
Effects of Karst Forest Degradation on Pulmonate and Prosobranch Land Snail Communities in Sabah, Malaysian Borneo

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Abstract: *Limestone (karst) outcrops in Southeast Asia are rich in land snails. Certain groups of land snails, in particular Prosobranchia species, are restricted to limestone and show a high degree of short-range endemism. Karst habitats are, however, seriously degraded by quarrying, logging, agriculture, and burning. The effect of these disturbances on land snail fauna is unknown, so we studied paired primary and secondary forest localities on six separate limestone hills in Sabah, Malaysian Borneo. Land snails were sampled with a standard protocol and identified to species level. More than 16,000 individuals, belonging to 74 species, were recorded. In most sites, snail diversities did not differ between disturbed and undisturbed plots. However, pulmonate snails were significantly more abundant at disturbed localities than prosobranch snails, whereas abundances for both groups were similar at undisturbed sites. Because Prosobranchia contain many site-endemic species, our findings suggest that continued exposure to these disturbances will eventually lead to extinctions in this group.*

Key Words: conservation, endemism, limestone, Mollusca, quarrying, Southeast Asia, terrestrial Gastropoda

Efectos de la Degradación del Bosque sobre Comunidades de Caracoles Terrestres Pulmonados y Prosobranquios en Sabah, Malasia

Resumen: *Los afloramientos de roca caliza (karst) en el sureste de Asia son ricos en caracoles terrestres. Ciertos grupos de caracoles terrestres, particularmente especies de Prosobranchia, están restringidos a calizas y muestran un alto grado de endemismo de distribución corta. Sin embargo los hábitats karst están seriamente degradados por la explotación de canteras, la extracción de madera, la agricultura e incendios. Se desconoce el efecto de estas perturbaciones sobre la fauna de caracoles terrestres, así que estudiamos localidades pareadas de bosque primario y secundario en seis colinas separadas en Sabah, Malasia. Los caracoles fueron muestreados con un protocolo estándar e identificados a nivel de especie. Registramos más de 16,000 individuos, pertenecientes a 74 especies. En la mayoría de los sitios, la diversidad de caracoles no fue diferente en las parcelas perturbadas y no perturbadas. Sin embargo, los caracoles pulmonados fueron significativamente más abundantes que los caracoles prosobranquios en localidades perturbadas, mientras que las abundancias de ambos grupos fueron similares en sitios no perturbados. Lo anterior sugiere que la exposición continua a estas perturbaciones conducirá eventualmente a extinciones en Prosobranchia, debido a que contiene muchas especies endémicas.*

Palabras Clave: conservación, endemismo, explotación de cantera, Gastropoda terrestres, Mollusca, sureste de Asia, roca caliza

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Introduction

In Southeast Asia eroded limestone outcrops (karst) form a prominent part of the landscape. Because rates of limestone weathering are higher in the humid tropics than in temperate climates (Crowther 1986; Gale 1986), erosion here has resulted in scattered, isolated limestone hills with steep flanks that are called karst towers. The ecosystems on these karst towers are recognized for their great biodiversity value (Wong et al. 2003). The strongly irregular geomorphology and the good drainage of the limestone substrate, with many underground caves and cavities, result in a variegated vegetation (Whitmore 1998). In addition, the high calcium carbonate content and consequently alkaline pH of the limestone provide suitable conditions for organisms with high calcium requirements or low acidity tolerance.

Malaysia contains no fewer than 800 separate limestone outcrops, ranging from hills tens of meters across to plateaus many square kilometers in size (Wilford 1964; Lim & Kiew 1997; Price 2001). Most, however, are just a few hundred meters in diameter and are separated from each other by noncalcareous substrates. Although occupying only 0.3% of the land surface (Price 2001), these hills are the sole habitat of, for example, hundreds of obligate calcicolous plant species (MacKinnon et al. 1996; Kiew 2001), including several limestone-restricted dipterocarp trees (Whitmore 1984). Among animals, land snails are one of the most distinctive groups of karst inhabitants. These organisms have high calcium requirements

for their shells and reproduction (Graveland et al. 1994), and their abundance is usually strongly positively correlated with both calcium carbonate (CaCO_3) concentration and pH (Waldén 1995; Schilthuizen et al. 2003). In some groups of land snails, their calcium requirements are so great that they are found exclusively on limestone.

