

## **Limestone Karsts of Southeast Asia: Imperiled Arks of Biodiversity**

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# Limestone Karsts of Southeast Asia: Imperiled Arks of Biodiversity

REUBEN CLEMENTS, NAVJOT S. SODHI, MENNO SCHILTHUIZEN, AND PETER K. L. NG

*The overexploitation of the world's biomes for natural products calls for the prioritization of biologically important ecosystems for conservation. Here we show that limestone karsts are "arks" of biodiversity and often contain high levels of endemism. Humans have exploited karsts for a variety of products and services, but unsustainable practices have caused population declines and extinctions among site-endemic taxa. Limestone quarrying is the primary threat to karst biodiversity in Southeast Asia, where quarrying rates exceed those in other tropical regions. Several socioeconomic, political, and scientific issues undermine the stewardship of these karsts. Mitigation of these problems will involve (a) better land-use planning to prevent karst resources from being exhausted in developing regions, (b) comprehensive assessments of a karst's economic and biological value before development, (c) improved legislation and enforcement to protect karst biodiversity, and (d) increased research and activities to promote public awareness of the importance of karsts and the threats facing them.*

*Keywords: carbonate, karstic, mining, outcrop, protected area*

**H**umans are extracting natural resources at unprecedented levels. About half the world's original forest cover has already been cleared for agriculture and forest products, while another 30% has subsequently become degraded or fragmented (UNFPA 2004). If the current pace of habitat loss continues, species extinctions in many areas may reach catastrophic levels (Sodhi and Brook 2006). To mitigate such a disaster, scientists are identifying areas within "biodiversity hotspots" (regions exceptionally rich in endemic species and facing massive habitat loss; Myers et al. 2000) for priority conservation. Economically valuable ecosystems within hotspots, however, may not be adequately protected because of vested commercial interests, weak legislation, or deficient biological data. Limestone karsts are a prime example of an ecosystem in this predicament.

Limestone karsts (hereafter referred to simply as karsts) are sedimentary rock outcrops that consist primarily of calcium carbonate. Most karsts were formed millions of years ago by calcium-secreting marine organisms (e.g., corals and brachiopods) before tectonic movements lifted them above sea level. Over the years, the softer sediments covering these karsts were removed by mechanical and chemical weathering. This process usually produces "tower" and "cockpit" karst formations in the tropics. Tower karsts are characterized by tall, precipitous (60-degree [°] to 90° gradient) cliffs riddled with caves and sinkholes (figure 1a), while cockpit karsts are generally cone-shaped and have gentle slopes (30° to 40° gradient) (MacKinnon et al. 1996).

In Southeast Asia, karsts cover an area of around 400,000 square kilometers (km<sup>2</sup>), with geological ages ranging from the Cambrian to the Quaternary (Day and Ulrich 2000). Karsts in this region, which are most extensive in Indonesia, Thailand, and Vietnam (figure 2), possess impressive geological features, such as the world's largest cave chamber (Good Luck Cave in Sarawak, Malaysia) and one of the world's longest underground rivers (St. Paul Subterranean River in Palawan, Philippines). On the highly fragmented Sunda Shelf, karsts have formed "islands within islands," and these are known to contain high levels of endemism. Many of these outcrops, which have historically been spared from agricultural development because of their rugged terrain, may function as biodiversity reservoirs, or "arks," that restock degraded environments during ecosystem reassembly (Schilthuisen 2004). Besides serving as natural laboratories for biogeographical, ecological, evolutionary, and taxonomic research (Ng 1991, Schilthuisen et al. 1999, 2005a), karsts also have huge

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**Figure 1.** Examples of land uses around karsts. (a) A pristine tower karst in Sarawak, Malaysia. (b) Karst quarried for limestone in Perak, Malaysia. (c) Karst used as a Hindu temple in Selangor, Malaysia. (d) Karst as an aesthetic backdrop for a resort in Perak, Malaysia. Photographs: Reuben Clements.

potential for archaeological and paleontological discoveries (e.g., fossils of the dwarf hominid *Homo floresiensis* were recently excavated from a karst cave in Indonesia; Morwood et al. 2004). For these and other reasons, karsts are recognized as important ecosystems and have been included for many years in national conservation plans within the region (MacKinnon and MacKinnon 1986).

