LAND SNAIL DIVERSITY IN A SQUARE KILOMETRE OF TROPICAL RAINFOREST IN SABAH, MALAYSIAN BORNEO

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ABSTRACT

We surveyed the land snail fauna in a single square kilometre of undisturbed tropical rainforest on acidic soil in the Danum Valley Conservation Area, Sabah, Malaysian Borneo. A malacofauna assessment protocol developed for a Cameroonian rainforest (de Winter & Gittenberger, 1998) was adapted to the present study. In each of 36 0.04 ha plots we searched for two person-hours, beat all trees between one and five cm in diameter at chest height over an inverted umbrella, and collected four litres of litter, from which the shells were later extracted by flotation. We also hand-collected additional snails and slugs while transferring from plot to plot. Species were identified where possible or assigned to morphospecies. In total, 546 individuals were found, belonging to 61 species and at least 14 families. Extrapolation suggests that the true diversity lies around 85 species. Several species were found that had previously only been known from limestone areas. Our study shows that, contrary to expectation, land snail diversity in southeast Asian rainforests can be high in spite of low abundance. The diversity in Danum Valley is similar to that of a four ha locality in New Zealand (60 species), and exceeded only by the site in Cameroon (97 species).

INTRODUCTION

Given the plethora of taxa and techniques currently in use for assessing biodiversity in tropical rainforests (e.g., Gaston, 1995), it is surprising that land snails have hardly received any attention yet. In principle, this group of animals has several of the characteristics that make a taxon useful as an indicator for diversity assessment. First of all, the fauna can be sampled easily and non-destructively, by collecting empty shells from litter. Second, since shells of any ecological group of snails (be they herbivorous, carnivorous, terrestrial, arboreal, or even canopy-dwelling) eventually end up on the forest floor, even cryptic portions of the malacofauna can be adequately sampled.

One of the reasons that land snails have not been popular as indicators of rainforest biodiversity may be that they are generally thought to be neither common nor diverse there. Solem (1984) argued that the lack of available nutrients, negligible litter, and abundance of predators make the tropical rainforest an unfavourable habitat for snails. Instead, he claimed that temperate, stable, moderately moist, and litter-rich forests are the places where land snail diversity reaches its pinnacle. A single site in the Waipipi Reserve on the mid-North island of New Zealand, for example, yielded 60 species (Solem, Climo & Roscoe, 1981).

Since then, however, several studies have appeared which prove that tropical rainforests can in fact contain rich and diverse malacofaunas. Gargominy & Ripken (1998) found 34 species of land snail in 280 litres of soil from a square kilometre of forest in French Guyana. In a patch of lowland rainforest in Madagascar, Emberton (1995) found 52 species, whereas Tattersfield (1997) reported 50 species from 27 0.16 ha plots in a 26,500 ha forest in western Kenya. De Winter & Gittenberger (1998), finally, discovered no less than 97 species in a square kilometre of forest in Cameroon.

In tropical Southeast Asia, malacological field work has always concentrated on limestone hills, which are a common feature of the region's geology (Tweedie, 1961; Vermeulen, 1993, 1996). Limestone hills have alkaline soils and are rich in calcium. These factors induce an abundance of living land snails, and also retard the breakdown of empty shells in the soil, which make these areas favoured spots for shell collectors. Moreover, limestone has a very patchy distribution in large parts of Southeast Asia, which, for certain snail taxa, has resulted in high degrees of endemism on individual hills. Consequently, current knowledge of the malacofauna of the region is almost exclusively restricted to limestone areas, which often make up less than one percent of the total land surface (Gobbett, 1965). Very

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little is known about the land snail fauna of the acidic, calcium-poor rainforests away from limestone.

In this paper, we offer a detailed study of the malacofauna of a small patch of forest on non-calciferous soil in Southeast Asia. For reasons of comparison, we have used a sampling protocol that is essentially identical to the one developed by de Winter & Gittenberger in their Cameroon study. Our primary objective was to obtain estimates of total diversity and spatial segregation of diversity (alpha and beta diversity, respectively; Rosenzweig, 1995) in a typical southeast Asian primary forest, and to compare these with the extremely rich situation in Cameroon.