It is these calcicolous groups of land snails that show the greatest diversity and endemism on limestone outcrops in Malaysia (Fig. 1). Tweedie (1961) listed the presence of 106 species of obligately calcicolous snails on 28 karst hills and found that 70 were restricted to a single hill. Vermeulen and Whitten (1999) reported that 50 land snail species are endemic to one large karst outcrop in the state of Sarawak. Calcicolity and endemism appear to be more pronounced in prosobranch than in pulmonate land snails. In general, Prosobranchia (which have an open mantle cavity) are less adapted to the desiccating effects of terrestrial life than are Pulmonata (Solem 1974, 1984). In Malaysia about 50% of all land snail species are prosobranchs, but they tend to have more patchy distributions than pulmonates (Schilthuizen et al. 2002), which may reflect their more narrow tolerance ranges for low humidity and perhaps other abiotic factors.

With limestone outcrops supporting such a large component of the land snail fauna in this part of the world, it is important to know how the malacofauna reacts to human disturbance of karst habitats. Limestone throughout Southeast Asia is prone to degradation from a variety of human activities. Quarrying for cement, marble, and surfacing material for roads is the most destructive of these,

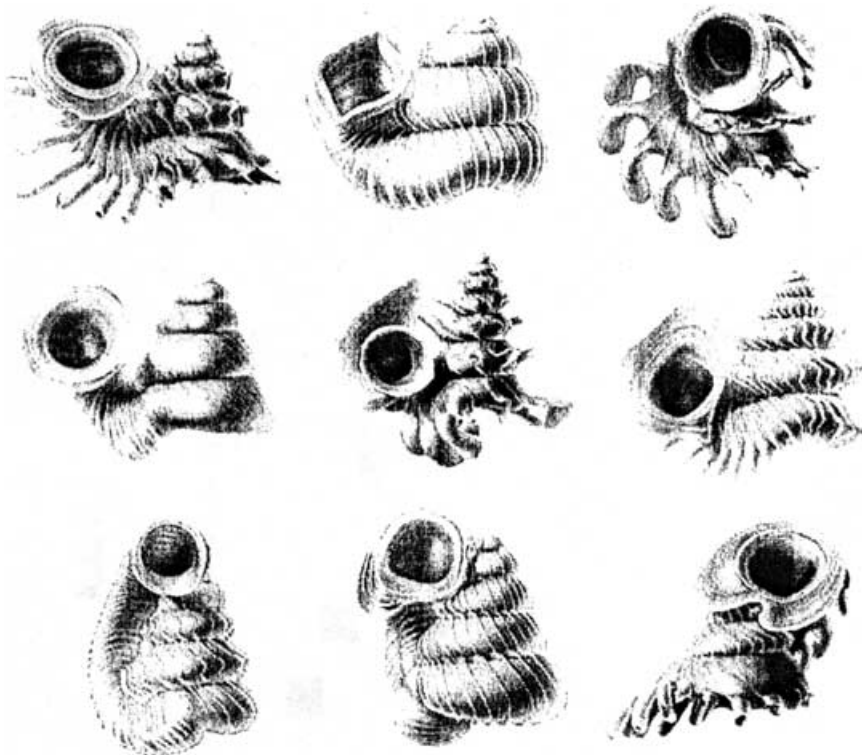


Figure 1. Nine representative Bornean members of the prosobranch genus Opisthostoma (shells not to scale, but all approximately 2 mm tall), showing the great diversity in shell shape. Many of these species are restricted to a single limestone outcrop (drawings by J. J. Vermeulen).

Table 1. Summary of numbers of snail species and individuals found at all primary and secondary plots and a measure of diversity (H').

Study site ^a (km ²)	Locality	S ^b	N ^c	H' ^d
Batu Tai (0.22)	Tai-primary	37	1844	2.13
Batu Tai (0.22)	Tai-secondary	10	677	0.38
Bukit Mawas (0.07)	Mawas-primary	37	2175	2.53
Bukit Mawas (0.07)	Mawas-secondary	36	1793	2.87
Batu Tomanggong Kecil (0.04)	Kecil-primary	26	408	2.62
Batu Tomanggong Kecil (0.04)	Kecil-secondary	32	1027	2.62
Batu Tomanggong Besar (0.07)	Besar-primary	35	1061	2.28
Batu Tomanggong Besar (0.07)	Besar-secondary	30	273	2.75
Batu Materis (0.33)	Materis-primary	31	1271	2.12
Batu Materis (0.33)	Materis-secondary	36	2690	2.15
Batu Kampung (0.19)	Kampung-primary	34	1339	2.59
Batu Kampung (0.19)	Kampung-secondary	35	1720	2.39

^aThe size of each limestone outcrop in parentheses.

^bTotal number of species.

^cTotal number of individuals.

^dShannon's index of diversity.

and several hills have completely disappeared, leading to the documented extinction of some site-endemic species (Vermeulen 1994).