Karsts in Southeast Asia, however, are threatened by modern destructive practices. Many outcrops are being quarried for limestone (figure 1b), an important raw material used to manufacture commercially valuable products such as cement. A cement company in Malaysia, which owned limestone quarries totaling 1.3 km<sup>2</sup>, generated about US\$150 million in revenue from just one year of cement production (CIMA 2004). Quarrying is now regarded as the primary threat to the survival of karst-associated species, and it will certainly exacerbate the biodiversity crisis in Southeast Asia, a mega-diverse region that has the highest rate of natural habitat loss among the tropics (Sodhi and Brook 2006).



**Figure 2.** Distribution of karsts (in black) throughout Southeast Asia (excluding Myanmar), modified from a map courtesy of Elery Hamilton-Smith.

In this overview of karsts in Southeast Asia, we discuss (a) karsts' role as arks of biodiversity, (b) their importance to humanity, (c) the conservation status of karst-associated species, (d) the threats posed by anthropogenic disturbances, and (e) the challenges facing karst conservation. Karsts are severely understudied (Vermeulen and Whitten 1999, Dennis and Aldhous 2004), and we hope this article will result in further research and conservation initiatives on these vulnerable ecosystems.

### Biodiversity arks

The high species diversity on karsts arises from a multitude of ecological niches afforded by complex terrains (e.g., fissured cliffs and extensive caves) and variable climatic conditions. High species endemism can also occur on karsts with different tectonic and eustatic histories, degrees of isolation, and incidences of random events. Karsts can be divided into surface and cave levels, both of which provide ideal conditions for speciation. On karst surfaces, edaphic (soil-related) isolation produces a unique flora that includes many calcicoles (species adapted to growing on limestone). At the same time, such vegetation supports animal species somewhat different from those in nonkarstic areas. Because of their poor dispersal capabilities, plants and some animals, such as invertebrates, have to adapt to highly alkaline conditions, thin soil layers, and desiccation on porous limestone bedrock. In caves, animals such as arthropods and fishes must evolve specializations to cope with fluctuating levels of light, water quantity, temperature, humidity, gas concentrations, and organic material (Culver et al. 2000). Examples of karst-associated taxa and their levels of richness and endemism are discussed below.

**Surface flora.** The presence of numerous karst microhabitats can support high floral diversity. For example, the slopes and gullies of some karsts have greater soil depths to sustain large trees such as dipterocarps, while rock faces and summits with thinner soil layers are usually colonized by herbaceous species (e.g., aroids, balsams, begonias [figure 3a], gesneriads, pandans, and slipper orchids) and bryophytes (Kiew 2001). Abiotic factors also exert strong influences on the composition of karst vegetation. In Sarawak, karsts in high-precipitation zones are usually covered by acidic peat soils that support plants unlike those typically associated with limestone substrates (e.g., casuarinas and pitcher plants), while cool temperatures at high-altitude karsts (e.g., the Api and Benarat karsts at about 1700 meters [m] above sea level) can support submontane species dissimilar from those found on karsts at lower altitudes (Kiew 1991). High floral richness has been recorded from karsts in Southeast Asia. In Peninsular Malaysia, 1216 angiosperm species, or 14% of the total Malayan flora, have been found on karsts (Chin 1977). The karsts of the Bau district in Sarawak also contain a large proportion (15% to 60%; figure 4) of regional limestone plant, moss, and orchid species (see Yong et al. 2004).

