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# Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts

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## ABSTRACT

Limestone karsts on tropical land masses are considered de facto habitat islands due to their isolation from one another by non-calcareous substrata; this spatial configuration limits gene flow and induces high levels of species endemism. Apart from their biological importance, karsts are also highly valued for the ecosystem services and resources they provide if left intact. Unfortunately, conservation planning for karsts has generally lacked scientific basis. Ideally, factors affecting the richness and distribution of karst-endemic taxa should be incorporated into quantitative guidelines for karst reserve selection. Using land snail data from 43 different karstic towers in Malaysia, we: (1) identified biogeographical factors (i.e., area, isolation, surrounding soil type and geological age) hypothesized to influence endemic richness; and (2) investigated how species distributions varied among karsts in different regions. Generalized linear mixed-effect models revealed the relatively important effects of surrounding soil type and karst area on land snail endemism; the most parsimonious model contributed to 63.6% of the Akaike's Information Criterion weight and explained over 18% of the deviance in karst-endemic richness (of which 10.0% was explained by surrounding soil type). Non-metric multi-dimensional scaling indicated that karsts in different regions of Malaysia had distinct malacofaunas. Therefore, conservation planners should take into account karst size, surrounding soil type and the influence of geographic barriers to maximize the protection of land snails and possibly other karst-endemic taxa, which are increasingly threatened by quarrying throughout Southeast Asia.

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## 1. Introduction

Modern conservation planning involves the identification (and prioritization) of biodiversity ‘hotspots’ (Myers et al., 2000) and their variants for protection. Among tropical ecosystems, limestone karsts have been recognized as ‘hotspots’ for the large number of endemic plants and animals they support (Clements et al., 2006), and for the heightened risk they face from habitat degradation and destruction from quarrying activities (Vermeulen and Whitten, 1999). Limestone karsts (hereafter referred to as ‘karsts’) are defined here as sedimentary rock outcrops made up primarily of calcium carbonate. Karsts were formed millions of years ago by calcium-rich organisms under the sea, but were uplifted relatively recently by tectonic events.

In Malaysia, more than 800 karsts can be found scattered across the Eastern (Sabah and Sarawak) and Western (Peninsular Malaysia) regions (Lim and Kiew, 1997; Price, 2001). Karsts in this region mostly occur as sheer-sided tower outcrops riddled with caves and sinkholes. Due to their isolation from one another by non-calcareous substrata (Paton, 1961), gene flow between karsts has been restricted, with the result that certain taxa on these habitat islands exhibit high levels of endemism via allopatric (van Benthem-Jutting, 1958; Tweedie, 1961) and/or parapatric (Schilthuizen et al., 2002) modes of speciation. For example, 21% of 1216 karst-associated plant species are endemic to West Malaysia and 11% are strictly confined to karsts (Chin, 1977). Karsts are also considered evolutionary hotspots for land snail speciation (Davison, 1991; Schilthuizen, 2004; Clements et al., 2006). In Borneo, the small (0.2 km<sup>2</sup>) Sarang karst contains at least six site-endemics, while no less than 50 species are endemic to the large (15 km<sup>2</sup>) Subis karst (Vermeulen and Whitten, 1999). In karst caves, high endemism in animal communities (e.g., fishes, bats, arthropods, etc.) can also result due to evolutionary changes arising from prolonged cohabitation of species from different ecological and biogeographical origins (e.g., Culver et al., 2000; Gibert and Deharveng, 2002). Apart from preserving karsts for their biological importance, certain karsts should be conserved for the useful ecosystem services and resources (e.g., groundwater, pollination and pest control services, eco-tourism sites, non-timber forest products, guano, bird’s nest, cement, etc.) they can provide if managed sustainably (Clements et al., 2006).

Unfortunately, conservation plans for karsts have been difficult to justify due to insufficient baseline data (Dennis and Aldhous, 2004). The number and size of karsts set aside for preservation are almost always dictated by economic (e.g., commercial interests from mining companies) and political (e.g., different jurisdictions of state governments) forces (Soberón, 1992). In Malaysia, several karsts that were identified decades ago for preservation due to their biological importance have not received any form of protection to date (Davison, 1991; Kiew, 1991). By overlaying the localities of karsts sampled in this study onto a year 2000 forest cover map (Stibig and Malingreau, 2003), it is apparent that a majority of them are already situated at forest edges or within defor-

ested landscapes (Fig. 1). Given that karst biodiversity is particularly susceptible to disturbances from human traffic (Kiew, 2001), recreational activities (McMillan and Larson, 2002; McMillan et al., 2003), crop cultivation (MacKinnon et al., 1996) and quarrying (Clements et al., 2006), there is clearly a pressing need to develop and utilize scientifically-sound criteria for karst conservation planning to prevent further population reductions (Schilthuizen et al., 2005) and extinctions (Vermeulen, 1994) of karst-endemic species.

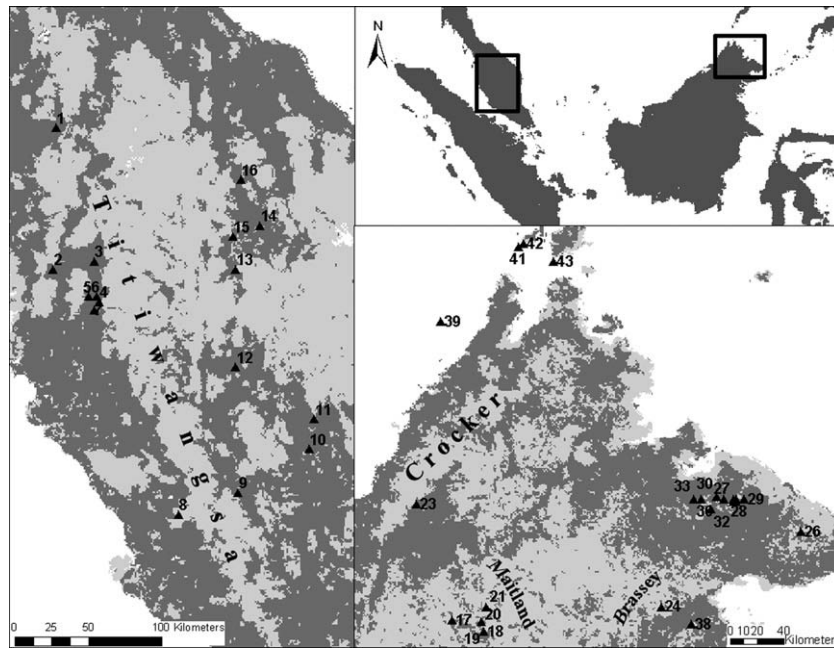
Biogeographical information has proved useful in setting conservation priorities (Daily et al., 2003; Lourie and Vincent, 2004), but knowledge of karst species endemism and distribution patterns remains inadequate for such purposes. For example, what are the effects of karst area and isolation on species endemism? Such correlates of endemism can potentially be used to identify biologically important karsts for preservation. In addition, how do species compositions vary across karsts in different regions? Understanding such large-scale distribution patterns can also reduce bias in reserve selection because basing reserve design on species richness or endemism data alone does not necessarily result in efficient biodiversity preservation policies (Born et al., 2007).

Given their patterns of high allopatric diversity (Solem, 1984; Tattersfield, 1996), and the persistence of shells that facilitate relatively easy sampling and species identification (Emberton et al., 1999), land snails are a suitable taxon to address the abovementioned questions. Here, we use land snail data from 16 different karsts in Malaysia to identify correlates of endemism from a set of factors (i.e., karst area, isolation, surrounding soil type and geological age) hypothesized to affect species endemism using generalized linear mixed-effect models. Next, we use ordination methods to investigate how land snail species compositions varied among these 16 karsts in West Malaysia (using the same dataset), and among 27 other karsts in East Malaysia that were sampled in previous studies (e.g., Schilthuizen et al., 2002, 2005). This study is timely because extensive quarrying activities threaten large numbers of karst-endemic plants and animals in Malaysia and, to a larger extent, Southeast Asia (Clements et al., 2006).

## 2. Materials and methods

### 2.1. Study area

Sixteen karsts were sampled in West Malaysia (between longitudes 100°52'E and 102°28'E, and latitudes 3°18'N and 5°40'N; Fig. 1; Appendix A) and 27 karsts in East Malaysia (between 116°10'E and 118°44'E, and between 4°38'N and 7°13'N; Fig. 1; Appendix B). The climate in Malaysia is typical of equatorial countries, with continuous warm temperatures (mean annual temperature around 27 °C) and high rainfall (annual rainfall between 1400 and 4000 mm) that vary with the arrival of the northeast (November–March) and southwest (May–September) monsoons (Framji et al., 1981). Limestone vegetation is an edaphic climax formation (Symington, 1943) and the canopy typically consists of trees such as *Vitex*, *Memecylon* and *Garcinia*, while the base of karsts are dominated by



**Fig. 1** – Overlay of sampled karsts in West Malaysia (1–16), sampled karsts in East Malaysia (17–43) and major mountain barriers (Titiwangsa, Crocker, Maitland and Brassey) on a sub-regional forest map from the year 2000 (Stibig and Malingreau, 2003). (Light grey = forest; dark grey = non-forest). See Appendix A and B for corresponding karst names.

bryophytes, shrubs and herbs such as *Begonia*, *Monophyllaea* and *Paraboea* (Crowther, 1982).