Other disturbances of limestone outcrops include logging and agricultural activities. Although the terrain of a limestone outcrop itself is usually too rugged for large-scale forestry or agriculture, timber extraction for local consumption is common, and cultivation usually reaches up to the fertile footsoils of the hill (MacKinnon et al. 1996). Burning is often used to prepare surrounding flat land for planting, and fires easily sweep up the well-drained, steep limestone slopes. All these activities result in loss of vegetation cover, increased influx of solar radiation, increased risk of fire, desiccation, and the resulting loss of topsoil. Limestone hills damaged by these factors are often eventually overgrown by secondary vegetation of grasses, invasive climbers, and pioneer tree species (Vermeulen & Whitten 1999) and can take decades to recover (Kiew 2001). Meanwhile, some of the more drought-intolerant snail species may go into decline, and anecdotal reports of this happening are available (Vermeulen & Whitten 1999). Here, we report on the effects of disturbance on the pulmonate and prosobranch malacofauna of limestone hills in Sabah, Malaysian Borneo.

Methods

Our study sites were six limestone outcrops in the Lower Kinabatangan Valley of eastern Sabah (in the rectangle between longitudes 118°00'E and 118°20'E and latitudes 5°26'N and 5°33'N). The natural vegetation in this region (mean annual rainfall and temperature of 3000 mm and 27° C) is periodically inundated lowland riverine forest (Boonratana 2000). After intensive logging and subsequent conversion to oil palm plantations over most of the area, the combined remaining patches of forest, some of

which are on and around limestone outcrops, were designated as wildlife sanctuary in 2002. All six hills suffered moderate to severe damage over part of their surface, mainly resulting from quarrying, timber extraction, and fire in the 1982–1983 El Niño event (Kiew 2001), but each hill also retained patches of pristine vegetation.

At each outcrop, we identified two localities 100–1000 m apart, which differed in degree of forest disturbance (Table 1). In view of snails' limited mobility, we assumed that the snail populations in both localities would have independent histories, at least over the past two or three decades. Localities with mature primary forest trees were considered "primary," and all other localities (mostly stands of pioneer tree species) were referred to as "secondary." Recordings we made with data loggers at a few selected sites showed that such secondary localities in the Kinabatangan Valley have an average daytime air temperature 1–2° C higher and receive 10–100 times more sunlight than a pristine primary forest control. At each locality, we established a 20 × 20 m plot and examined six habitat parameters: (1) proportion of moss cover on rocks, (2) depth of leaf and wood litter layer, (3) proportion of canopy cover, number of trees (4) more and (5) less than 30-cm diameter at breast height (dbh), and (6) proportion of herb cover. A principal component analysis (Fig. 2) confirmed that the primary localities were separated from the secondary ones and were characterized by significantly more canopy and herb cover, more old trees, fewer young trees, and less leaf and wood litter.

At each plot land snails were sampled in 2 person-hours of manual searching and sieving and flotation of 5 L of litter and topsoil. This method, which is based on de Winter and Gittenberger (1998), is described in more detail in Schilthuizen and Rutjes (2001) and Cameron et al. (2003). We collected, cleaned, and stored all living and dead snails, including identifiable fragments. The method yielded chiefly empty shells, especially for microsnails,

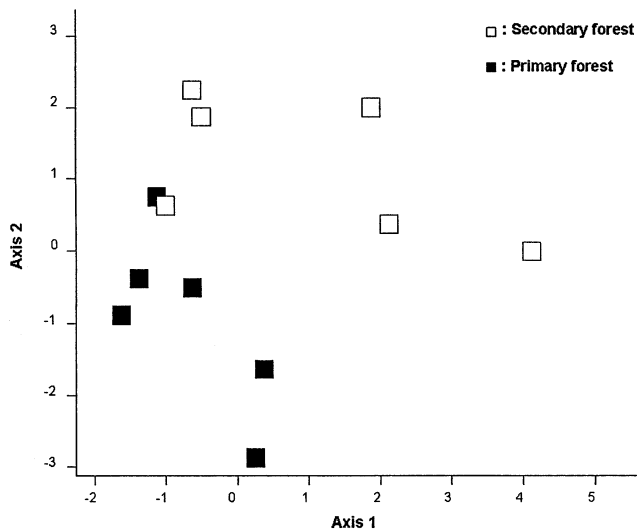


Figure 2. Principal component analysis based on six ecological parameters for all primary and secondary sites. The first principal component (Axis 1) correlated with reduced canopy cover and increased herb cover. The second principal component (Axis 2) correlated with increased leaf and wood litter; reduced number of trees >30 cm dbh, and increased number of trees <30 cm dbh.

most of which are rarely found alive. Microsnail shells are expected to survive in the soil for weeks (de Winter & Gittenberger 1998), but perhaps considerably longer under alkaline conditions. Thus, the sample may have partly contained individuals from previous years. Using an unpublished identification guide to the land snails of Sabah by J.J. Vermeulen and M. Schilthuizen and the BORNEENSIS reference collection of Universiti Malaysia Sabah, we identified all individuals to the species level. Voucher specimens were deposited in the BORNEENSIS collection under reference numbers BOR/MOL/1900-2206, 2242-2313, 2474-2499, 2579-2653, and 2839-2863.

