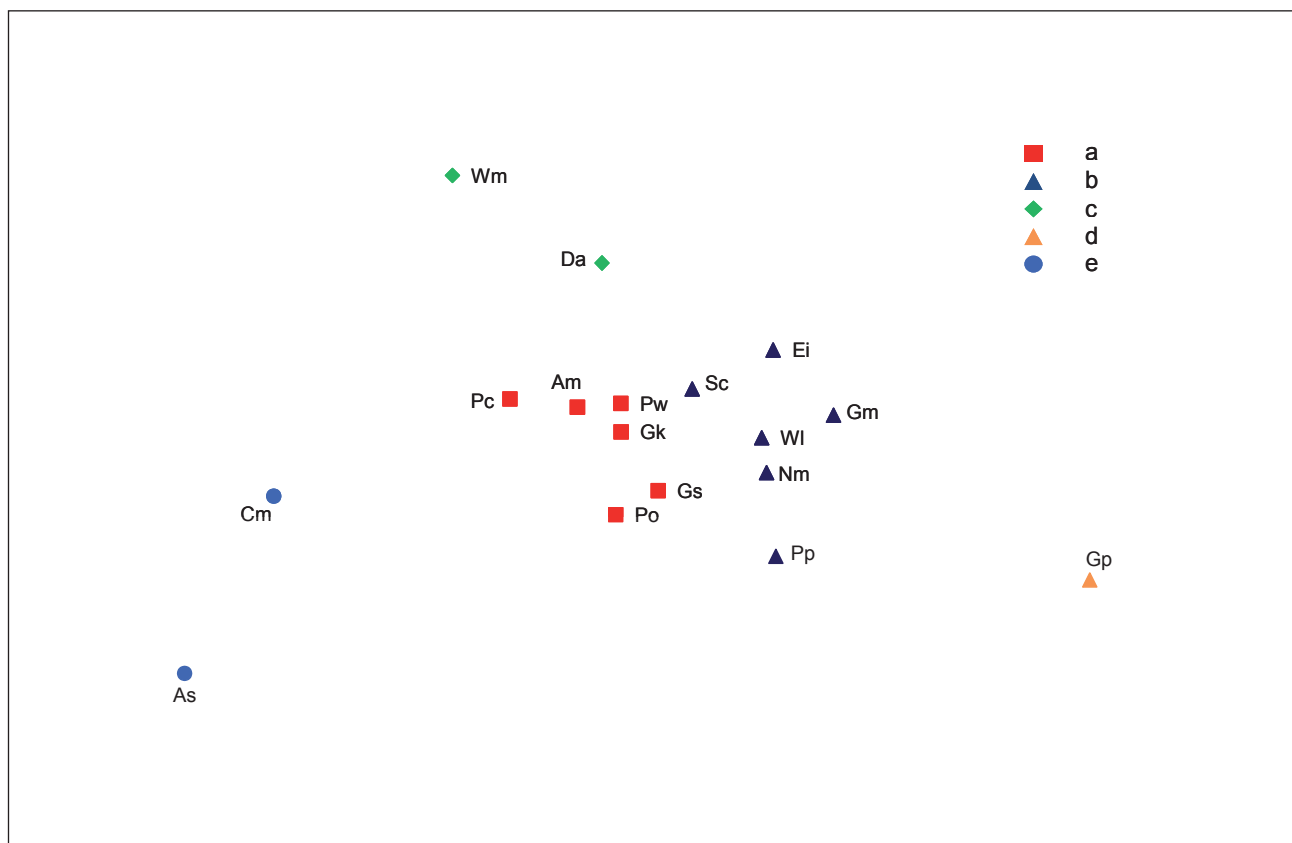


FIGURE 7 Non-metric MDS plot of non-camaenid species according to their co-occurrences on the Kimberley islands based on the Two-step association measure (2D stress = 0.05). UPGMA classification clusters are indicated by dot shape and colour on the plot.