MATERIALS AND METHODS

The study area

(Unless stated otherwise, the data in this section have been taken from Marsh (1995).) Our field work was carried out in Danum Valley Conservation Area (DVCA), 60 km west of Lahad Datu, on the east coast of Sabah, Malaysian Borneo (4°58′N 117°48′E; see fig. 1). DVCA is a 43,800 ha area of undisturbed, mainly lowland dipterocarp rainforest within the 972,000 ha concession area of the Sabah Foundation, which is mostly selectively logged. DVCA occupies much of the upper catchment of the Segama river. Rainfall averages about 2,700 mm per year, although severe droughts regularly occur. The most recent drought was associated with the 1997/1998 El Niño Southern Oscillation: during the first four months of 1998, a monthly average of only 92 mm was measured, with April 1998 registering no more than 11 mm (Danum Valley Management Committee, 1999). Normally, seasonality is not pronounced; two wet seasons correspond with the north-eastern monsoon from November to March and the south-western monsoon from May to August, but monthly rainfall in the intervening dry periods rarely falls below 100 mm. Mean annual temperature is 26.7°C and mean annual relative humidity at 8.00 A.M. is 94.5%. Until the establishment of the Danum Valley Field Centre, human influence in the region had been almost non-existent. No traces of permanent settlement have been found within a distance of 20 km from the DVCA perimeter.

We selected a single square kilometre patch demarcated by the main trails west of the Danum Valley Field Centre. The soils in this area, which are composed chiefly of sandstone, shale and assorted rocks (Wright, 1975), have an acidity of pH 5.3 to pH 4.0. The altitude is c. 300 m above sea-level. Forest type is large-crowned lowland dipterocarp rainforest, with crown-sizes of more than 18 m, and a dense canopy cover of 60-90%.