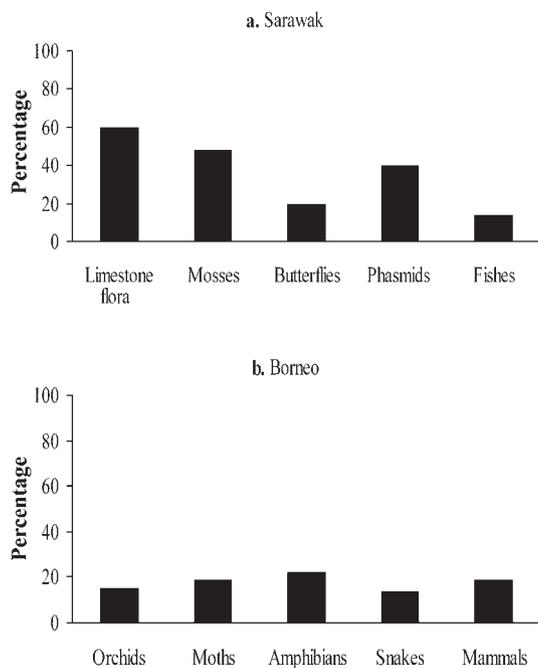
Current figures of karst floral richness, however, may be underestimated as a result of the difficulty of sampling inaccessible areas such as cliff faces and summits. Using data sets of understory flora and summit trees from 20 karsts in Bau (see Yong et al. 2004), we show that numerous species remained undiscovered even after 30 months of sampling, as the numbers of observed and estimated species for both plant groups were still rising and showed no sign of converging (figure 5). Isolation within edaphically unusual karsts also exerts strong selective forces, which may lead to the evolution of endemic plant species (Kruckeberg and Rabinowitz 1985). Numerous species of bryophytes (Mohamed et al. 2005) and vascular plants (Kiew 1991, 2001, MacKinnon et al. 1996, IUCN 2000) are restricted to karsts in Southeast Asia. In Peninsular Malaysia, 21% of 1216 karst-associated plant species are endemic to the peninsula, and 11% are strictly confined to karsts (Chin 1977). Proctor and colleagues (1982) have also shown the floral composition of karsts to be unique: 60% of the 73 plant species recorded from the Mulu karsts in Sarawak could not be found in other lowland forest types. Botanical expeditions to remote karst areas continue to uncover endemic plants new to science. In Vietnam, biologists recently described a critically endangered genus of conifer (*Xanthocyparis vietnamensis*) that appears to be confined to karsts (Farjon et al. 2002).

**Surface fauna.** Invertebrate groups on karst surfaces can be very speciose. A recent survey showed that a significant proportion (19% to 40%; figure 4) of regional butterfly, macro-moth, and phasmid species inhabit the Bau karsts of Sarawak (see Yong et al. 2004). Land snails, in particular, flourish on karsts because the calcium-rich soils favor their growth and reproduction (Graveland et al. 1994). One subgenus (*Plectostoma*; figure 3b) even shows obligate calcicolous (depend-



**Figure 3. Examples of karst biodiversity. (a) Site-endemic begonia, *Begonia amphioxus*, from Sabah, Malaysia. (b) Site-endemic prosobranch land snail, *Opisthostoma (Plectostoma) obliquedentatum*, from Sabah, Malaysia. (c) Blind troglobitic crab, *Cancrocaeca xenomorpha*, genus from Sulawesi, Indonesia. (d) Cave-dwelling insectivorous bat, *Hipposideros diadema*, from Sarawak, Malaysia. Photographs: Peter Koomen (a), Menno Schilthuizen (b), Louis Deharveng (c), and Kelvin K. P. Lim (d).**