Key: Pw – *Pleuropoma walkeri*, As – Assimineid n. gen., n. sp., Po – *Pupisoma orcula*, Pc – *Pupisoma circumlitum*, Nm – *Nesopupa mooreana*, Gp – *Gastrocopta pediculus*, Gs – *Gastrocopta stupefacians*, Gm – *Gastrocopta macdonnelli*, Gk – *Gastrocopta kessneri*, Pp – *Pupoides pacificus*, Am – *Amimopina macleayi*, Ei – *Eremopeas interioris*, Da – *Discocharopa aperta*, Sc – *Stenopylis coarctata*, Cm – *Coneuplecta microconus*, WI – *Westracystis lissus*, Wm – *Wilhelminaia mathildae*.

two main groups showed that *Gastrocopta kessneri*, *G. stupefacians*, *Aminopina macleayi*, *Pleuropoma walkeri* and *Pupisoma orcula* contributed to 50.1% of the average dissimilarity between the groups. All of these species are known to be more common in areas of high rainfall (Solem and McKenzie 1991). Of the combinations of the six attributes considered, the BIOENV procedure found that rainfall on its own had the strongest relationship with compositional similarity of the islands (Spearman's rho = 0.50). A rainfall gradient was also evident in the nMDS ordination plot, with the high-rainfall islands tightly clustered and distant from the other islands (Figure 6). The remaining islands had an average annual rainfall of less than 1,000 mm, except for Un-named (~1,000 mm). Adding additional attributes only reduced the correlation,

indicating they added little to explaining the compositional patterns.

Species similarity of the non-camaenids among islands decreased significantly with geographical distance (Mantel $r = -0.521$, $P < 0.01$). When we corrected for the effect of geographical distance, the correlation of species similarity with rainfall remained significant (Mantel $r = -0.404$, $P < 0.01$).

An examination of species based on their co-occurrences on the same island revealed five main groups (Figure 7). The species in group 'a' are known to occur in the high rainfall rainforests of the Kimberley and the Northern Territory (Solem 1988b, 1991; Pokryszko 1996; Solem and McKenzie 1991; Köhler et al. 2012). Group 'b' includes the more widespread species. Most have been recorded in a

variety of habitats (including semi-arid areas) in the Kimberley, Northern Territory, New South Wales and Queensland (Solem 1988b, 1991; Pokryszko 1996; Stanisic et al. 2010; Köhler et al. 2012). Group 'c' contains two species (*Discocharopa aperta* and *Wilhelminaia mathildae*), which were recorded on relatively few islands. *Discocharopa aperta* appears to tolerate drier areas, extending into the arid zone of central Australia (Solem 1988b) whereas *Wilhelminaia mathildae* occurs mainly in the high rainfall rainforests of the Kimberley and Northern Territory (Solem 1988b; Köhler et al. 2012). It is also distributed from coastal southern New South Wales to northern Queensland (Stanisic et al. 2010; Köhler et al. 2012). *Gastrocopta pediculus* forms group 'd', occurring on only five islands, all located in the northern section of those sampled. This species is common in semi-arid areas of the Kimberley and Northern Territory (Solem 1991; Pokryszko 1996; Köhler et al. 2012). The final group 'e' consists of two species, one newly discovered ('Assimineid n. gen. n. sp.') occurring only on Middle Osborn Island and *Coneuplecta microconus*, occurring on Middle Osborn and Boongaree. Both these islands contain volcanic substrates. *Coneuplecta microconus* is restricted to rainforests in the wetter areas of the Kimberley, Northern Territory and Queensland (Solem 1991; Stanisic et al. 2010; Köhler et al. 2012).

DISCUSSION

CAMAENID LAND SNAILS

CORRELATES OF SPECIES RICHNESS

Some studies have indicated that species richness is largely a function of sampling effort (e.g. Cowie 1995; Stanisic et al. 2007). In our case, sampling effort, as estimated by the number of locations sampled for land snails on an island, had a low contribution to explaining species richness, suggesting that the number of camaenid species recorded on an island was not biased by sampling effort.

Species richness on islands is a function of both colonisation and extinction events, as well as within-island speciation (Losos and Ricklefs 2009, 2010). Geographical and ecological factors such as island area, insularity, island age, elevation, habitat availability and diversity, as well as intrinsic factors such as dispersal capability and ecological tolerance are likely to influence the relative importance of these processes (Parent and Crespi 2006). On the continental islands along the Kimberley coast, we found that the richness of camaenid land snail species was strongly influenced by a rainfall gradient, with richness increasing with rising average annual rainfall. In this case, rainfall is

likely to be a surrogate of habitat availability and structure. Rainfall was highly correlated with the extent of rainforest on an island. Rainforests are considered to be the best habitat for most camaenid land snail species as they provide a moist and protective environment suitable for these desiccation-prone organisms (Solem 1991). Solem and McKenzie (1991) similarly found that species richness of camaenids was related to rainfall over a broader area of the Kimberley. The number of camaenid species was also higher on larger islands, those with a higher elevation and a larger extent of rock scree. All these variables are indirect/direct measures of habitat complexity or niche space (Cowie 1995; Parent and Crespi 2006). Larger and higher islands typically contain a greater range of potential habitats, which promotes higher speciation rates (Losos and Schluter 2000; Losos and Ricklefs 2009).