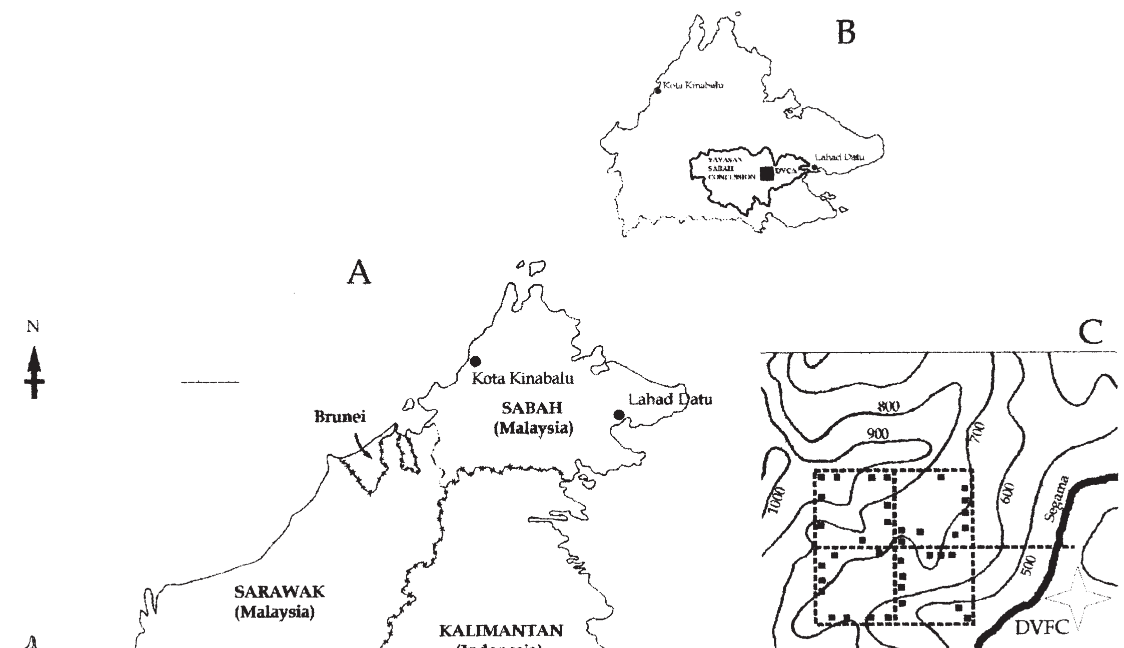

Figure 1. The localities described in this paper. **A.** The northern half of the island of Borneo, showing the location of the Malaysian state of Sabah. **B.** The state of Sabah, at the same scale as in A, showing the location of the Yayasan Sabah concession, and the Danum Valley Conservation Area (DVCA). **C.** The area directly adjacent to the Danum Valley Field Centre (DVFC), showing the trails (dashed lines) and the sample sites (filled squares); contours in map C are given in feet above sea level.

Sampling

All sampling was carried out between 9.v.2000 and 30.v.2000. Thirty-six plots of 20 × 20 m each were selected along the trails bounding and intersecting the one km^2 area (Fig.1). For each plot, slope, leaf litter thickness, canopy cover, understorey density, and the amount of decaying wood were recorded. At every plot, we intensively searched for snails and slugs, paying particular attention to habitats favoured by these animals, such as rotting logs, the bark and buttresses of large trees, and the undersides of palm and epiphyte leaves. We beat thin saplings, vines and palms (between one and five cm width at breast height) over an inverted umbrella, and collected the snails thus assembled in the field. Also, four litres of litter from a variety of micro-habitats were collected. Searching was done during two person-hours (i.e., two searchers active for one hour, or three searchers for 40 minutes). All snails, slugs, empty shells and shell fragments were collected. Living animals were relaxed in deoxygenated water and preserved in 70% ethanol. Litter samples were sieved with a one cm mesh width in the field; upon arrival in the laboratory, the samples were submerged in water and the floating debris (including small and minute shells) was collected, dried, and exhaustively searched under a dissection microscope. While walking between our field plots, snails encountered along the paths were also collected. All specimens have been deposited in the 'Borneensis' collection of the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah.

The sampling protocol above is essentially the same as the one used by de Winter & Gittenberger (1998) in 36 20 × 20 m plots within one square kilometre of forest in Cameroon. However, for logistic reasons, we deviated in the following respects: (1) we did not separate our samples into arboreal and soil fractions; (2) the field site was visited only once, rather than twice in different seasons; (3) soil samples were sieved only coarsely and then further enriched by flotation, rather than by successive sieving with decreasing mesh-width; (4) we collected some additional material outside the plots, which de Winter & Gittenberger do not report.

Although we did not systematically segregate samples from arboreal and litter origin, notes were made during the field work on the position and activity of living individuals. Snails were also observed in the canopy, using the tree platforms erected in the vicinity of the Danum Valley Field Centre.

Identifications

The land snail fauna of Borneo is rich and complex, and the taxonomic literature is scattered and mostly 19th-century. Only a few genera have recently been taxonomically revised, so reliable identifications could only be carried out on a minor fraction of the samples. The other samples were given tentative taxonomic names, mostly following suggestions by Dr. J.J. Vermeulen (Singapore Botanical Gardens), or they were identified to the genus (and, in one case, family) level and assigned morphospecies codes. With the exception of the single slug species, identifications were carried out on the basis of shell characters only. Some juvenile specimens of the genera *Everettia* (Ariophantidae) and *Japonia* (Cyclophoridae) could not reliably be identified to species level. Also, the identity of some smaller shell fragments could not be ascertained. For the calculation of snail abundance, these unidentifiable specimens were included. For the calculation of diversities, unidentifiable fragments were excluded, while unidentifiable juveniles were included where no adults were found.

Estimations of true diversity

We carried out estimations of the total number of species by performing 100 randomisations on the data from the 36 plots, and calculating S using the estimators Chao2 and second-order jackknife in the program EstimateS6.0b1 (Colwell, 2000).

RESULTS

In total, we collected 546 individuals, 14 of which were shell fragments which could not be assigned to any species. Hence, the following is based only on the remaining 532 identifiable specimens (Table 1). Of these, 158 (29%) were collected outside the plots. Each plot yielded between two and 28 specimens (mean 10.8; standard deviation 6.3). The diversity per plot ranged from two to 14 species (mean 6.1; s.d. 3.5). The total number of species found inside the 36 plots was 52, with nine additional species found outside the plots. The total land snail diversity in the single square kilometre thus stands at 61 species.