We used the full data set to derive five measures of species diversity, namely Shannon's, Simpson's, Margalef's, and Fisher's alpha indices, along with the Q statistic. These indices were chosen because they cover a wide breadth of sensitivities to, for example, degree of sampling efficiency and influence of low-, medium-, or high-abundance species (Magurran 1988). For each of these indices, Wilcoxon's signed-rank test was performed to test for the effect of disturbance. We graphed rank versus abundance for each plot for Pulmonata and Prosobranchia separately. To remove the stochastic effects of very rare species, we also analyzed the rank-abundance patterns for the 10 most abundant species in each plot. Because a chi-square test did not reject the null hypothesis of homogeneity of variance across all plots ($\chi^2 = 1.857$, $df = 5$), we also tested the effect of disturbance on Pulmonata versus Prosobranchia in a contingency table, across all

plots. We carried out statistical tests in SPSS for Windows (version 11.0.0, SPSS, Chicago, Illinois).

Results

We collected 16,278 identifiable snails belonging to 74 species, including 40 species of Pulmonata and 34 species of Prosobranchia (29 Caenogastropoda and 5 Neritopsina). The identifiable snails were mostly empty shells. Less than 1% of what we collected were living individuals. Full lists of species and numbers of individuals are available from the authors on request. The 12 plots yielded species numbers ranging from 26 to 37 species, with the exception of one very degraded locality (grass and climbers with almost no canopy cover), "Tai-secondary," at which only 10 species were found. None of the diversity measures gave a significant overall difference between primary and secondary plots (Wilcoxon's signed-rank test, $t = 7-10$; $n = 6$; $p \gg 0.05$).

A distinct shift in species composition was seen, however, in the dominance of Pulmonata in the disturbed plots. In three of the six sites (Batu Tai, Bukit Mawas, and Batu Tomangong Besar), the proportion of Prosobranchia was markedly reduced in the secondary plot compared with the primary plot (Fig. 3). In the other three sites, no change in relative proportions of Prosobranchia and Pulmonata was obvious. The greater representation of Pulmonata over Prosobranchia in the secondary plots was also apparent when only the 10 most abundant species for each plot were considered (Fig. 4). A chi-square test showed that this shift was significant at $p < 0.005$ ($\chi^2 = 8.06$, $df = 1$).

Discussion

Land snails tend to have very small ranges and are prone to extinction by habitat destruction. This is exemplified by the fact that of all 693 documented animal extinctions since AD 1500, 260 have been snails (Lydeard et al. 2004). Prosobranch snails on limestone outcrops in Southeast Asia have a combination of biogeographic features that put them at risk of a similar fate. These animals show a relatively strong dependence on limestone, and many species are restricted to a single limestone hill or a cluster of hills. For example, the Prosobranch family Diplommatinidae has 158 species on the island of Borneo, of which one-third appear to be restricted to a single karst locality (J. Vermeulen, personal communication). These karst localities, moreover, are being degraded and removed by human activities at an increasing pace.

Our results show that, at least in our field sites in Borneo, it is this rich and endemic Prosobranchia component of the land snail fauna of limestone hills that