Rocky habitat is often associated with land snail occurrence (Solem and McKenzie 1991; Slatyer et al. 2007; Stanisic et al. 2007). Not only does it provide shelter, particularly for aestivating land snails, but it also provides protection from fire, a prominent feature in the Kimberley landscape. The high complexity of the rock scree habitat in the Kimberley also creates a diversity of niche space. Exposed, layered, rocks provide stable microclimatic conditions as they are cool, moist and relatively buffered from short- and long-term climatic changes. Couper and Hoskin (2008) suggested that rock habitats act as 'litho-refugia' for the persistence of a number of primary rainforest faunal groups in areas where once more widespread rainforest is marginal or absent. A similar evolutionary importance of rocky habitats can also be postulated for the Camaenidae.

The degree of habitat isolation can be deterministic in terms of species diversification. There is less chance of gene flow between areas of isolated habitat due to lower opportunities for colonisation (Losos and Ricklefs 2009). In the case of the camaenids, we found that distance of an island to a larger landmass (i.e. potential source of colonisation) was of little importance in determining species richness. This may indicate that species richness of the camaenids is not a function of colonisation/extinction dynamics, but is largely a function of *in situ* speciation. The limited dispersal ability of most camaenid land snails (Solem and McKenzie 1991; Cameron 1992) lends weight to this argument. As does that we found little evidence of species similarity among islands decreasing with geographical distance (see below). Dispersal capacity of land snails has been shown to be correlated with body size (e.g. Hausdorf 2000). Specifically, passive dispersal capacity tends to decrease with increasing body

size (Hausdorf 2000). The camaenid land snails are relatively large compared to the non-camaenid families and they have certain anatomical features that increase their susceptibility to desiccation and lower their chances of passive dispersal (Solem and McKenzie 1991). A study by Johnson et al. (2010), focusing on *Amplirhagada* species from just parts of the Bonaparte Archipelago in the Kimberley, found that these island populations show little evidence of gene flow, despite periodic connections among islands and only small distances separating them. One possible explanation is that, much like on the mainland, camaenid species are restricted to habitat patches (such as rainforests) on the islands themselves, and if these habitats remain disjunct even when connected to the mainland or other islands, then gene flow is less likely (Johnson et al. 2010; Köhler 2010b). Such restricted gene flow is likely to encourage allopatric differentiation among islands and *in situ* speciation within islands. When we treated the two campsites on the larger islands separately, we found some evidence of dispersal across an island. The campsites on the same island were more similar to each other than any other campsite sampled (Appendix 2). However, the occurrence of species turnover between campsites on the same island is consistent with the significance of geographical distance as an isolating factor, even in the absence of marine barriers.

PATTERNS IN COMPOSITION OF THE GENERA

At the level of genus, patterns in composition of camaenid land snail assemblages also appeared to correspond largely with a rainfall gradient. Islands with a high average annual rainfall contained a higher number of genera that are characteristic of the wettest part of the Kimberley (i.e. central area of its north-west) and restricted to rainforest habitats, whereas the lower rainfall islands located in the north-eastern and southern-most sections along the coastline contain genera that have distributions that extend into semi-arid areas and will also occur in more open woodland (Solem 1991; Solem and McKenzie 1991; Köhler 2011b). The close association of rainfall with species composition of land snails has also been observed in many other countries (e.g. Hermida et al. 1994; Kadmon and Heller 1998; Tattersfield et al. 2001; Steinitz et al. 2005), and is likely to be an indirect effect with rainfall determining the soil moisture, vegetation and productivity at a site (Nekola 2003; Chiba 2007; Slatyer et al. 2007).

The extent of rock scree also played a role in terms of explaining assemblage composition. Genera containing species less reliant on rock scree have a higher representation in one of the island groups identified. Specifically, two of the three genera in one of the groups (*Xanthomelon*

and *Rhagada*) contain species that are free-sealers (i.e. to avoid desiccation they secrete mucus across their shell opening), as opposed to a rock-sealer (which seals with mucus to a rock), and therefore are not dependent on rock scree to provide shelter during aestivation, but can burrow in soil or leaf litter (Solem and McKenzie 1991). Island area and insularity did not appear to contribute to the patterns in assemblage composition observed, however, these attributes are more likely to play a role in determining species diversity (as evidenced above).