Fourteen snail families were represented, of which the two most prominent were the Ariophantidae (17 species) and the Cyclophoridae (10 species). As far as is known, all 61 species are herbivores s.l. and detritivores. Few species were abundant, with the exception of *Everettia* spec. 1 (143 individuals), *Leptopoma sericatum* (Pfeiffer) (43 individuals), *Hemiplecta densa* (Adams & Reeve) (37 individuals), *Amphidromus martensi* (Boettger) (27 individuals), *Opisthoporus* spec. 2 (27 individuals), *Philalanka kusana* (Aldrich) (25 individuals), *Everettia* spec. 4 (21 individuals) and *Videna metcalfei* (Pfeiffer) (21 individuals). All other species were represented by fewer than twenty individuals, and of 24 species only a single individual was found (Fig. 2).

For the 52 species collected in the 36 plots, Whittaker's Index I amounted to 8.6 (calculated as the overall species richness $S = 52$ divided by the mean number of species per plot $\alpha = 6.06$). This figure indicates a substantial degree of beta diversity, i.e., differentiation among the plots. However, possibly due to small sample sizes, we were unable to relate any of the ecological parameters (slope, leaf litter thickness, canopy cover,

Table 1. A list of all 61 (morpho)species found in a single square kilometre of rainforest in Sabah. Specimens were retrieved from 36 0.04 ha plots (column 'IP' = inside plots) and also while hand collected while transfering between plots (column 'OP' = outside plots). A tentative indication of the species' preferred microhabitat (column 'MH') is given with the letter A (for arboreal), F (for forest floor), and I (for indifferent). Species for which insufficient ecological field data were available are indicated with a question mark.

	OP	IP	MH
Helicinidae			
Sulfurina spec.	0	1	?
Cyclophoridae			
Alycaeus spec.	2	0	?
Cyclophorus spec.	1	0	?
Cyclotus s.l. spec. 1	0	1	?
Cyclotus s.l. spec. 2	9	0	F
Japonia spec. 1 (spec. nov.)	0	5	A
Japonia spec. 2	0	1	?
Leptopoma sericatum (Pfeiffer, 1851)	6	37	A
Leptopoma undatum (Metcalfe, 1851)	5	2	A
Opisthoporus spec. 1	14	13	F
Opisthoporus spec. 2	1	1	F
Diplommatinidae			
Arinia stenotrochus anisopleuron Vermeulen, 1996	0	3	F
Arinia paricostata Vermeulen, 1996	0	1	?
Diplommatina centralis Vermeulen, 1993	0	4	I
Diplommatina soror Vermeulen, 1993	0	3	F
Diplommatina sykesi Fulton, 1901	0	3	F
Diplommatina whiteheadi E.A. Smith, 1898	0	5	F
Pupinidae			
Pupina spec.	1	0	?
Veronicellidae			
Laevicaulis? spec.	1	0	?
Subulinidae			
Lamellaxis clavulinus (Potiez & Michaud, 1838)	0	11	F
Lamellaxis gracilis (Hutton, 1834)	0	5	F
Lamellaxis spec. (spec. nov.)	0	1	?
Paropeas achatinaceum (Pfeiffer, 1846)	1	1	F
Clausiliidae			
Phaedusa spec.	10	4	A
Achatinidae			
Achatina fulica Bowdich, 1822	3	0	I
Endodontidae			
Philalanka kusana (Aldrich, 1889)	0	25	?
Philalanka spec. 2	0	1	?
Euconulidae			
Coneuplecta spec. 1	0	1	?
Coneuplecta spec. 2	0	1	?
Liardetia spec. 1	0	1	?
Liardetia spec. 2	0	1	?
Liardetia angigyra (von Moellendorff, 1897)	0	17	A
Liardetia cf. *C. microconus* (Mousson, 1865)	0	1	A
Helicarionidae			
Geotrochus spec. 1	0	8	I
Geotrochus spec. 2	0	1	?
Geotrochus conicoides (Metcalfe, 1851)	2	1	I
Helicarion spec. 1	0	1	?