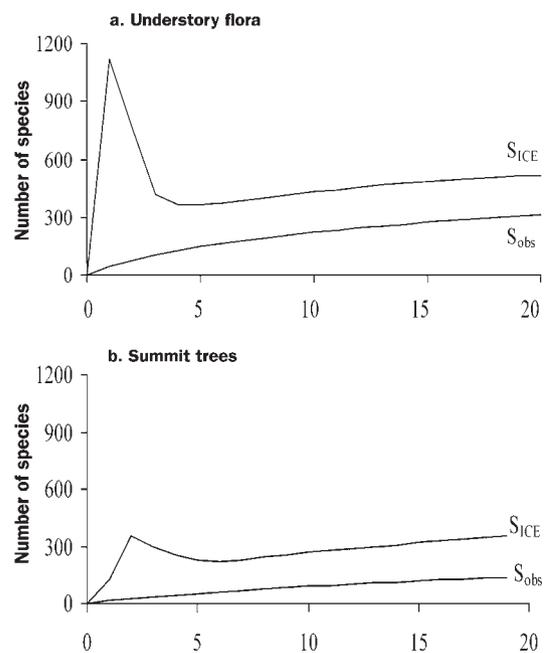
ency on calcareous substrates for survival), with all 44 Bornean species recorded only from karsts (Schilthuizen 2004). In Malaysia, around 80% of the total land snail fauna occurs on karsts that make up less than 1% of the country's land area (Schilthuizen 2000). Land snail endemism peaks on karsts because of their low dispersal capabilities and isolation effects, both of which facilitate radiation at small spatial scales (Schilthuizen et al. 1999). Among just eight selected land snail genera, a large number of species (78) were found to be site endemics (species restricted to single isolated karsts) in Peninsular Malaysia (Davison 1991). 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). Other invertebrates, such as butterflies, also exhibit endemism on karsts, albeit to lesser



**Figure 4.** Percentages of total flora and fauna (selected taxa) from (a) Sarawak and (b) Borneo recorded on the Bau karsts. These percentages show that karst landscapes can harbor significant proportions of a region's biodiversity. Data are from Yong and colleagues (2004).

degrees. For instance, the montane butterfly fauna at the Mulu karsts in Sarawak has more endemic species (possibly due to specificity for karst-associated host plants) than nearby sandstone outcrops (Holloway 1986).

Vertebrates are relatively well represented around karsts. For example, birds are known to use limestone crags as refugia and breeding grounds; high avifaunal richness (129 species from 40 families) was recently recorded from the Bau karsts in Sarawak (see Yong et al. 2004). Considerable percentages (14% to 22%; figure 4) of Sarawak's and Borneo's total fish, amphibian, snake, and mammal species were also observed from the same karsts (see Yong et al. 2004). As most vertebrates have high dispersal capabilities, only a few mammals (e.g., François's leaf monkey [*Trachypithecus francoisi*] and the serow [*Capricornis sumatraensis*]) and birds (e.g., the limestone wren-babbler [*Napothera crispifrons*]) are believed to be restricted to karsts. Nevertheless, the potential for discovering new vertebrate taxa at poorly sampled karsts remains quite high. Recently, the Khammouan karsts in Laos yielded a new mammal family (Laonastidae) and two new genera of rodents (*Laonastes* and *Saxatilomys*), both of which appear morphologically suited for karstic terrain (Jenkins et al. 2005, Musser et al. 2005). Fishes, on the other hand, are subjected to stronger evolutionary pressures in isolated water bodies. For example, the ichthyofauna of Inlé Lake in Myanmar, which is situated on a limestone plateau 1000 m above sea level, comprises several endemic cyprinid genera (e.g., *Inlecypris* and *Sawbwa*) and species (Annandale 1918).



**Figure 5.** Observed ( $S_{obs}$ ) and estimated ( $S_{ICE}$ ) species of (a) understory flora and (b) summit trees, as a function of sampled karsts in Bau, Sarawak. The lack of convergence between  $S_{obs}$  and  $S_{ICE}$  curves indicates that sampling saturation has not been reached despite 30 months of sampling. Data are from Yong and colleagues (2004), and curves were generated with presence/absence data using EstimateS (Colwell 2005). Abbreviation: ICE, incidence-based coverage estimator.