The 'distance decay' pattern, where sites located in close proximity to each other tend to have more species in common than sites separated by large distances, has been attributed to a combination of environmental relationships and dispersal processes (Nekola and White 1999). This pattern is expected to be stronger for organisms with poor dispersal ability (Steinitz et al. 2006). In this case, we found little evidence of distance decay among camaenid species, although we did find the pattern at the higher taxonomic resolution of genus, suggesting that geographic distances between islands played a role in defining compositional groups at this resolution. However, rainfall and rock scree still influenced composition even after controlling for geographical distance indicating a combined effect of all these factors.

Among camaenid land snails, sympatric species have been shown to belong to different genera, with each genus displaying unique adaptations with respect to aestivation behavior, body size or shell shape, suggesting that they use distinct ecological niches (Solem 1985). Studies of land snails elsewhere have shown that even within a genus, shell morphology of the species has a clear relationship with habitat use (Cameron and Cook 1989; Chiba 2004; Stankowski 2011). For instance, high-spined shells are generally associated with vertical surfaces and flat shells with horizontal surfaces (Barker 2001). Our study also showed that co-occurring genera among the islands do tend to have a different shell shape (i.e. as indicated by height v diameter). Additionally, those genera that share a similar shell shape generally belong to different compositional groups (Figure 5). In this case, we used a 'broad-brush' approach and averaged the shell dimensions for each genus regardless of the island they occurred on and related that to the compositional pattern. Even so, the standard errors were very small (Appendix 3). This result indicates that species coexistence of camaenid land snails could be related to niche differentiation. Further studies will investigate co-occurring species on islands, relating shell morphology specifically to habitat/substrate preference.

NON-CAMAENID LAND SNAILS

CORRELATES OF SPECIES RICHNESS

For the more widely distributed non-camaenid land snail species, annual rainfall was again the most important attribute defining species richness, with the model including rainfall alone explaining 65% of the deviance. While many of these species are known to tolerate a variety of environmental conditions (Solem 1988b; Cameron 1992), the patches of rainforest of the high rainfall zone are optimal habitat for land snails in general (for reasons explained above).

The confounding effect of sampling effort on species richness was evidenced here, with the influence of sampling effort moderately supported in the models. The small size of the non-camaenid species (1–10 mm) and the large proportion of arboreal species (Solem and McKenzie 1991) make them particularly difficult to detect. The vast majority of non-camaenids are found by searching through leaf litter, where they can be easily overlooked (V. Kessner, pers. comm.). Sampling effort therefore, is likely to bias estimates of species richness to some degree. However, among the islands as a whole, the species accumulation curve does not indicate gross deficiencies.

The remaining attributes, including island area and distance to a larger landmass, were only weakly supported in terms of explaining species richness. However, the high passive dispersal capacity of the non-camaenids, including their ability to cross substantial barriers such as the ocean (Solem and McKenzie 1991; Cameron 1992), and the relatively small distances between the islands and the mainland (majority less than 4 km), permits colonisation into most areas supporting suitable habitat. This pattern is typical of other groups with high passive dispersal such as perennial plants, as well as highly mobile species such as birds (McKenzie et al. 1991b; Steinitz et al. 2006). The lack of obvious speciation of the non-camaenids on the islands also suggests a high dispersal rate, as sufficient gene flow between islands will prevent divergence of populations (Losos and Ricklefs 2009). Lack of evidence of diversification also points to extinction/colonisation dynamics, rather than within-island speciation, as the main driver of species diversity of the non-camaenid land snails on the islands.

PATTERNS IN SPECIES COMPOSITION

In contrast to the extraordinarily high inter-island turnover in the camaenid species, a large majority of the non-camaenid species were recorded on several islands. This difference in geographical

range has been attributed to the ease of passive dispersal of the smaller non-camaenid species (Solem and McKenzie 1991; Cameron 1992). A significant negative correlation between body size and range size has been recorded for other groups of land snails also implying that dispersal capacity is correlated with body size (Hausdorf 2000; Pokryszko et al. 2011).