## 2.2. Sampling protocol

All karsts were sampled at their cliff bases to control for species heterogeneity among karst microhabitats (e.g., karst summits may have different species compositions). Sampling in West Malaysia involved a total of 16 karsts, which were chosen equally from the eastern and western regions (eight karsts on each side) of a possible vicariant barrier (i.e., Titiwangsa Mountain Range) to minimize bias and to achieve greater representativeness (Fig. 1). Furthermore, these eight karsts were evenly distributed into four categories of area and isolation (Appendix A): (1) small and isolated; (2) large and isolated; (3) small and not isolated; and (4) large and not isolated. These 16 karsts were sampled during the dry southeast monsoon in July 2005 and 2006. On each karst, six replicate plots ( $4 \times 2$  m) were located at least 5 m apart. Due to the patchy distribution of land snails and small plot sizes, systematic sampling was adopted for higher spatial interspersation (Hurlbert 1984; Cameron and Pokryszko, 2005). To minimize confounding effects of human disturbance at karsts near human settlements, a plot was located more than 5 m away from the previously sampled plot if it had shown signs of artificial habitat modification. Sampling involved the collection of topsoil (depth: 5 cm; volume: 4 L) from suitable microhabitats (e.g., rock crevices or between tree roots) within the plot. In East Malaysia, 27 karsts were sampled by Schilthuis et al. (2003, 2005) between March 2000 and December 2005, irrespective of monsoon seasons. Sampling on these

karsts was derived from a mixture of systematic and random searches.

## 2.3. Sorting and identification

Shells were extracted using a combination of flotation and sieving. Although this method yielded mostly empty shells that could have belonged to individuals from previous years (Schilthuis et al., 2005), these essentially provided a history of the total number of endemic land snail species on each karst. Shells from West Malaysia were identified to species by RC, while those from East Malaysia were identified by MS. Nomenclature follow van Benthem-Jutting (1950, 1954a,b, 1961a,b) and Vermeulen and Whitten (1998). Additional verifications were made with type specimens from the Musée National d'Histoire Naturelle (Paris) and the Natural History Museum (London). Voucher specimens were deposited in the Raffles Museum of Biodiversity Research (Singapore) and the Universiti Malaysia Sabah's "Borneensis" collection. We considered a land snail species to be 'endemic' if its range is restricted to a single karst, or a group of karsts from the same limestone bedrock within a distinct biogeographical region (e.g., West Malaysia or Borneo). As endemism can be an artefact of under-sampling of neighbouring karsts, we sought to reduce this potential bias by using genera known for their endemism based on current and historical sampling records (e.g., Tweedie, 1961; Maassen, 2001; Vermeulen et al., unpublished data): *Diplommatina*, *Opisthostoma*, *Gyllothachela*, *Boysidia*, *Paraboysidia*, *Hypselostoma*, *Alycaeus*, *Chamalalycaeus*, *Rhiostoma*, *Sinoennea*, *Discartemon*, *Haplotychius*, *Arinia*, *Georissa*, *Everettia*, *Atopos* and *Japonia*.



## 2.4. Analyses

Based on completeness ratios (i.e., no. of observed species/estimated species: Soberón et al., 2000), sampling saturation was calculated for karsts in West Malaysia, but not for those in East Malaysia due to spatial (i.e., plot size) and temporal (i.e., sampling effort was spread over 6 years) variation among sampling plots. Using presence/absence data from each karst in West Malaysia, expected species accumulation curves (i.e., sampled-based rarefaction curves) were first computed based on equations derived by Colwell et al. (2004) and extrapolated to obtain estimated species richness (to calculate completeness ratios) with the incidence-based coverage estimator (Colwell and Coddington, 1994). All curves and estimators were computed using EstimateS Version 7.5 (Robert K. Colwell, Connecticut, USA).

As sampling completeness ratios could only be calculated for karsts in West Malaysia, we investigated the determinants of land snail endemism for this region only. We fitted generalized linear mixed-effect models (GLMM) to the data using the `lmer` function implemented in the `lme4` library of the R Package (R Development Core Team, Vienna, Austria). For each GLMM, we coded the number of endemic species per karst as a Poisson-distributed response variable and karst area (90 m digital elevation model from the Shuttle Radar Topography Mission viewed on ArcGIS 9; ESRI, Redlands, USA), degree of karst isolation (1:25,000, topographical maps series DNMM6102), soil type surrounding karsts (1:800,000 Generalized Soil Map, Peninsula Malaysia 1970) and karst geological age (1:500,000 Geological Survey of Malaysia 1985) as linear predictors (fixed effects – see below), assigning each model a Poisson error distribution and a log link function. Isolation was estimated using two metrics: either (a) the minimum straight-line distance to the nearest adjacent karst, or (b) the number of karsts within a 10-km radius of the focal karst. Area and isolation were treated as covariates, and soil type and geological age as categorical factors. Other covariates such as perimeter and cliff height were considered, but were removed due to autocorrelation. The number of models that

could be considered in the model set was constrained by the small sample size in our study, so we omitted models with climatic covariates in favour of more traditional drivers of endemism (e.g., area, isolation, etc.). In addition, we did not have reliable historical climatic data for each karst.

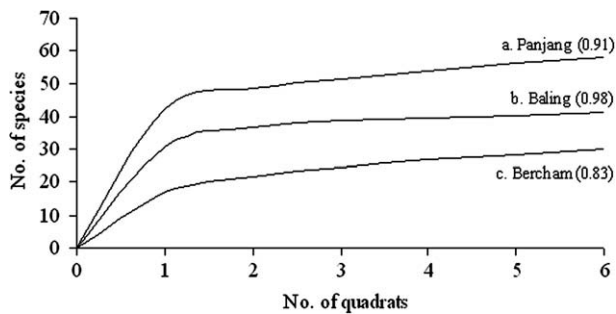
Random effects models are particularly useful here because they control for spatial pseudoreplication and potential autocorrelation (Crawley, 2005). Since plots were replicates within a karst, the term ‘karst’ was included as a random effect to control for repeated sampling of the same statistical unit; this effectively reduces the degrees of freedom to the number of karsts, and not replicates. This is a standard procedure in GLMM to account for non-independence of units (repeated measures). Coding the ‘isolation’ term explicitly as a fixed covariate essentially accounts for spatial autocorrelation by examining the relative importance of distance among karsts on endemism patterns. Given the small number of karsts sampled ( $n = 16$ ) and replicates ( $n = 96$ ), we restricted our *a priori* model set to include only seven models that represented major thematic hypotheses to test (Table 1). These models represented particular combinations of the terms of interest, with karst area considered as a ‘control variable’ (i.e., a covariate present in each model). We did not include the total number of species as a control variable given the expected positive relationship between karst area and total species richness; preliminary analyses actually revealed a rather strong univariate log-linear relationship between total species richness and karst area ( $r^2 = 0.44$ ; ignoring the karst random effect; Fig. 3a). As such, it made little sense to include both of these highly correlated terms in each model as control variables.

An index of Kullback–Leibler (K–L) information loss was used to assign relative strengths of evidence to the different competing models and Akaike’s Information Criterion corrected for small sample sizes ( $AIC_c$ ) was used to compare relative model support (Burnham and Anderson, 2002). One could also employ other methods to compare models such as the dimension-consistent Bayesian Information Criterion (BIC); however, BIC may only be preferable when sample sizes are large (Burnham and Anderson, 2004; Link and Barker,

**Table 1 – The *a priori* model set used to examine the relationship between the number of endemic species and correlates using generalized linear mixed-effects modelling for 16 karsts in West Malaysia, the major analytical (hypothesis) theme represented by each model, and the information-theoretic ranking of models investigating the correlates of endemic species richness according to Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ )**

Model no.	Model	Analytical theme	k	–LL	$\Delta AIC_c$	wAIC <sub>c</sub>	%DE	$\Delta\%DE$
1	EN ~ AR + SL	Area + soil type	6	–45.682	0	0.656	18.1	9.3
2	EN ~ AR + IS + SL	Area + isolation + soil type	7	–45.455	1.874	0.257	18.5	0.4
3	EN ~ AR	Area only	4	–50.858	5.848	0.035	8.8	–
4	EN ~ AR + GA	Area + geological age	6	–49.000	6.635	0.024	12.1	3.3
5	EN ~ AR + IS	Area + isolation	5	–50.837	8.032	0.012	8.8	<0.1
6	EN ~ AR + IS + GA	Area + isolation + geological age	7	–48.889	8.741	0.008	12.3	3.5
7	EN ~ AR + IS + AR * IS	Area + isolation + their interaction	6	–50.034	8.704	0.008	10.3	1.5

Term abbreviations are defined as follows: EN = number of endemic species, AR = karst area, IS = isolation index (minimum straight-line distance to nearest karst), GA = geological age (Permian and Lower Triassic, Carboniferous or Palaeozoic), SL = major soil type (yellow–grey podzols, red–yellow podzols or ‘other’), k = number of parameters, –LL = negative log-likelihood,  $\Delta AIC_c$  = difference in  $AIC_c$  for each model from the most parsimonious model, wAIC<sub>c</sub> =  $AIC_c$  weight, and %DE = percent deviance explained in the response variable by the model under consideration.