**Cave fauna.** The relative stability and antiquity of subterranean ecosystems enable relict faunas to persist (Gibert and Deharveng 2002). In Sarawak, some of the 200 cave species found in the Mulu karsts belong to ancient animal groups that have mostly disappeared from the surface (IUCN 2000). On the other hand, the ecotone at the epigeal–cave interface can also generate cave-adapted species (e.g., the endemic land snail *Georissa filiasaulae*) that remain parapatrically connected (i.e., with contiguous but nonoverlapping geographic distributions) with their ancestors on the surface (Schilthuizen et al. 2005b).

Invertebrates make up the majority of cave faunas, and as a result of their sheer diversity, surveys consistently yield new genera and species from Southeast Asian karsts (Juberthie and Decu 2001). In just three hours of sampling a well-documented karst cave in Peninsular Malaysia, 28% of the 53 invertebrate species collected by Dittmar and colleagues (2005) were new records, and a further 6% were likely to be new to science. In karst caves, most invertebrates (e.g., flies, cockroaches, and snails) primarily or ultimately depend on guano for food, and several arthropods, such as certain families of millipedes (Glyphiulidae) and beetles (Aderidae), are even restricted to life on guano piles (Deharveng and Bedos 2000). Primary consumers such as raphidophorid crickets can reach

giant proportions (e.g., in the Mulu karsts; Chapman 1982), and in turn are consumed by larger cave predators (e.g., centipedes, whip-scorpions, and crabs). Some invertebrates are troglobites, completing their life cycles entirely within caves, and most have undergone regressive evolution. For example, the troglobitic crab *Cancrocaeca xenomorpha* (figure 3c) from the Maros karsts in Indonesia is characterized by ocular degeneration, pale coloration, and abnormally long appendages after years of isolation in perennial darkness (Ng 1991). Despite the poor sampling effort, troglobitic richness in Southeast Asia (16 to 28 species per cave,  $n = 4$ ; Deharveng and Bedos 2000) appears to be higher than in other well-sampled tropical regions (e.g.,  $\leq 14$  species per cave,  $n > 100$ , in Central America; Peck and Finston 1993). Surveys of karst caves in Southeast Asia have hinted at high levels of troglobitic endemism, particularly among isopods, diplopods, and collembolids from the genus *Troglopedetes*, which has about 12 species restricted to the caves of western Thailand (Deharveng and Bedos 2000). Crabs of the genus *Orcovita* are also known to be endemic to anchialine karst caves (caves in marine or brackish water bodies with no surface connection to the sea) in countries such as the Philippines (Ng et al. 1996).

Bats are probably the most conspicuous cave-dwelling vertebrates, as they prefer caves to other roosting habitats (Hutson et al. 2001). The Mulu karsts have one of the region's richest bat faunas (28 species), and more than a million wrinkle-lipped bats (*Chaerephon plicata*) can occupy a single cave (IUCN 2000). Swiftlets roosting in caves can also reach staggering numbers, with about 300,000 individuals occurring at the Niah karsts (Lim and Cranbrook 2002).

Because of their isolation from surface streams, fishes are probably the only vertebrates that are truly endemic to karst caves, and many species possess bizarre morphological and behavioral adaptations. Since 1988, 13 cave-restricted fishes have been described from the karsts of five Southeast Asian countries, including a highly depigmented and blind cave loach (*Cryptotora thamicola*) from Thailand that climbs onto rocks using its large lateral fins (Kottelat 1988). Apart from several reptilian taxa (e.g., geckos, skinks, and snakes), other vertebrates found exclusively in karst caves include the world's smallest mammal (the bumblebee bat [*Craseonycteris thonglongyai*]), which has a skull size of only 11 millimeters and inhabits a few karsts in Kanchanaburi, Thailand (Hill 1974).