Like the camaenids, patterns in species composition of the non-camaenids were tightly correlated with average annual rainfall with the highest number of co-occurring species on islands (>11) receiving at least 1,000 mm and islands that support low numbers of species (<4) receiving less than 850 mm. A cohort of species tended to occur across all islands, regardless of rainfall, while another appeared to be largely restricted to high rainfall islands. This pattern may in part be due to false absences as indicated by the correlation between species richness and sampling effort. However, rainfall was still the most important attribute influencing species richness, and it is also likely to be a significant driver of species compositional patterns. Solem and McKenzie (1991) also determined rainfall to be the most significant factor influencing species compositional patterns of the non-camaenids within rainforests of the Kimberley more generally.

Patterns in similarity of species composition of the non-camaenids were also influenced by geographical distance between islands. Rainfall still influenced species composition, even after controlling for geographical distance, indicating that both dispersal characteristics of the non-camaenids and a rainfall gradient influenced compositional similarity.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

As has been found on the Kimberley mainland, the camaenid land snails demonstrated high overall species richness, restricted geographical ranges (most to a single island) and almost complete turnover of species among islands. In comparison, the overall number of the smaller non-camaenid land snail species was much lower and their wider distribution was reflected by a lower level of species turnover among islands. These results are consistent with the differing dispersal abilities of the two groups, one fostering *in situ* speciation and the other inter-island colonisation. An examination of phylogenetic patterns will help to elucidate this pattern further and will be the subject of another study (authors, unpublished data). We also show that dispersal ability was not the only driver of species richness and composition of land snail species on islands, but that rainfall, island area and availability of habitat also played a role.

The high level of short-range endemism of the camaenid land snails on the islands sampled, in sharp contrast to the wide ranges of the non-camaenids, implies that conservation effort should be focused on the former. However, as similar environmental attributes were important determinants of species richness and patterns of species composition for both groups of snails, conservation strategies specified for the camaenids are also likely to benefit the non-camaenid land snails.

Of the 89 camaenid species detected in this study, 73 were endemic to the islands, many to single islands. This high level of endemism coupled with such a high turnover rate among islands indicates that all the islands sampled are significant in terms of representing the diversity of the camaenid fauna. This is a conservation issue for many range-restricted endemic fauna (Harvey 2002). In terms of prioritising islands for land snail conservation, those located in the high rainfall zone (i.e. >1,000 mm), are clearly important. Among these, the relatively larger islands and those with a greater extent of rock scree are of particular significance, such as Boongaree, Augustus, Bigge and Storr. To encompass differences in composition, at least at the level of genus, Middle Osborn, Coronation and Wargul Wargul are also priorities. Additionally, some islands contain endemic genera known only from there, such as NW Molema (*Molema*), Bigge (*Kimberleydiscus*) and Middle Osborn (*Kimberleymelon*).

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Abbreviations: AD – Adolphus, AU – Augustus, BI – Bigge, BO – Boongaree, BM – Byam Martin, CO – Coronation, HI – Hidden, JU – Jungulu, KA – Katers, KF – Kingfisher, LA – Lachlan, LO – Long, MA – Mary, MO – Middle Osborn, NM – NW Molema, GM – Sir Graham Moore, SO – South West Osborn, AN – St Andrew, ST – Storr, SU – Sunday, UN – Unnamed, UW – Uwins, WW – Warqul Warqul, WU – Wulalam