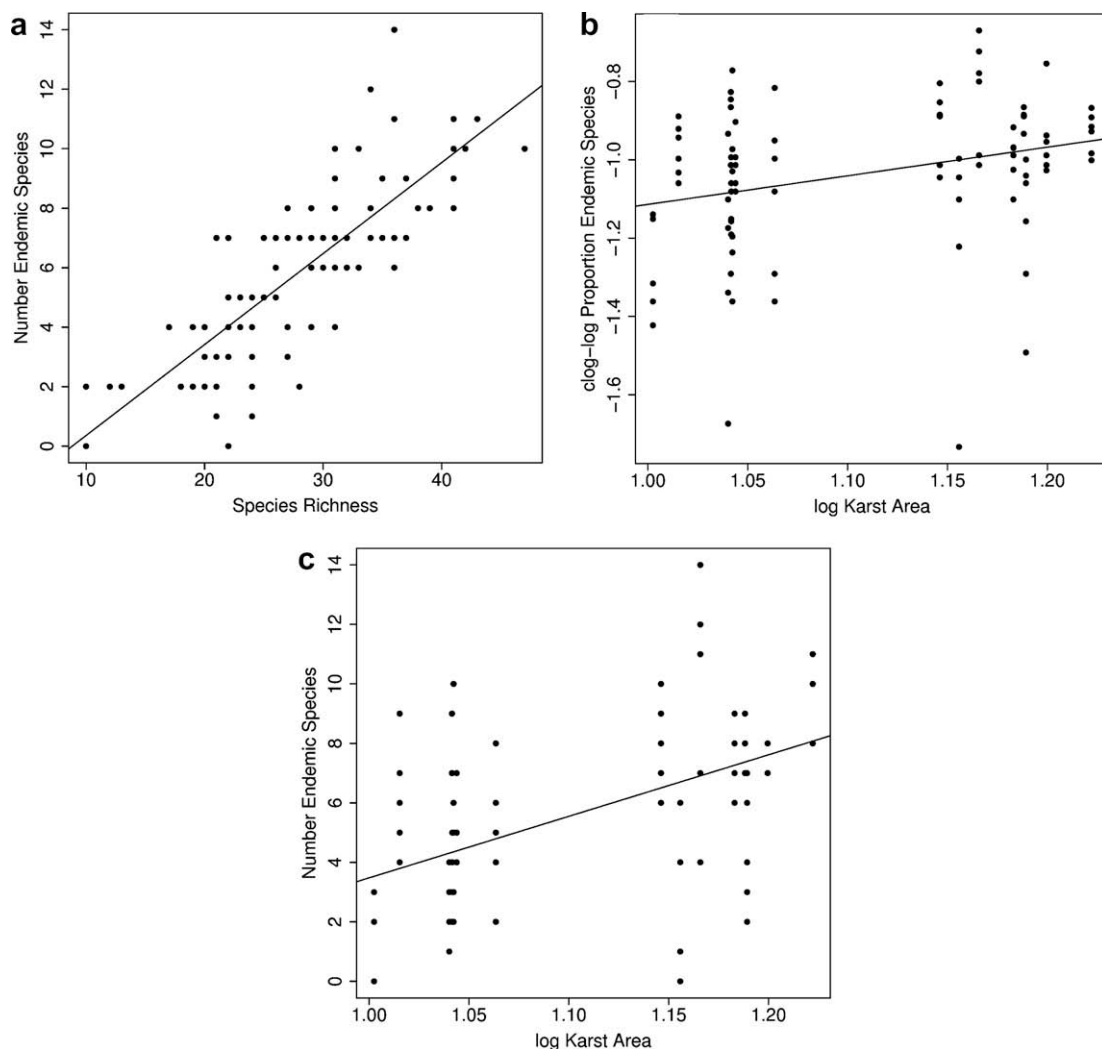


**Fig. 2** – Expected species accumulation curves for three (i.e., Panjang, Baling and Bercham karsts) of the 16 karsts in West Malaysia with the: (a) highest species richness; (b) highest completeness ratio; and (c) lowest completeness ratio.

2006). The relative likelihoods of candidate models were calculated using  $AIC_c$  (Burnham and Anderson, 2002), with the

weight ( $wAIC_c$ ) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. For each model considered, we also calculated the percentage deviance explained (%DE) as a measure of goodness-of-fit, and compared each model's %DE to that of the next most parsimonious model to examine what proportion of the variance in the response was attributable to individual terms considered.

Compositional patterns of land snail communities across 27 karsts in East Malaysia and 16 karsts in West Malaysia were investigated using non-metric multi-dimensional scaling (NMDS; Kruskal, 1964) on a species presence/absence data matrix using PC-ORD Version 4.14 (MjM Software, Oregon, USA). NMDS is a distance-based ordination analysis that searches for the best positions of  $n$  entities (samples) on  $k$  dimensions (axes) that minimize the departure from monotonicity in the relationship between the original dissimilarity data of the  $n$  samples and the reduced  $k$ -dimensional ordination space of these samples. NMDS is considered one of the most effective ordination methods for ecological community



**Fig. 3** – Positive univariate relationships between (a) number of endemic land snail species and total land snail species richness, (b) the log-log transformation of the proportion of land snail species that are endemic and  $\log_{10}$  karst area and (c) the total number of endemic land snail species and  $\log_{10}$  karst area.

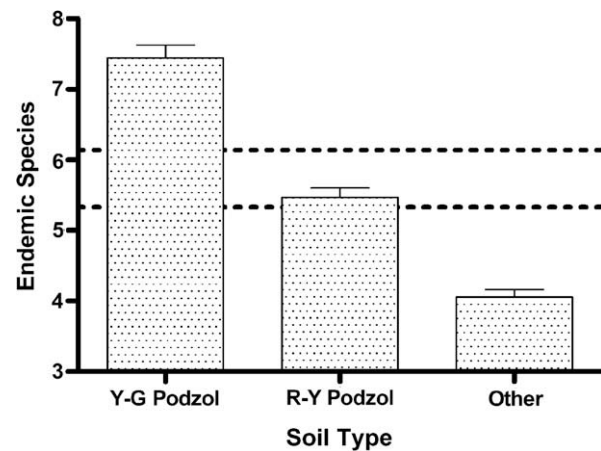
data because it does not assume linear relationships (McCune and Grace, 2002). After conducting a preliminary NMDS analysis on the complete datasets, species with pan- and paleotropical distributions were excluded (7% of East Malaysia datasets and 5% of West Malaysia datasets) from the second NMDS analysis to investigate distribution patterns for local and regional malacofauna only.

After identifying outliers using the ‘outlier analysis’ function, NMDS was run in the ‘autopilot (slow and thorough)’ mode with random starting configurations and Sørensen distance as the dissimilarity measure. The resulting ordination consisted of the two axes representing the highest proportion of variance (obtained by calculating the coefficient of determination between distances in the ordination space and distances in the original space; McCune and Grace, 2002) in species data of the final  $k$ -dimensional ordination space. A Monte Carlo permutation test was done on the resulting ordinations to evaluate whether NMDS was extracting stronger axes than expected by chance. Multi-response permutation procedures (MRPP: Mielke and Berry, 2001) were also done to provide a non-parametric test of differences between resulting groups of karsts from each ordination. No correlations between climatic variables (e.g., rainfall and temperature) and the final NMDS scores were made because, as mentioned earlier, reliable historical data was unavailable for each karst.

### 3. Results

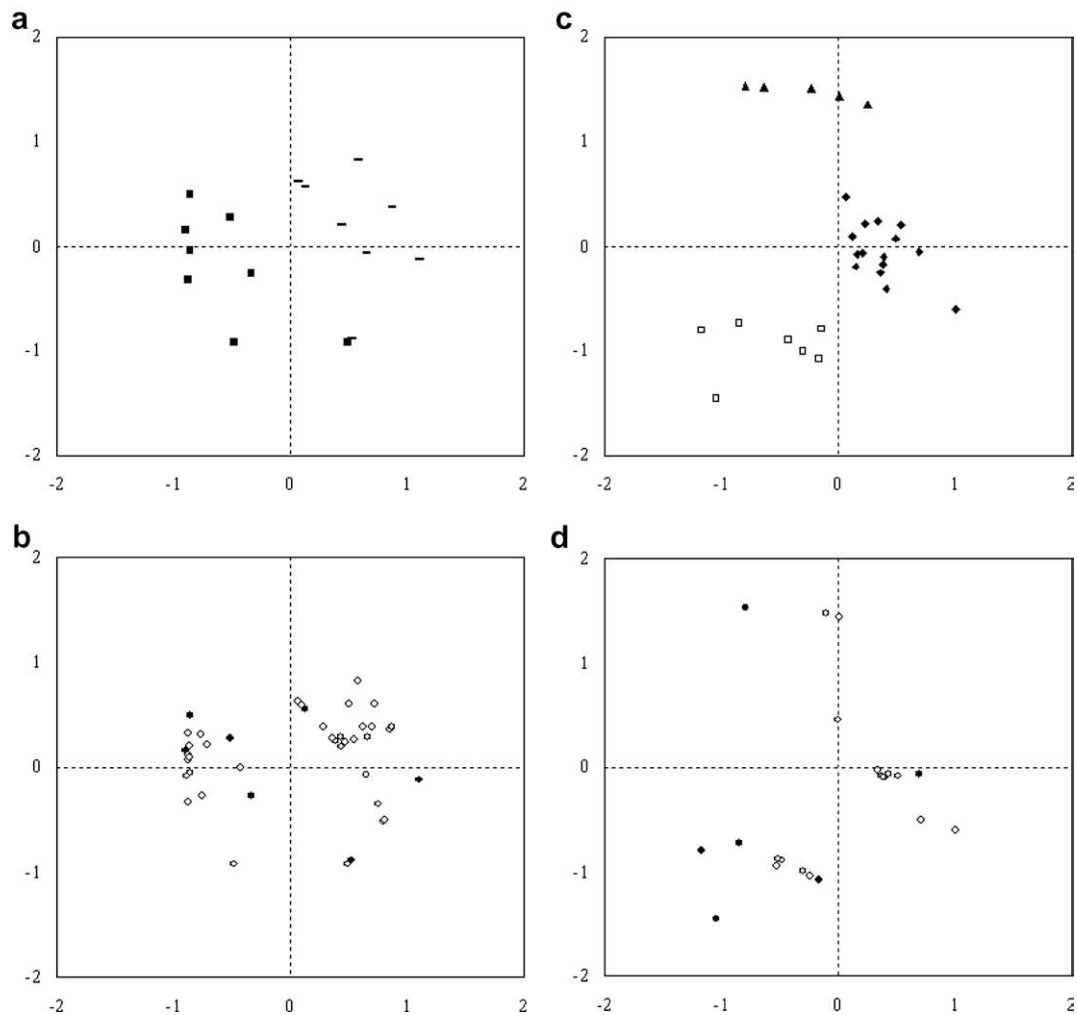
Sampling from 16 karsts in West Malaysia yielded a total of 198 land snail species from 49 genera and 19 families (Appendix C), while 173 species from 64 genera and 23 families were sampled from 27 karsts in East Malaysia (Appendix D). Based on their completeness ratios (0.83–0.98; Fig. 2), sampling saturation was high for each of the 16 karsts in West Malaysia. The two model sets using the two different measures of karst isolation (total straight-line distance to the nearest karst and number of karsts within a 10-km radius) revealed nearly identical model rankings and %DE explained, so we only reported the results using the latter isolation measure. The contrasted generalized linear mixed-effects models (GLMM) revealed an important contribution of surrounding soil type (Table 1) beyond the effect of karst area on endemic richness (Table 1). The positive, but weak relationship between karst area and endemic richness (Fig. 3b and c), however, requires further corroboration with larger sample sizes.