Table 1. (*Continued*).

	OP	IP	MH
Ariophantidae			
Dyakia densestriata (Schepman, 1895)	5	2	I
Everettia spec. 1	31	112	I
Everettia spec. 2	0	7	I
Everettia spec. 3	0	1	?
Everettia spec. 4	10	11	I
Everettia spec. 5	0	2	I
Quantula spec.	0	1	?
Hemiplecta densa (Adams & Reeve, 1848)	22	15	I
Macrochlamys spec. 1	0	3	I
Macrochlamys spec. 2	0	1	?
Microcystina spec. 1	0	2	?
Microcystina spec. 2	0	1	?
Microcystina spec. 3	0	1	?
Microcystina spec. 4	0	7	?
Microcystina spec. 5	0	3	?
Microcystina spec. 6	0	3	?
Vitrinula padasensis (E.A. Smith, 1895)	0	1	?
Trochomorphidae			
Bertia brookei (Adams & Reeve, 1848)	1	0	I
Videna metcalfei (Pfeiffer, 1845)	2	3	I
Camaenidae			
Amphidromus martensi (Boettger, 1894)	23	4	A
Chloritis spec. 1	1	2	I
Chloritis spec. 2	1	0	?
Chloritis spec. 3	0	1	?
Trachia spec.	2	11	I
totals	**158**	**374**	

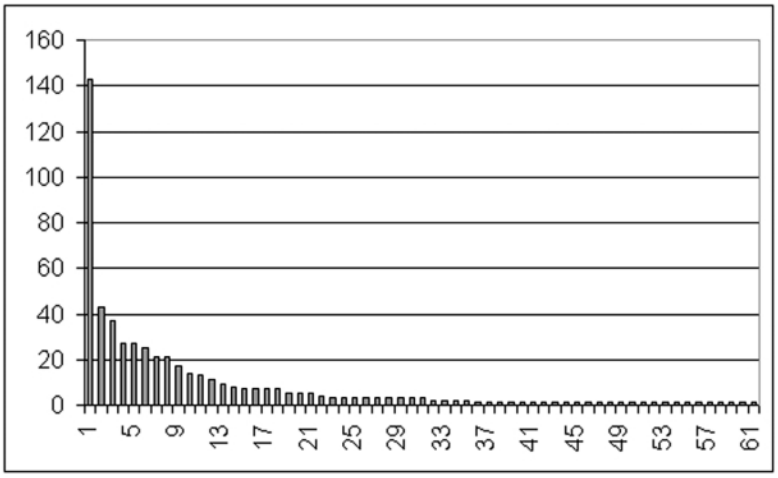

Figure 2. Absolute abundances of the 61 species found in the study.

understorey density, and the amount of decaying wood) to either snail abundance or diversity (results not shown). Estimated true diversity, based on 100 randomisations of the data for all 36 plots, was 81 species (s.d. = 21) for Chao2, and 88 species for the second-order jackknife.

DISCUSSION

Our study revealed a surprisingly rich malacofauna in Danum Valley. Sixty-one species were recorded in a single square kilometre, which is similar to the diversity recorded by Solem et al. (1981) in New Zealand and almost two-thirds of the diversity in Cameroon (de Winter & Gittenberger, 1998). This study in a Southeast Asian rainforest, like those in tropical regions in other parts of the world, disproves the generally held notion that land snail biodiversity in equatorial rainforests is comparatively low.

We have reasons to suspect that the true diversity in Danum Valley will lie even higher than the 61 species recorded, however. First of all, no less than 24 species were found as single individuals, which suggests that more rare species remain to be discovered. This is borne out by the estimation of true species richness, using the Chao 2 (Chao, 1987) and second-order jackknife (Smith & Van Belle, 1984) estimators, which are particularly suitable for small sample sizes, as is the case here (Colwell & Coddington, 1995). Chao 2 richness estimator and second-order jackknife give estimates of 81 and 88 species, respectively, which is considerably higher than the total number of species actually found in the plots (i.e., 52 species). In fact, subsequent studies in the near vicinity of the sites described here, have already resulted in five additional species (Schilthuizen, unpublished data).