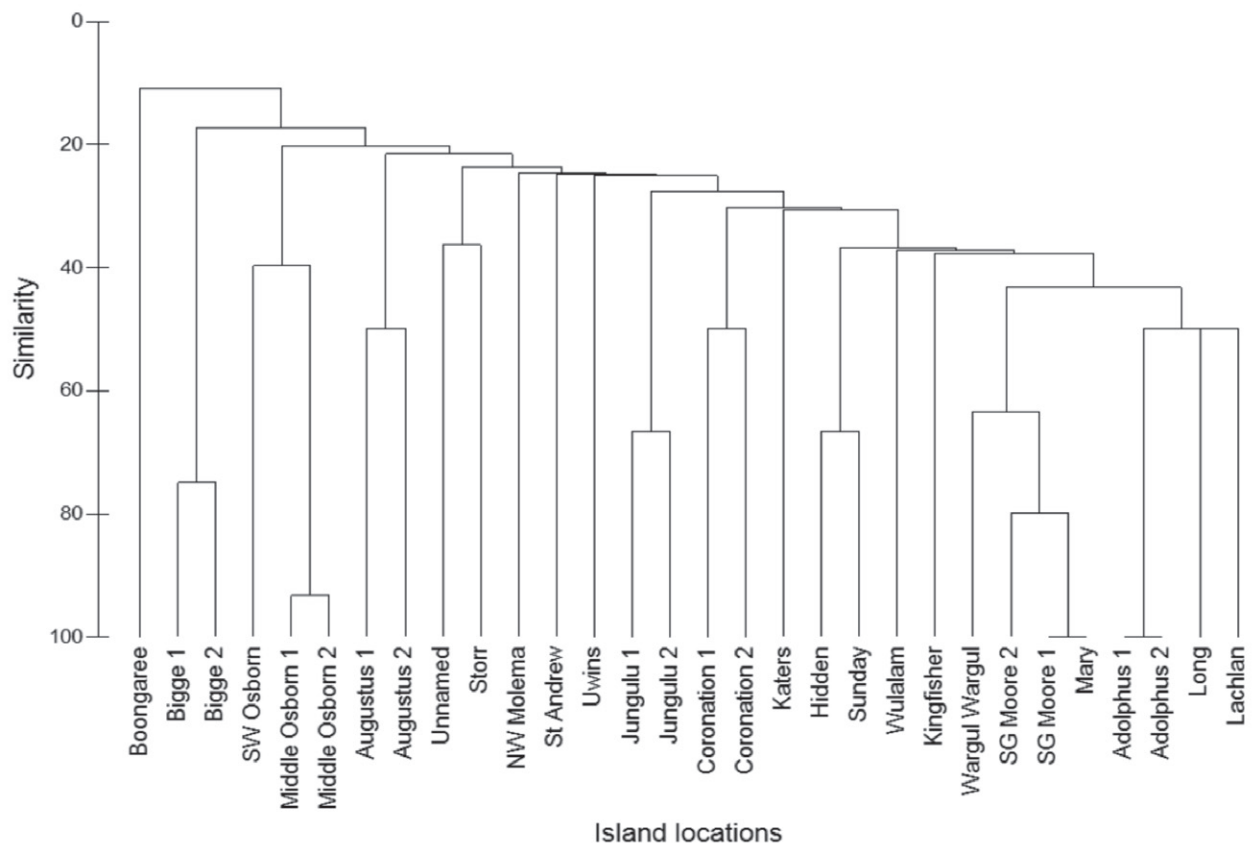
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Species	AD	AU	BI	BO	BM	CO	HI	JU	KA	KF	LA	LO	MA	MO	NM	GM	SO	AN	ST	SU	UN	UW	WW	WU
<i>Setobaudinia quinta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Setobaudinia rectilabrum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Setobaudinia umbadayi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Setobaudinia wuyurru</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Setobaudinia</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia allouarni</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia aquilonia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Torresitrachia brookei</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia dampieri</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia flindersi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia freycineti</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia girgarinae</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia hartogi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Torresitrachia houtmani</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Torresitrachia janszi</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia leichhardti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Torresitrachia tasmani</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torresitrachia urvillei</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Xanthomelon obliquirugosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Total per island	1	11	9	13	3	6	2	5	3	2	1	1	1	5	4	2	3	4	6	2	3	4	3	2

APPENDIX 2 Classification of camaenid land snail species according to their co-occurrences at each island location.



APPENDIX 3 Average shell height and diameter of each camaenid land snail genus across all islands sampled. Standard errors (SE) are also shown.

	Height (mm)	SE	Diameter (mm)	SE
<i>Amplirhagada</i>	15.23	0.14	20.34	0.10
<i>Carinotrachia</i>	10.27	0.08	16.95	0.11
<i>Kimberleydiscus</i>	9.23	0.17	19.28	0.26
<i>Kimberlymelon</i>	21.03	0.81	23.21	0.81
<i>Australocosmica</i>	11.83	0.19	15.20	0.15
<i>Kimboraga</i>	16.29	0.30	21.73	0.21
<i>Baudinella</i>	3.10	0.03	6.89	0.04
<i>Molema</i>	3.16	0.09	8.42	0.18
<i>Setobaudinia</i>	4.45	0.11	8.82	0.20
<i>Rhagada</i>	9.94	0.18	14.96	0.23
<i>Retroterra</i>	7.76	0.48	17.70	0.42
<i>Kimberleytrachia</i>	9.45	0.34	17.17	0.52
<i>Torresitrachia</i>	8.27	0.07	15.66	0.10
<i>Xanthomelon</i>	22.37	0.40	24.20	0.43
<i>Globorhagada</i>	27.16	0.63	25.62	0.64