The most parsimonious model had 65.6% of the  $AIC_c$  weight and explained over 18% of the deviance in the total number of endemic species per karst (of which 9.3% was explained by surrounding soil type and 8.8% by area; Table 1). Karsts surrounded by yellow-grey podzols had the highest predicted number of endemic species, with karsts surrounded by red-yellow podzols having a neutral effect and karsts surrounded by other soil types containing the lowest levels of endemism (Fig. 4). Although the next highest-ranked model contained the isolation term ( $wAIC_c = 25.7\%$ ), its addition only accounted for another 0.4% of the deviance explained (Table 1). All other models had weak support ( $wAIC_c < 3.5\%$ ).



**Fig. 4 – Predicted number of endemic land snail species per karst surrounded by the following soil type: yellow-grey (Y-G) podzols, red-yellow (R-Y) podzols and all ‘other’ soils. The observed 95% confidence interval of the number of endemic species per karst (dotted horizontal lines) was determined by a 10,000 iteration bootstrap of the probabilities predicted by the model  $EN \sim AR + SL$ . Changes to the predicted number of endemic species relative to each soil type level were calculated by adjusting the original dataset so that all karsts were surrounded by the same soil type (each soil type in turn), keeping the ‘area’ term in the model as in the original dataset. Error bars represent the 10,000 iteration bootstrapped upper 95% confidence limits.**

For karsts in West Malaysia, NMDS yielded a final optimum three-dimensional ordination space that collectively explained 81% of the variance in the species data. The Monte Carlo test of 400 iterations with randomized data indicated the minimum stress of the solution was lower than would be expected by chance ( $p = 0.02$ ). The final solution had a stress value of 8.79, which was considered a good ordination with no real risk of drawing false inferences (McCune and Grace, 2002). Sample scores (i.e., 16 karsts) were plotted in species space (i.e., 189 species after omitting non-native species) on the two axes that represented the highest proportion of the variance (46 and 26%; Fig. 5a). The ordination for West Malaysia showed that karst groups in the eastern and western regions were distinct (MRPP multiple pairwise comparison tests;  $p < 0.001$ ) from each other based on their species compositions (Fig. 5a). A graphical overlay of only endemic species scores (Fig. 5b) from the West Malaysia ordination did not reveal high affinities of endemic species with any particular group of karsts on either side of the Titiwangsa Mountain Range. For karsts in East Malaysia, sample scores (i.e., 27 karsts) were plotted in species space (i.e., 161 species after omitting non-native species) on the two axes that explained the highest proportion of the variance (31 and 56%; Fig. 5c). The Monte Carlo test indicated the minimum stress of the solution was lower than would be expected by chance ( $p = 0.02$ ). Based on the East Malaysia ordination, karst groups offshore, and in the eastern and western regions were also significantly



**Fig. 5** – Non-metric multi-dimensional scaling joint plot of: (a) 16 karst scores and (b) 189 land snail species scores for West Malaysia; and (c) 27 karst scores and (d) 161 species scores for East Malaysia. '■' and '—', respectively represent karsts in the western and eastern regions of West Malaysia, while '▲', '□' and '◆', respectively represent karsts offshore, and in the western and eastern regions of East Malaysia. The distances between each karst scores reflect their relative dissimilarity in species compositions. To ascertain if certain karst groups warrant urgent conservation attention due to the presence of unusually high number of endemic species, only endemic land snail species scores were reflected here. '●' and '○', respectively represent species endemic to a single karst, or to a group of karsts on the same or adjacent body of limestone bedrock.

different (MRPP multiple pairwise comparison tests;  $p < 0.001$ ) from one another based on their species compositions (Fig. 5c). Similarly, the graphical overlay of only endemic species scores (Fig. 5d) from the East Malaysia ordination did not show high affinities of endemic species with any particular group of karsts.

#### 4. Discussion

As predicted from studies examining the total species–area (Preston, 1948; Diamond, 1969; MacArthur, 1972; Rosenzweig,

1995) and endemic species–area relationships (Hubbell, 2001), karst area appears to be a relatively important determinant of both land snail species richness and endemism (Table 1; Fig. 3). Indeed, area has been shown to be the most important factor determining land snail species richness on other island systems (Welter-Schultes and Williams, 1999), but our results also indicate its positive effect on land snail endemism. For other taxa such as fish and orchids, area predicts both species richness and endemism as well (Ackerman et al., 2007; De Silva et al., 2007). Larger areas are believed to support higher numbers of endemic species (Roos et al., 2004), in part due



to their greater habitat diversity which promotes higher speciation rates (Losos and Schluter, 2000). As such, larger karsts probably contain a higher number and diversity of microhabitats that are conducive for land snail speciation. In future studies, the relative importance of area and isolation on land snail endemism could be investigated further by comparing distribution patterns among small karsts adjacent to large karsts versus small karsts situated far away from large karsts. However, such analyses were beyond the scope of our study due to the limited sample size (i.e., number of karsts and plots).

We also found evidence that the soil type surrounding karsts exerts an influence on land snail endemism. Several studies have documented the impact of soil qualities (e.g., pH and moisture) on land snail abundance, densities and species richness (Graveland et al., 1994; Graveland and van der Wal, 1996; Schilthuisen et al., 2003; Martin and Sommer, 2004), but none have demonstrated potential effects of soil type on land snail endemism. In Malaysia, podzolic soils are generally acidic (Andriesse, 1968); such conditions may have promoted speciation because they would have created formidable barriers to the dispersal of land snails away from karsts, especially among groups that exhibit obligate calcicolity. Our measures of isolation and geological age, however, did not have any measurable effects on the patterns of land snail endemism. Isolation is not always a question of distance (Whittaker, 1998) and so its effect on land snail endemism might not have been detected using these metrics. Although differences in geology may determine the degree to which land snail communities are isolated (van Benthem-Jutting, 1958; Welter-Schultes and Williams, 1999), such factors are difficult to quantify for individual karsts (Chin, 1977) and are beyond the scope of this study. Other factors such as forest cover around karsts are unlikely to affect endemism patterns unless deforestation, which occurred only recently (over the last century) relative to evolutionary time scales (over millions of years), already caused catastrophic extinctions that we were unable to detect.

We have demonstrated quantitatively that groups of karsts in different parts of East and West Malaysia warrant conservation attention as each cluster supports unique malacofaunas (Fig. 5a and c). Other studies have similarly reported the influence of geography on land snail diversity (Nekola, 2003; Kiss et al., 2004). In West Malaysia, the Titiwangsa Mountain range traverses the middle of the region and effectively separates the eastern part from the west (Fig. 1), and these two karst groups contain different land snail communities. NMDS of plant datasets from 15 different karsts on either side of the Titiwangsa Range also revealed a similar pattern (Clement's, unpublished data). Vicariant processes probably began when the once-continuous karst region was bisected by the mountain's intrusion during the Mesozoic era (van Benthem-Jutting, 1958). In the Amazon, phylogenetic relationships of various taxa appear to be shaped by geographical barriers such as ridges as well (Loughheed et al., 1999). In East Malaysia, our results also showed that land snail communities on karsts offshore (Fig. 1) are dissimilar to those on the mainland. Radiation of island land

snails can be attributed to their limited dispersal abilities over oceanic barriers and relatively low natural immigration and colonization rates (Cowie, 1995; Welter-Schultes and Williams, 1999). On mainland East Malaysia, karsts situated in the eastern and western parts also contain distinct malacofaunas that were possibly influenced by the vicariant effects of major mountain ranges (i.e., Crocker, Maitland and Brassey; Fig. 1). Several karsts in each of the identical three areas of East Malaysia (i.e., offshore, east and west) have also been regarded as centres of plant diversity (Davis et al., 1995).