### Importance to humanity

Karsts are mainly exploited for limestone, an important mineral with over 100 industrial uses (Davison 2001), which include the production of cement and marble products. Several karst species are commercially valuable as well. Rare slipper orchids are often sold or hybridized on a large scale in the billion-dollar orchid industry, while endemic cycads, palms, and various herbaceous plants (e.g., *Chirita* and *Paraboea*) are sought after by horticulturalists (Kiew 1991). Nests built by swiftlets (e.g., *Collocalia fuciphagus* and *Collocalia maximus*) on karst cave walls are highly prized as Asian culinary delicacies. At 15 caves in the Gomantong karsts of Sabah, nest

yields of about 5 metric tons can fetch more than US\$2.5 million annually (Lim and Cranbrook 2002). Guano deposited by bats and swiftlets onto cave floors is also harvested for fertilizer. At the Niah karsts, for example, the Sarawak Museum operates a cooperative that sells guano to fertilize local black pepper fields (MacKinnon et al. 1996).

Services provided by karsts and their biodiversity are less tangible but significant nonetheless. Karsts readily store rain, and apart from maintaining the hydrological integrity of a watershed (MacKinnon et al. 1996), they also serve as sources of groundwater for consumption and irrigation. In Indonesia, quarrying has caused water shortages in human settlements because, in the absence of water storage in karsts, rain flows directly into underground streams that empty into the sea (Bambang and Utomo 2003). Animals in karst caves are also known to perform valuable ecosystem services. Bats pollinate and disperse the seeds of many economically important plants. In the Niah karsts, resident populations of cave nectar bats (*Eonycteris spelaea*) are vital pollinators of the durian tree (*Durio*), which has a yearly market of approximately US\$1.5 billion in East Asia (Ross 1997). Around karsts, insectivorous bats, such as the Diadem roundleaf bat (*Hipposideros diadema*; figure 3d), and swiftlets also help to control agricultural pests; these animal groups consume up to 7.5 and 11 metric tons, respectively, of insects at the Niah karsts each day (Vermeulen and Whitten 1999).

Karsts feature prominently in several cultures and religions within the region. Caves have been used as places of worship (e.g., by the Buddhists and Hindus; figure 1c) or burial sites (e.g., by the Dayak people in Borneo) for several centuries. The economies of countries such as Malaysia and Thailand ultimately benefit from cultural and religion-based tourism, especially during important festivals held at karst temples. Similarly, many countries have profited from tourism at karsts of high aesthetic value (e.g., the sea-flooded karst towers of Ha Long Bay, Vietnam). By protecting and maintaining the natural states of Niah and Mulu karsts, the state of Sarawak obtains US\$80,000 from eco- and geotourism each year (see Yong et al. 2004).

### Conservation status

We compiled the total number of karst-associated species listed by the IUCN (The World Conservation Union) as critically endangered, endangered, or vulnerable. Our findings showed that 143 species known from karstic habitats are globally threatened, and of these, 31 occur in Southeast Asia (table 1). These figures, however, must be regarded as very conservative for several reasons. First, we found the numbers of threatened karst species to be geographically skewed and not representative of the true conservation status of karst species worldwide. More than 50% of globally threatened karst plants and molluscs were highlighted from just one country (table 1). Second, other karst species may not have been detected during our searches on the IUCN search engine, which broadly classified the habitats of several species. For example, the François's leaf monkey (*T. francoisi*) and serow (*C. suma-*

**Table 1. Taxonomic breakdown of IUCN threatened species.**

Group	Habitats worldwide	Karsts worldwide	Karsts in Southeast Asia
Molluscs	974	20 <sup>a</sup>	18 <sup>a</sup>
Insects	559	0	0
Fishes	800	2 <sup>a</sup>	0
Amphibia	1770	27	4
Reptiles	304	4	0
Birds	1213	0	0
Mammals	1101	2	1 <sup>a</sup>
Plants	8321	88 <sup>a</sup>	8 <sup>a</sup>
Total	15,042	143	31

Note: For information on karst-associated species, three habitat categories (karst and other subterranean hydrological systems, caves and subterranean habitats, rocky areas) and one threat category (mining) were searched using the expert search engine in the 2004 IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)).

a. More than 50% of species highlighted in these taxa were from only one country.