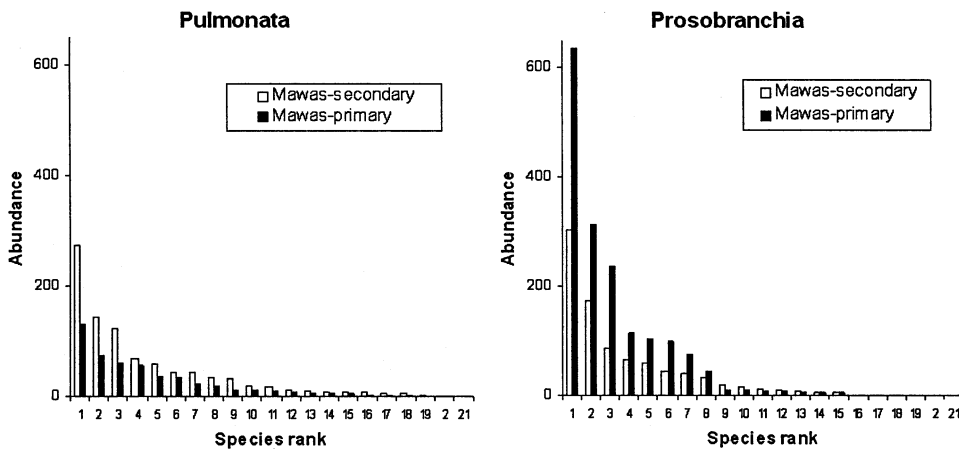


Figure 3. Rank-abundance curves for Pulmonata and Prosobranchia for the primary (mature primary forest trees) and secondary plots (not primary) at Bukit Mawas.

appears to decline first after habitat degradation. We could not detect any decline in richness or diversity in localities that retained some canopy cover. Only one highly degraded locality, from which all tree cover had disappeared, had a strongly reduced diversity. However, there was a clear overall downward shift in relative abundance of the prosobranchs in disturbed localities, with a corresponding upward shift of pulmonates. The known introduced and invasive land snail species in Southeast Asia are without exception Pulmonata, which further underscores their ability to survive in disturbed habitats (Vermeulen & Whitten 1998). Disturbance of limestone hills in our study area started only about 20 years ago. It is thus conceivable that continued exposure to raised temperatures, reduced humidity, and increased competition from the more tolerant pulmonate species will eventually lead to local extinctions of prosobranch species. Simple control measures such as the establishment or preservation of narrow forested buffer zones around a hill may be sufficient to reverse this trend.

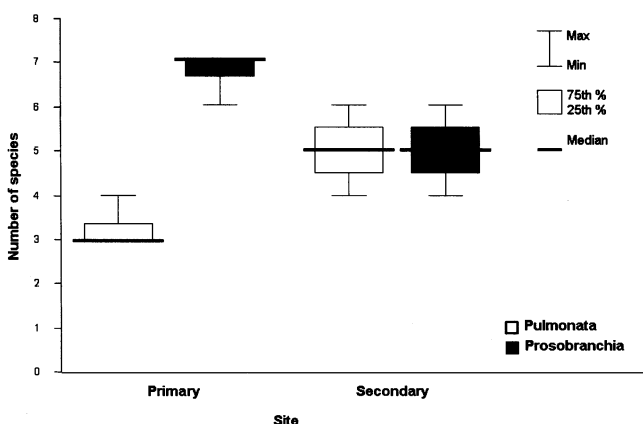


Figure 4. Relative contributions of Prosobranchia and Pulmonata to the 10 most abundant species in each plot (primary, mature primary forest trees; secondary, plots that were not primary).

It is surprising that, despite this shift in community structure, diversity seemed unaffected. Regardless of diversity index, p values for the test for difference between primary and secondary sites were always between 0.75 and 1.00. Possibly, this discrepancy is a consequence of our sampling method, which focused on shells. Some species may thus have already disappeared from a site, but their empty shells can still be found. Another possible cause may be the distribution of land snails, which is patchy even at spatial scales smaller than that of a single limestone hill (Schilthuizen et al. 2002). Prosobranch species that disappear from a site may thus be replaced by pulmonate species from elsewhere on the hill, keeping the site diversity constant until the diversity of the entire hill begins to drop.

In temperate regions of the world, it is increasingly recognized that land snails form an important and vulnerable component of the biota of limestone areas (Solem 1984; Waldén 1995; McMillan et al. 2003). In the tropics, the biological significance of limestone areas is much less understood, and land snails are rarely included in conservation projects. Their importance, however, is probably as great as in temperate karst regions, if not greater. The more fragmented nature of karst in Southeast Asia results in higher degrees of endemism, particularly in the prosobranch snails, which are nowhere as prominent a component of the terrestrial snails as in this part of the world. Unfortunately, few karst localities in this region have been placed under sufficient protection (Vermeulen & Whitten 1999; Wong et al. 2003), and with the demand for construction materials still rising, many more sites may be lost to quarrying and logging in the near future.

We recommend that the value of land snail communities be explicitly included in management plans for limestone areas in Southeast Asia in the future. Until now, the conservation values of these areas have often been recognized only when they harbor large colonies of bats, cave-nesting Swiftlets (*Collocalia* spp.), or other vertebrates. Also, conservation plans in areas with many limestone hills often focus on the conservation of one or a

few large outcrops (Wong et al. 2003). The high degree of short-range endemism in land snails suggests that these strategies may not be sufficient to conserve the malaco-fauna effectively.

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