## 5. Conclusions and conservation remarks

Based on our results, conservation planners in Malaysia should focus on preserving relatively larger outcrops (i.e., >1 km<sup>2</sup>) surrounded by yellow-grey podzolic soils because they potentially contain higher numbers of endemic land snail species. In addition, larger karsts within groups of karsts bisected by geographical barriers such as mountains should warrant even greater conservation attention. For example in West Malaysia, larger karsts on both sides of the Titiwangsa Mountain Range should be preserved to maximise protection of endemic malacofaunas. While fewer and larger reserves have proven to be more feasible from biogeographical, financial and political perspectives (Whittaker, 1998), future studies should investigate if fewer and larger karst reserves within a particular geographic region will preserve more or less endemic species than many smaller ones of the same total area. In addition, the feasibility of conserving extensive karsts more than 100 km<sup>2</sup> should be re-evaluated because land snail endemism in extremely large areas may approach asymptotic levels (e.g., if species-area curves follow logistic models; He and Legendre, 2003). Nevertheless, we now have the first set of recommendations developed within a scientific framework to aid karst reserve selection in Malaysia. By examining larger datasets of snails and other karst-endemic taxa (e.g., plants, arthropods), and using additional biogeographical factors obtained from karsts in other countries, these guidelines may be refined further for utilization in karst conservation planning throughout the rest of Southeast Asia.

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**Appendix A. Summary information of 16 karsts sampled in West Malaysia**

No.	Karst name	Region	Geographical coordinates	Category	Area (km <sup>2</sup> )	Soil type	Geological age	Isolation – straight-line distance to nearest karst (km)	Isolation – no. of karsts within 10 km
1	Baling	■	5°40'N 100°53'E	LI	5.20	2	3	57.7	0
2	Pondok	■	4°48'N 100°52'E	LI	4.16	2	2	12.42	0
3	KE 001	■	4°51'N 101°07'E	SI	0.02	3	3	0.45	5
4	Datok	■	4°36'N 101°09'E	LN	7.53	2	3	1.34	33
5	Tasek	■	4°38'N 101°05'E	SN	0.06	2	3	3.91	24
6	Bercham	■	4°38'N 101°08'E	SN	0.06	2	3	1.24	24
7	Rapat	■	4°33'N 101°07'E	LN	5.01	2	3	1.69	37
8	Takun	■	3°18'N 101°38'E	SI	0.06	2	2	8.66	1
9	Cintamanis	—	3°26'N 102°00'E	SI	0.10	2	3	43.56	0
10	Senyum	—	3°42'N 102°26'E	LI	2.31	1	1	18.80	0
11	Gelanggi	—	3°53'N 102°28'E	LI	1.21	1	1	18.80	0
12	Sai	—	4°12'N 101°59'E	SI	0.06	3	1	3.69	1
13	Panjang	—	4°48'N 101°59'E	LN	17.51	1	1	2.92	42
14	Ciku 7	—	5°04'N 102°08'E	SN	0.06	1	1	5.02	15
15	Hill 001	—	5°00'N 101°58'E	LN	1.65	3	1	7.81	45
16	Ikan	—	5°21'N 102°01'E	SN	0.03	1	1	3.29	22

‘■’ and ‘—’ represent karsts in the western and eastern site of the Titiwangsa Mountain Range respectively. Codes for category are as follows: codes for soil type are as follows: yellow grey podzols – 1; red–yellow podzols – 2; and others (i.e., lithosols on limestone crags, alluvial and gley soils, reddish brown lateritic soils) – 3. Codes for geological age are as follows: Permian and Lower Triassic – 1, Carboniferous – 2; and Palaeozoic – 3.

**Appendix B. Summary information of 27 karsts sampled in East Malaysia**

No.	Karst name	Region	Geographical coordinates
17	Temurung	□	4°43'N 116°24'E
18	Tinahas	□	4°38'N 116°37'E
19	Punggul	□	4°38'N 116°37'E
20	Pungiton	□	4°42'N 116°36'E
21	Sinobang	□	4°48'N 116°38'E
22	Sanaron	□	4°42'N 116°36'E
23	Lian	□	5°29'N 116°10'E
24	Danum	◆	4°48'N 117°48'E
25	Tomanggong Besar	◆	5°30'N 118°18'E
26	Tabin	◆	5°18'N 118°44'E
27	Tomanggong Kecil	◆	5°30'N 118°17'E
28	Tomanggong 2	◆	5°31'N 118°18'E
29	Sungai Resang	◆	5°31'N 118°21'E
30	Batu Tai	◆	5°32'N 118°10'E
31	Pangi	◆	5°31'N 118°18'E
32	Mawas	◆	5°27'N 118°08'E
33	Materis	◆	5°31'N 118°01'E
34	Keruak	◆	5°31'N 118°17'E
35	Kampung	◆	5°30'N 118°17'E
36	Gomantong	◆	5°31'N 118°04'E
37	Bod Tai	◆	5°31'N 118°13'E
38	Baturong	◆	4°41'N 118°00'E
39	Mantanani Besar	▲	6°42'N 116°20'E
>40	Mantanani Kecil	▲	6°42'N 116°20'E
>41	Balambangan (Bt. Sireh)	▲	7°12'N 116°51'E
>42	Balambangan (Kok Simpul)	▲	7°13'N 116°53'E
>43	Banggi (Karakit)	▲	7°06'N 117°05'E

‘▲’, ‘□’ and ‘◆’ represent karsts offshore, and in the western and eastern regions, respectively.

### Appendix C. List of 198 mollusc species sampled from 16 karsts in West Malaysia

Family	Genus	Species
Ariophantidae	<i>Achatina</i>	<i>fulica</i>
Ariophantidae	<i>Dyakia</i>	<i>salangana</i>
Ariophantidae	<i>Hemiplecta</i>	<i>cymatium</i>
Ariophantidae	<i>Hemiplecta</i>	<i>humphreysiana</i>
Ariophantidae	<i>Hemiplecta</i>	<i>gemina</i>
Ariophantidae	<i>Macrochlamys</i>	<i>resplendens</i>
Ariophantidae	<i>Macrochlamys</i>	<i>tersa</i>
Ariophantidae	<i>Microcystina</i>	<i>striatula</i>
Ariophantidae	<i>Microcystina</i>	sp.1 to 7
Ariophantidae	<i>Pseudoplecta</i>	<i>bijuga</i>
Ariophantidae	<i>Quantula</i>	<i>striata</i>
Assimineidae	<i>Cyclotropis?</i>	sp.1
Camaenidae	<i>Amphidromus</i>	<i>atricollosus</i>
Camaenidae	<i>Chloritis</i>	<i>penangensis</i>
Camaenidae	<i>Chloritis</i>	sp.1 to 2
Camaenidae	<i>Landouria</i>	sp.1
Camaenidae	<i>Trachia</i>	<i>gabata</i>
Charopidae	<i>Charopa</i>	sp.1 to 3
Clausiliidae	<i>Phaedusa</i>	<i>filicostata</i>
Cyclophoridae	<i>Alycaeus</i>	<i>balingensis</i>
Cyclophoridae	<i>Alycaeus</i>	<i>gibbosulus</i>
Cyclophoridae	<i>Alycaeus</i>	<i>kelantanensis</i>
Cyclophoridae	<i>Alycaeus</i>	<i>liratulus</i>
Cyclophoridae	<i>Alycaeus</i>	<i>perakensis</i>
Cyclophoridae	<i>Alycaeus</i>	<i>perakensis</i> var. <i>minor</i>
Cyclophoridae	<i>Alycaeus</i>	<i>thieroti</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>diplochilus</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>jousseauae</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>microconus</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>microdiscus</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>mixtus</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>oligopleuris</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>parvulus</i>
Cyclophoridae	<i>Chamalycaeus</i>	sp.1 to 6
Cyclophoridae	<i>Cyclophorus</i>	<i>malayanus</i>
Cyclophoridae	<i>Cyclophorus</i>	<i>semisulcatus</i>
Cyclophoridae	<i>Cyclophorus</i>	<i>zebrinus</i>
Cyclophoridae	<i>Cyclophorus</i>	<i>perdix</i>
Cyclophoridae	<i>Cyclotus</i>	<i>penangensis</i>
Cyclophoridae	<i>Cyclotus</i>	<i>setosus</i>
Cyclophoridae	<i>Cyclotus</i>	<i>solutus</i>
Cyclophoridae	<i>Cyclotus</i>	sp.1 to 3
Cyclophoridae	<i>Geotrochus</i>	sp.1
Cyclophoridae	<i>Lagochilus</i>	<i>townsendi</i>
Cyclophoridae	<i>Leptopoma</i>	<i>perlucidum</i>
Cyclophoridae	<i>Platyrhapha</i>	<i>lowi</i>
Cyclophoridae	<i>Rhiostoma</i>	<i>asiphon</i>
Cyclophoridae	<i>Rhiostoma</i>	<i>jousseauae</i>
Cyclophoridae	<i>Rhiostoma</i>	<i>speleotes</i>
Diplommatinidae	<i>Diplommatina</i>	<i>canaliculata</i>
Diplommatinidae	<i>Diplommatina</i>	<i>crosseana crosseana</i>
Diplommatinidae	<i>Diplommatina</i>	<i>demorgani</i>
Diplommatinidae	<i>Diplommatina</i>	<i>diminuta</i>
Diplommatinidae	<i>Diplommatina</i>	<i>laidlawi</i>
Diplommatinidae	<i>Diplommatina</i>	<i>maduana</i>