The high diversity was found in spite of very low abundance. We found only one-fifth of the number of specimens collected by de Winter & Gittenberger (1998), even though those authors already considered the abundance in their study site low. Possibly, the low snail density in Danum Valley was a delayed effect of the severe drought of 1997/1998, during which snail mortality must have been high. However, it should be noted that all abundant species are the very large and conspicuous ones, which suggests that many small ones were overlooked, and that the relative abundance of these minute species is higher than the data suggest.

Although the species diversity in Danum Valley is comparable to that in Cameroon, the taxonomic composition is very different. This is not unexpected, since many families and superfamilies which are common in Africa (e.g., Achatinidae and Urocyclidae) are not or poorly represented in Southeast Asia, and vice versa (e.g., Ariophantidae, Camaenidae, and Cyclophoridae). However, the ecological composition shows large discrepancies as well. De Winter & Gittenberger report the presence of 33 species of carnivorous Streptaxidae, a situation that is common in the Ethiopian faunal region (Tattersfield, 1996; Emberton, Pierce, Kasigwa, Tattersfield & Habibu, 1997). Probably, these carnivorous snails depend on molluscan prey. In our study, no streptaxids or other known carnivores were present. However, some shells were found which carried marks of abrasion similar to those inflicted by the carnivorous oleacinid snail *Poiretia* (Schilthuizen, Kemperman & Gittenberger, 1994), which suggests that some predators may be hidden among the species assemblage found. Nevertheless, given the absence of many mollusc species with a known carnivorous mode of life, it is likely that many more predators of land snails in our study site are non-molluscan than in Cameroon.

Although we did not systematically segregate samples from arboreal and litter origin, notes made in the field clearly show signs of considerable ecological specialisation. Representatives of certain genera (*Hemiplecta, Everettia, Chloritis*) were found at the foot and lower portions of large trees, while others (*Amphidromus, Phaedusa*) were only seen high in the trees, up to 40 metres above the ground. Species from yet other genera, like *Japonia, Leptopoma, Coneuplecta,* and *Liardetia*, appeared to forage on leaves of palms, trees and saplings. Finally, Subulinidae and Diplommatinidae were mostly seen alive in soil litter. Further studies should be able to circumscribe the ecological niches of the various species and the degree of niche overlap. For the time being, we have no reason to believe that the prevalences of the various ecological groups is very different from those in the Cameroonian study, where 28% of the species were arboreal, 19% were 'indifferent', and 46% were floor-dwellers (plus an additional seven percent unclassified species). Applying the same ecological classifications to the species in our study (Table 1), the figures are 11% arboreal, 25% indifferent, 16% floor-dwellers, and 48% unclassified due to the fact that only a single or several dead individuals were collected.

Whittaker's *I* took a high value of 8.6. This suggests substantial differentiation in species-composition among the plots. However, given the small sample sizes, this is probably largely the result of sampling error rather than reflecting actual beta-diversity.

Surprisingly, our collection also includes several species that belong to the Diplommatinidae, most of which are considered obligate calcicoles. *Arinia paricostata* Vermeulen, *Diplommatina soror* Vermeulen, *D. centralis* Vermeulen and *D. sykesi* Fulton are all species which had so far been recorded exclusively from limestone rocks (Vermeulen, 1993, 1996). This suggests that many of these so-called limestone species actually occur at low densities on non-calciferous soils, a situation that had already been predicted on the basis of distribution patterns (Tweedie, 1961), and population genetics (Schilthuizen, Vermeulen, Davison & Gittenberger, 1999).

In conclusion, it can be stated that southeast Asian lowland dipterocarp forest on acidic soil is surprisingly rich in land snail species, similar to other localities with a rich malacofauna, such as tropical rainforest in

Africa and Madagascar and temperate forests in New Zealand. It may also be suspected that, although the abundance is low, the diversity in Danum Valley is similar to that of limestone hills in the region.

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