*traensis*) were placed under the general habitat category of “forests,” although both these species were reported as being restricted to karsts (MacKinnon et al. 1996, Vermeulen and Whitten 1999). Ultimately, these low figures suggest that karst species are severely underrepresented in lists of endangered species, in part as a result of undersampling and data deficiency on uncharismatic taxa such as cave invertebrates. To our knowledge, most troglobitic organisms have not even been subjected to any form of threat analysis.

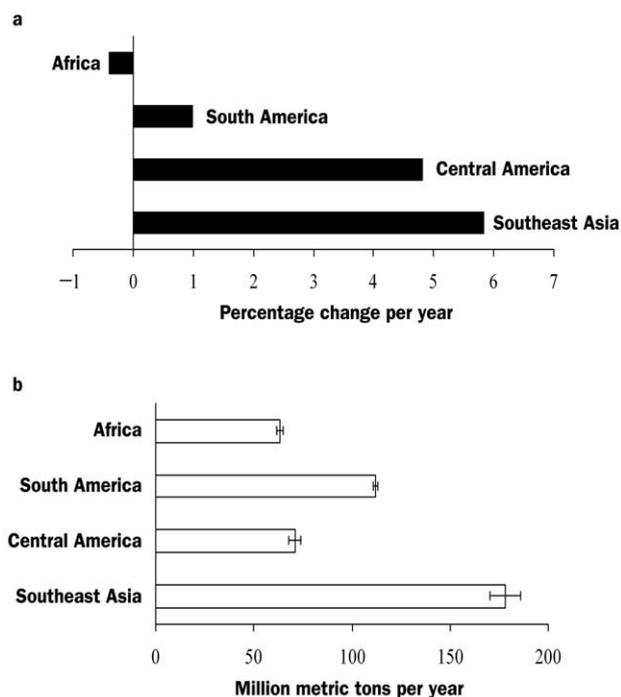
Site-endemic species face the greatest extinction risk when a karst is completely quarried. Extinctions of at least 18 karst plant species have already been documented in Peninsular Malaysia (Kiew 1991). Molluscs are also extinction prone as a result of their low vagility, poor tolerance for desiccation, and high degree of site endemism (Schilthuizen 2004). In Sabah, two site-endemic land snail species (*Opisthostoma otostoma* and *Opisthostoma decrespignyi*) are presumed extinct because the karsts where they were found were demolished for an airstrip (Vermeulen 1994). Some purported extinctions, however, cannot be established unequivocally, because karsts have generally been poorly sampled. For instance, recent surveys at the karsts of Negros Island in the Philippines resulted in the rediscovery of the Negros fruit bat (*Dobsonia chapmani*), a species previously thought to be extinct (Alcala et al. 2004). Nevertheless, many species extinctions have probably gone unnoticed on karsts that were destroyed before they could be sampled. Unless biodiversity surveys of karsts are intensified, the true magnitude of extinctions will never be ascertained.

### Anthropogenic threats

Large-scale operations involving the mining of limestone and basement minerals (e.g., antimony, gold, and iron; Davison 2001) are a primary threat to karst biotas because they cause irreversible ecosystem damage and extirpations of site-endemic taxa (Vermeulen 1994). To estimate the magnitude of limestone-quarrying activities in the tropics, we compiled mineral statistics over a five-year period (1999–2003) for

four regions. Southeast Asia appears to have greater mean annual increases in limestone quarrying rates (5.7% per year; figure 6a) and significantly higher ( $\chi^2 = 16.9$ ,  $p = 0.001$ , degrees of freedom = 3, Kruskal-Wallis test, SPSS 11.5) mean annual limestone quarrying rates (178 million metric tons per year; figure 6b) when compared with larger tropical regions such as Africa, South America, and Central America (including the Caribbean). Furthermore, quarrying rates for each region are likely to be underestimates because they do not include statistics from village-level quarries. The gravity of these figures will become clear only when remaining limestone resources for the whole of Southeast Asia have been quantified. Nevertheless, they suggest a bleak outlook for the future of regional karst biodiversity.