### Appendix C (continued)

Family	Genus	Species
Diplommatinidae	<i>Diplommatina</i>	<i>nelvilli</i>
Diplommatinidae	<i>Diplommatina</i>	<i>pentaechma</i>
Diplommatinidae	<i>Diplommatina</i>	<i>sinistral</i>
Diplommatinidae	<i>Diplommatina</i>	sp.1
Diplommatinidae	<i>Diplommatina</i>	<i>streptophora</i>
Diplommatinidae	<i>Diplommatina</i>	<i>superba</i>
Diplommatinidae	<i>Diplommatina</i>	<i>superba brevior</i>
Diplommatinidae	<i>Diplommatina</i>	<i>tweediei</i>
Diplommatinidae	<i>Diplommatina</i>	<i>ventriculus</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>tenuicostatum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>coronatum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>crassipupa</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>hypermicrum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>megalomphalum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>michaelis</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>micridium</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>paranomon</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>paulucciae</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>plagiostomum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>retrovertens</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>sinyumensis</i>
Diplommatinidae	<i>Opisthostoma</i>	sp.1 to 17
Diplommatinidae	<i>Opisthostoma</i>	<i>umbilicatum</i>
Endodontidae	<i>Philalanka</i>	<i>kusana</i>
Endodontidae	<i>Philalanka</i>	sp.1 to 3
Euconulidae	<i>Coneuplecta</i>	<i>microconus</i>
Euconulidae	<i>Coneuplecta</i>	<i>olivacea</i>
Euconulidae	<i>Liardetia</i>	<i>angigyra</i>
Euconulidae	<i>Liardetia</i>	<i>doliolum</i>
Euconulidae	<i>Liardetia</i>	sp.1 to 5
Euconulidae	<i>Queridomus</i>	<i>fimbrius</i>
Euconulidae	<i>Queridomus</i>	sp.1
Ferussaciidae	<i>Ceciloides</i>	<i>caledonica</i>
Helicarionidae	<i>Geotrochus</i>	sp.1
Hydrocenidae	<i>Georissa</i>	<i>monterosatiana</i>
Hydrocenidae	<i>Georissa</i>	<i>semisculpta</i>
Hydrocenidae	<i>Acmella</i>	sp.1 to 2
Hydrocenidae	<i>Hydrocena</i>	sp.1 to 3
Pomatiopsidae	<i>Tricula?</i>	sp.1 to 6
Pupinidae	<i>Pupina</i>	<i>arula</i>
Pupinidae	<i>Pupina</i>	<i>excise</i>
Pupinidae	<i>Pupina</i>	sp.1 to 2
Streptaxidae	<i>Discartemon</i>	<i>collingei</i>
Streptaxidae	<i>Discartemon</i>	<i>leptoglyphus</i>
Streptaxidae	<i>Discartemon</i>	<i>platymorphus</i>
Streptaxidae	<i>Discartemon</i>	<i>plussensis</i>
Streptaxidae	<i>Gullela</i>	<i>bicolor</i>
Streptaxidae	<i>Haplotychius</i>	<i>atopospria</i>
Streptaxidae	<i>Haplotychius</i>	<i>balingensis</i>
Streptaxidae	<i>Haplotychius</i>	<i>eutropha</i>
Streptaxidae	<i>Sinoennea</i>	<i>apicata</i>
Streptaxidae	<i>Sinoennea</i>	<i>attenuate</i>
Streptaxidae	<i>Sinoennea</i>	<i>baculum</i>
Streptaxidae	<i>Sinoennea</i>	<i>butleri</i>
Streptaxidae	<i>Sinoennea</i>	<i>callizonus</i>
Streptaxidae	<i>Sinoennea</i>	<i>chintamanensis</i>

**Appendix C (continued)**

Family	Genus	Species
Streptaxidae	<i>Sinoennea</i>	<i>crumenilla</i>
Streptaxidae	<i>Sinoennea</i>	<i>hungerfordiana</i>
Streptaxidae	<i>Sinoennea</i>	<i>lepida</i>
Streptaxidae	<i>Sinoennea</i>	<i>perakensis</i>
Streptaxidae	<i>Sinoennea</i>	sp.1 to 3
Streptaxidae	<i>Sinoennea</i>	<i>subcylindrica</i>
Streptaxidae	<i>Sinoennea</i>	<i>tiarella</i>
Streptaxidae	<i>Sinoennea</i>	<i>tweediei</i>
Subulinidae	<i>Allopeas</i>	<i>clavulinum</i>
Subulinidae	<i>Allopeas</i>	<i>gracile</i>
Subulinidae	<i>Prosopeas</i>	<i>tchehelense</i>
Subulinidae	<i>Subulina</i>	<i>octana</i>
Trochomorphidae	<i>Videna</i>	sp.1 to 2
Trochomorphidae	<i>Vitrinopsis</i>	sp.1
Valloniidae	<i>Pupisoma</i>	sp.1 to 3
Vertiginidae	<i>Boysidia</i>	sp.1
Vertiginidae	<i>Gyliotrachela</i>	<i>depressura</i>
Vertiginidae	<i>Gyliotrachela</i>	<i>hungerfordiana</i>
Vertiginidae	<i>Gyliotrachela</i>	sp.1 to 7
Vertiginidae	<i>Hypselostoma</i>	<i>perigra</i>
Vertiginidae	<i>Hypselostoma</i>	sp.1 to 3
Vertiginidae	<i>Hypselostoma</i>	<i>terae</i>
Vertiginidae	<i>Paraboydsidia</i>	<i>serpa</i>
Vertiginidae	<i>Paraboydsidia</i>	sp.1 to 3

**Appendix D. List of 173 mollusc species sampled from 27 karsts in East Malaysia**

Family	Genus	Species
Achatinellidae	<i>Achatinellid</i>	sp.1
Achatinellidae	<i>Elasmias</i>	<i>globulosum</i>
Achatinidae	<i>Achatina</i>	<i>fulica</i>
Ariophantidae	<i>Dyakia</i>	<i>hugonis</i>
Ariophantidae	<i>Everettia</i>	sp.1 to 4
Ariophantidae	<i>Hemiplecta</i>	<i>humphreysiana</i>
Ariophantidae	<i>Kalamantania</i>	<i>whiteheadi</i>
Ariophantidae	<i>Macrochlamys</i>	<i>indica</i>
Ariophantidae	<i>Macrochlamys</i>	<i>tersa</i>
Ariophantidae	<i>Microcystina</i>	<i>callifera</i>
Ariophantidae	<i>Microcystina</i>	<i>lissa</i>
Ariophantidae	<i>Microcystina</i>	<i>microrhynchus</i>
Ariophantidae	<i>Microcystina</i>	<i>muscorum</i>
Ariophantidae	<i>Microcystina</i>	<i>physotrochus</i>
Ariophantidae	<i>Microcystina</i>	<i>sinica</i>
Ariophantidae	<i>Microcystina</i>	<i>striatula</i>
Ariophantidae	<i>Parmarion</i>	sp.1
Ariophantidae	<i>Vitrinula</i>	<i>descrepignyi</i>
Assimineidae	<i>Acmella</i>	<i>cyrtoglyphe</i>
Assimineidae	<i>Acmella</i>	<i>nana</i>
Assimineidae	<i>Acmella</i>	<i>ovoidea</i>
Assimineidae	<i>Acmella</i>	<i>polita</i>
Assimineidae	<i>Acmella</i>	<i>striata</i>
Assimineidae	<i>Acmella</i>	<i>umbilicata</i>
Bradybaena	<i>Bradybaena</i>	<i>similaris</i>

**Appendix D (continued)**

Family	Genus	Species
Bradybaena	<i>Cochlostyla</i>	<i>trillii</i>
Camaenidae	<i>Amphidromus</i>	<i>adamsi</i>
Camaenidae	<i>Amphidromus</i>	<i>martensi</i>
Camaenidae	<i>Chloritis</i>	<i>kinibalensis</i>
Camaenidae	<i>Chloritis</i>	<i>plena</i>
Camaenidae	<i>Chloritis</i>	<i>sibutuensis</i>
Camaenidae	<i>Chloritis</i>	sp.1
Camaenidae	<i>Ganesella</i>	<i>acris</i>
Camaenidae	<i>Trachia</i>	<i>pubica</i>
Charopidae	<i>Beilania</i>	<i>philippinensis</i>
Charopidae	<i>Charopa</i>	<i>argos</i>
Charopidae	<i>Charopa</i>	<i>infrastrata</i>
Charopidae	<i>Charopa</i>	<i>jugalis</i>
Charopidae	<i>Charopa</i>	<i>lissobasis</i>
Charopidae	<i>Discocharopa</i>	<i>aperta</i>
Charopidae	<i>Pilsbrycharopa</i>	<i>kobelti</i>
Clausiliidae	<i>Phaedusa</i>	<i>filicostata filialis</i>
Cyclophoridae	<i>Alycaeus</i>	<i>jagori</i>
Cyclophoridae	<i>Chamalycaeus</i>	<i>everetti</i>
Cyclophoridae	<i>Chamalycaeus</i>	sp.1
Cyclophoridae	<i>Chamalycaeus</i>	<i>specus</i>
Cyclophoridae	<i>Cyclophorus</i>	<i>kinabaluensis</i>
Cyclophoridae	<i>Ditropopsis</i>	<i>constricta</i>
Cyclophoridae	<i>Japonia</i>	<i>anceps</i>
Cyclophoridae	<i>Japonia</i>	<i>balabacensis</i>
Cyclophoridae	<i>Japonia</i>	<i>compressa</i>
Cyclophoridae	<i>Japonia</i>	<i>janus</i>
Cyclophoridae	<i>Japonia</i>	<i>jucunda</i>
Cyclophoridae	<i>Japonia</i>	<i>keppeli</i>
Cyclophoridae	<i>Japonia</i>	<i>smithi</i>
Cyclophoridae	<i>Japonia</i>	<i>kinabaluensis</i>
Cyclophoridae	<i>Leptopoma</i>	<i>pellucidum</i>
Cyclophoridae	<i>Leptopoma</i>	<i>sericatum</i>
Cyclophoridae	<i>Leptopoma</i>	<i>undatum</i>
Cyclophoridae	<i>Opisthoporus</i>	<i>birostris</i>
Cyclophoridae	<i>Opisthoporus</i>	<i>iris</i>
Cyclophoridae	<i>Platyrhaphis</i>	<i>bongaoensis</i>
Cyclophoridae	<i>Platyrhaphis</i>	<i>linitus</i>
Cyclophoridae	<i>Pterocyclos</i>	<i>tenuilabius</i>
Cyclophoridae	<i>Pterocyclos</i>	<i>trusanensis</i>
Diplommatinidae	<i>Arinia</i>	<i>biplicata</i>
Diplommatinidae	<i>Arinia</i>	<i>boreoborneensis</i>
Diplommatinidae	<i>Arinia</i>	<i>borneensis</i>
Diplommatinidae	<i>Arinia</i>	<i>brevispira brevispira</i>
Diplommatinidae	<i>Arinia</i>	<i>brevispira orientalis</i>
Diplommatinidae	<i>Arinia</i>	<i>clausa</i>
Diplommatinidae	<i>Arinia</i>	<i>cylindrica cylindrica</i>
Diplommatinidae	<i>Arinia</i>	<i>paricostata</i>
Diplommatinidae	<i>Arinia</i>	<i>pertusa</i>
Diplommatinidae	<i>Arinia</i>	<i>simplex</i>
Diplommatinidae	<i>Arinia</i>	sp.1
Diplommatinidae	<i>Arinia</i>	<i>stenotrochus pachystoma</i>
Diplommatinidae	<i>Arinia</i>	<i>stenotrochus stenotrochus</i>
Diplommatinidae	<i>Arinia</i>	<i>turgida</i>
Diplommatinidae	<i>Diplommatina</i>	<i>antheae</i>

(continued on next page)

**Appendix D. (continued)**

Family	Genus	Species
Diplommatinidae	<i>Diplommatina</i>	<i>asynaimos</i>
Diplommatinidae	<i>Diplommatina</i>	<i>calvula</i>
Diplommatinidae	<i>Diplommatina</i>	<i>centralis</i>
Diplommatinidae	<i>Diplommatina</i>	<i>cyrtorhitis</i>
Diplommatinidae	<i>Diplommatina</i>	<i>gomantongensis</i>
Diplommatinidae	<i>Diplommatina</i>	<i>isseli</i>
Diplommatinidae	<i>Diplommatina</i>	<i>oedogaster</i>
Diplommatinidae	<i>Diplommatina</i>	<i>recta</i>
Diplommatinidae	<i>Diplommatina</i>	<i>rubicunda</i>
Diplommatinidae	<i>Diplommatina</i>	<i>soror</i>
Diplommatinidae	<i>Diplommatina</i>	<i>sykesi</i>
Diplommatinidae	<i>Diplommatina</i>	<i>whiteheadi</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>brevituba</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>concinnum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>cyrtopleuron</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>dormani</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>fraternum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>hailei</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>javanicum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>jucundum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>mirabile</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>obliquedentatum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>perspectivum</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>simplex</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>sp.1</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>telestoma</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>brachyacrum lambii</i>
Diplommatinidae	<i>Opisthostoma</i>	<i>lissopleuron</i>
Endodontidae	<i>Philalanka</i>	<i>kusana</i>
Endodontidae	<i>Philalanka</i>	<i>moluensis</i>
Endodontidae	<i>Philalanka</i>	<i>obscura</i>
Endodontidae	<i>Stenopylis</i>	<i>coarctata</i>
Euconulidae	<i>Kaliella</i>	<i>accepta</i>
Euconulidae	<i>Kaliella</i>	<i>angulata</i>
Euconulidae	<i>Kaliella</i>	<i>barrakporensis</i>
Euconulidae	<i>Kaliella</i>	<i>calculosa</i>
Euconulidae	<i>Kaliella</i>	<i>dendrophila</i>
Euconulidae	<i>Kaliella</i>	<i>doliolum</i>
Euconulidae	<i>Kaliella</i>	<i>microconus</i>
Euconulidae	<i>Kaliella</i>	<i>punctata</i>
Euconulidae	<i>Kaliella</i>	<i>scandens</i>
Euconulidae	<i>Queridomus</i>	<i>conulus</i>
Euconulidae	<i>Rahula</i>	<i>sp.1</i>
Ferussaciidae	<i>Ceciloides</i>	<i>caledonica</i>
Helicarionidae	<i>Atopos</i>	<i>sp.1</i>
Helicinidae	<i>Aphanoconia</i>	<i>usukanensis</i>
Helicinidae	<i>Geophorus</i>	<i>agglutinans</i>
Helicinidae	<i>Sulfurina</i>	<i>euchromia</i>
Helicinidae	<i>Sulfurina</i>	<i>martensi</i>
Hydrocenidae	<i>Georissa</i>	<i>bangueyensis</i>
Hydrocenidae	<i>Georissa</i>	<i>borneensis</i>
Hydrocenidae	<i>Georissa</i>	<i>filiassulae</i>
Hydrocenidae	<i>Georissa</i>	<i>gomantongensis</i>
Hydrocenidae	<i>Georissa</i>	<i>saulae</i>
Hydrocenidae	<i>Georissa</i>	<i>scalinelia</i>
Hydrocenidae	<i>Georissa</i>	<i>similis</i>

**Appendix D (continued)**

Family	Genus	Species
Hydrocenidae	<i>Georissa</i>	<i>sp.1 to 3</i>
Hydrocenidae	<i>Georissa</i>	<i>williamsi</i>
Pupinidae	<i>Pupina</i>	<i>hosei</i>
Rhytididae	<i>Macrocycloides</i>	<i>sp.1</i>
Streptaxidae	<i>Diaphera</i>	<i>wilfordii ectyphus</i>
Streptaxidae	<i>Diaphera</i>	<i>wilfordii wilfordii</i>
Streptaxidae	<i>Huttonella</i>	<i>bicolor</i>
Subulinidae	<i>Allopeas</i>	<i>clavulinum</i>
Subulinidae	<i>Allopeas</i>	<i>gracile</i>
Subulinidae	<i>Borneopeas</i>	<i>sp.1</i>
Subulinidae	<i>Opeas</i>	<i>hannense</i>
Subulinidae	<i>Paropeas</i>	<i>achatinaceum</i>
Subulinidae	<i>Subulina</i>	<i>octona</i>
Trochomorphidae	<i>Bertia</i>	<i>brookei</i>
Trochomorphidae	<i>Geotrochus</i>	<i>bongaoensis</i>
Trochomorphidae	<i>Geotrochus</i>	<i>labuanensis</i>
Trochomorphidae	<i>Geotrochus</i>	<i>meristotrochus</i>
Trochomorphidae	<i>Geotrochus</i>	<i>whiteheadi</i>
Trochomorphidae	<i>Videna</i>	<i>bicolor</i>
Trochomorphidae	<i>Videna</i>	<i>froggatti</i>
Trochomorphidae	<i>Videna</i>	<i>metcalfei</i>
Trochomorphidae	<i>Videna</i>	<i>repanda</i>
Trochomorphidae	<i>Videna</i>	<i>timorensis</i>
Valloniidae	<i>Pupisoma</i>	<i>pulvisculum</i>
Vertiginidae	<i>Boysidia</i>	<i>salpinx</i>
Vertiginidae	<i>Gastrocopta</i>	<i>avanica</i>
Vertiginidae	<i>Gastrocopta</i>	<i>pediculus</i>
Vertiginidae	<i>Gastrocopta</i>	<i>recondita</i>
Vertiginidae	<i>Nesopupa</i>	<i>malayana</i>
Vertiginidae	<i>Nesopupa</i>	<i>moreleti</i>
Vertiginidae	<i>Ptychopatula</i>	<i>orcella</i>
Vertiginidae	<i>Ptychopatula</i>	<i>orcula</i>

## REFERENCES

- Ackerman, J.D., Trejo-Torres, J.C., Crespo-Chuy, Y., 2007. Orchids of the West Indies: predictability of diversity and endemism. *Journal of Biogeography* 34, 779–786.
- Andriesse, J.P., 1968. A study of the environment and characteristics of tropical podzols in Sarawak (East Malaysia). *Geoderma* 2, 201–227.
- Born, J., Linder, H.P., Desrnet, P., 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34, 147–162.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Inference: A Practical Information – Theoretic Approach*. Springer, New York.
- Burnham, K.P., Anderson, D.R., 2004. Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33, 261–304.
- Cameron, R.A.D., Pokryszko, B.M., 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology* 38, 529–547.
- Chin, S.C., 1977. The limestone hill flora of Malaya: part 1. *Gardens' Bulletin Singapore* 30, 165–220.
- Clements, R., Sodhi, N.S., Schilthuizen, M., Ng, P.K.L., 2006. Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *Bioscience* 56, 733–742.



- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B* 345, 101–118.
- Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85, 2717–2727.
- Cowie, R.H., 1995. Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution* 49, 1191–1202.
- Crawley, M.J., 2005. *Statistics: An Introduction Using R*. John Wiley and Sons Ltd., West Sussex.
- Crowther, J., 1982. Ecological observations in a tropical karst terrain, West Malaysia. I. Variations in topography, soils and vegetation. *Journal of Biogeography* 9, 65–78.
- Culver, D.C., Master, L.L., Christman, M.C., Hobbs, H.H., 2000. Obligate cave fauna of the 48 contiguous United States. *Conservation Biology* 14, 386–401.
- Daily, G.C., Ceballos, G., Pacheco, J., Suszán, G., Sánchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17, 1814–1826.
- Davis, S.D., Heywood, V., Hamilton, A., 1995. Centres of plant diversity: a guide and strategy for their conservation. *Asia, Australasia and the Pacific*, vol. 2. Springer, Berlin.
- Davidson, G.W.H., 1991. Terrestrial molluscs of Peninsular Malaysia. In: Kiew, R. (Ed.), *The State of Nature Conservation in Malaysia*. Malayan Nature Society, Kuala Lumpur, pp. 101–104.
- De Silva, S.S., Abery, N.W., Nguyen, T.T.T., 2007. Endemic freshwater finfish of Asia: distribution and conservation status. *Diversity and Distributions* 13, 172–184.
- Dennis, C., Aldhous, P., 2004. Biodiversity: a tragedy with many players. *Nature* 430, 396–398.
- Diamond, J.M., 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Science of the United States of America* 64, 57–63.
- Emberton, K.C., Pearce, T.A., Randalana, R., 1999. Molluscan diversity in the unconserved Vohimana and the conserved Anosy mountain chains, southeast Madagascar. *Biological Conservation* 89, 183–188.
- Framji, K.K., Garg, B.C., Luthra, S.D.L., 1981. *Irrigation and Drainage in the World – A Global Review*. International Commission on Irrigation and Drainage, New Delhi.
- Gibert, J., Deharveng, L., 2002. Subterranean ecosystems: a truncated functional biodiversity. *Bioscience* 52, 473–481.
- Graveland, J., van der Wal, R., 1996. Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia* 105, 351–360.
- Graveland, J., van der Wal, R., Van Balen, J.H., van Noordwijk, A.J., 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature* 368, 446–448.
- He, F., Legendre, P., 2003. On species–area relations. *American Naturalist* 148, 719–737.
- Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, New Jersey.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187–211.
- Kiew, R., 1991. The limestone flora. In: Kiew, R. (Ed.), *The State of Nature Conservation in Malaysia*. Malayan Nature Society, Kuala Lumpur, pp. 42–50.
- Kiew, R., 2001. Towards a limestone flora of Sabah. *Malayan Nature Journal* 55, 77–93.
- Kiss, L., Magnin, F., Torre, F., 2004. The role of landscape history and persistent biogeographical patterns in shaping the responses of Mediterranean land snail communities to recent fire disturbances. *Journal of Biogeography* 31, 145–157.
- Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 1–27.
- Lim, S.P., Kiew, R., 1997. Gazetteer of limestone localities in Sabah, Borneo. *Gardens' Bulletin Singapore* 49, 111–118.
- Link, W.A., Barker, R.J., 2006. Model weights and the foundations of multimodel inference. *Ecology* 87, 2626–2635.
- Losos, J.B., Schluter, D., 2000. Analysis of an evolutionary species–area relationship. *Nature* 408, 847–849.
- Lougheed, S.C., Gascon, C., Jones, D.A., Bogart, J.P., Boag, P.T., 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). *Proceedings of the Royal Society of London Series B* 266, 1829–1835.
- Lourie, S.A., Vincent, A.C.J., 2004. Using biogeography to help set priorities in marine conservation. *Conservation Biology* 18, 1004–1020.
- Maassen, W.J.M., 2001. *A Preliminary Checklist of the Non-marine Molluscs of West-Malaysia*. Nationaal Natuurhistorisch Museum, Amsterdam.
- MacArthur, R.H., 1972. *Geographical Ecology*. Princeton University Press, New Jersey.
- MacKinnon, K., Hatta, G., Halim, H., Mangalik, A., 1996. The ecology of Indonesia series. *The Ecology of Kalimantan*, vol. III. Periplus Editions, Hong Kong.
- Martin, K., Sommer, M., 2004. Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. *Pedobiologia* 48, 193–203.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software, Oregon.
- McMillan, M.A., Larson, D.W., 2002. Effects of rock climbing on the vegetation of the Niagara Escarpment in southern Ontario, Canada. *Conservation Biology* 16, 389–398.
- McMillan, M.A., Nekola, J.C., Larson, D.W., 2003. Effects of rock climbing on the land snail community of the Niagara Escarpment in Southern Ontario, Canada. *Conservation Biology* 17, 616–621.
- Mielke Jr., P.W., Berry, K.J., 2001. *Permutation Methods: A Distance Function Approach*. Springer Series in Statistics, New York.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nekola, J.C., 2003. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Diversity and Distributions* 9, 55–71.
- Paton, J.R., 1961. A brief account of the geology of the limestone hills of Malaya. *Bulletin of the Raffles Museum* 26, 66–75.
- Preston, F.W., 1948. The commonness, and rarity, of species. *Ecology* 29, 254–283.
- Price, L., 2001. *Caves and karst of peninsular Malaysia*. Gua Publications, Kuala Lumpur.
- Roos, M.C., Kefler, P.J.A., Gradstein, S.R., Baas, P., 2004. Species diversity and endemism of five major Malesian islands: diversity–area relationships. *Journal of Biogeography* 31, 1893–1908.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Schilthuizen, M., 2004. Land snail conservation in Borneo: limestone outcrops act as arks. *Journal of Conchology Special Publication* 3, 149–154.
- Schilthuizen, M., Teravainen, M.I.F., Faezamaltha, N., Tawith, K., Ibrahim, H., Chea, S.M., Chuan, C.P., Daim, L.J., Jubaidi, A., Madjapuni, A., et al, 2002. Microsnails at micro-scales in Borneo: distributions of Prosobranchia versus Pulmonata. *Journal of Molluscan Studies* 68, 255–258.
- Schilthuizen, M., Chai, H.-N., Kimsin, T.E., Vermeulen, J.J., 2003. Abundance and diversity of land-snails

- (Mollusca: Gastropoda) on limestone hills in Borneo. *Raffles Bulletin of Zoology* 51, 35–42.
- Schilthuizen, M., Liew, T.-S., Bin Elahan, B., Lackman-Ancrenaz, I., 2005. Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. *Conservation Biology* 19, 949–954.
- Soberón, J.M., 1992. Island biogeography and conservation practice. *Conservation Biology* 6, 161.
- Soberón, J.M., Llorente, J.B., Onate, L., 2000. The use of specimen-label databases for conservation purposes: an example using Mexican Papilionid and Pierid butterflies. *Biodiversity and Conservation* 9, 1441–1466.
- Solem, A., 1984. A world model for land snail diversity. In: Solem, A., Bruggen, A.C.V. (Eds.), *Biogeographical Studies on Non-marine Mollusca*. Backhuys Publishers, Leiden, pp. 6–22.
- Stibig, H.-J., Malingreau, J.-P., 2003. Forest cover of insular Southeast Asia mapped from recent satellite images of coarse spatial resolution. *Ambio* 32, 469–475.
- Symington, C.F., 1943. *Foresters' Manual of Dipterocarps*. Penerbit Universiti Malaya, Kuala Lumpur.
- Tattersfield, P., 1996. Patterns of diversity and endemism in East African land snails, and the implications for conservation. *Journal of Conchology Special Publication* 2, 77–86.
- Tweedie, M., 1961. On certain Mollusca of the Malayan limestone hills. *Bulletin of the Raffles Museum* 26, 49–65.
- van Benthem-Jutting, W.S.S., 1950. The Malayan species of *Boysidia*, *Paraboysidia*, *Hypselostoma* and *Gyliotrachela* (Gastropoda, Pulmonata, Vertiginidae) with a catalogue of all the species hitherto described. *Bulletin of the Raffles Museum* 21, 5–47.
- van Benthem-Jutting, W.S.S., 1954a. The Malayan species of *Opisthostoma* (Gastropoda, Prosobranchia, Cyclophoridae), with a catalogue of all the species hitherto described. *Bulletin of the Raffles Museum* 24, 5–62.
- van Benthem-Jutting, W.S.S., 1954b. The Malayan Streptaxidae of the genera *Discartemon* and *Oophana*. *Bulletin of the Raffles Museum* 25, 71–106.
- van Benthem-Jutting, W.S.S., 1958. Non-marine mollusca of the limestone hills in Malaya. In: Purchon, R.O. (Ed.), *Proceedings of the Centenary and Bicentenary Congress of Biology*. University of Malaya Press, Singapore, pp. 63–68.
- van Benthem-Jutting, W.S.S., 1961a. Additional new species and new localities of the family Vertiginidae and the genera *Oophana* and *Opisthostoma* from Malaya. *Bulletin of the Raffles Museum* 26, 34–48.
- van Benthem-Jutting, W.S.S., 1961b. The Malayan Streptaxidae Genera *Huttonella* and *Sinoennea*. *Bulletin of the Raffles Museum* 26, 5–33.
- Vermeulen, J.J., 1994. Notes on the non-marine molluscs of the island of Borneo 6 the genus *Opisthostoma* (Gastropoda: Prosobranchia: Diplommatinidae), part 2. *Basteria* 58, 75–191.
- Vermeulen, J.J., Whitten, T., 1998. *Fauna Malesiana: Guide to the Land Snails of Bali*. Backhuys, Leiden.
- Vermeulen, J., Whitten, T., 1999. Biodiversity and Cultural Property in the Management of Limestone Resources – Lessons from East Asia. World Bank, Washington, DC.
- Welter-Schultes, F.W., Williams, M.R., 1999. History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography* 26, 239–249.
- Whittaker, R.J., 1998. *Island Biogeography: Ecology, Evolution and Conservation*. Oxford University Press, New York.