Land clearing for development is another major threat to karst biota. Logging activities around karsts (a) reduce shade and humidity and endanger sensitive plants (Kiew 1991), (b) drive away cave-visiting animals such as mammals and arthropods that supply organic matter to guano communities (Culver et al. 2000), (c) pollute cave streams and kill resident fauna, and (d) diminish bat populations that depend heavily on surrounding forests for foraging (Robinson and Webber 2000). The land surrounding karsts is sometimes burned to facilitate crop cultivation (e.g., for federal agricultural



**Figure 6. Scale of limestone quarrying in terms of (a) mean annual percentage change in quarrying rates and (b) mean ( $\pm$  standard error) annual quarrying rates for four major tropical regions over a five-year period (1999–2003). Quarrying rates in Southeast Asia appear to be the highest relative to other regions. Calculations excluded countries with incomplete statistics for all five years. Data are from the US Geological Survey (<http://minerals.usgs.gov/minerals>).**

land schemes in Malaysia; Davison 2001), but the fires resulting from such activities can easily sweep up karst slopes. Burnt karsts subsequently experience prolonged desiccation due to higher solar radiation and are more susceptible to further fires (Schilthuizen et al. 2005a). The resulting depauperate secondary vegetation that grows on burnt karsts not only takes decades to recover (Kiew 1991, 2001) but also results in population declines in taxa that are sensitive to disturbance (Schilthuizen et al. 2005a).

Unsustainable collection of endemic plants of medicinal and ornamental value can also result in population extinctions, and the indiscriminate harvesting of swiftlet nests in Borneo has reduced swiftlet populations (Lim and Cranbrook 2002). Excessive nest-harvesting activities may have indirectly contributed to the decline of bat populations as well; the abundance of naked bats (*Cheiromeles torquatus*) at the Niah karsts in Sarawak fell from approximately 30,000 to 1000 over a 42-year period (Hutson et al. 2001). Hunting pressure can also deplete populations of certain karst-associated animals if it continues unregulated. Bats from karst caves are sold for consumption in the markets of Thailand and Indonesia, and horn trophies of the threatened serow (*C. sumatraensis*) can be purchased at markets in Laos (Vermeulen and Whitten 1999). Other threats to karst species include the quarrying of speleothems (mineral formations in caves, such as stalactites), insecticide use, flooding caused by the damming of nearby rivers, treasure hunting, and spelunking (Kiew 1991, Davison 2001).

### Conservation challenges

Poverty and resource shortages resulting from overpopulation are likely to continue to marginalize karst conservation issues. Concepts of population extinctions and unsustainable extractions are usually of little concern to the poor. In Sarawak, a survey of 198 low-income households around the Bau karsts revealed that more than half (54%) were dependent on karst resources for subsistence, and a substantial minority (33%) were unwilling to accept conservation measures restricting their customary land rights (see Yong et al. 2004). For cash-strapped governments, royalties from cement manufacture are so substantial that policies for sustainable limestone quarrying are generally overlooked. The regency administration of Gunungkidul, which presides over one of the poorest areas in Indonesia (with a per capita income of approximately US\$153), issued quarrying permits to 13 mining companies in the past decade to revive its ailing economy (Bambang and Utomo 2003). To alleviate poverty and resource overexploitation in karst areas, land-use planning must be improved (using a landscape-scale conservation approach) to consider the welfare of poorer communities. For example, the managing agencies of the Pu Luong-Cuc Phuong karst conservation project in Vietnam allocated land to local residents for sustainable agroforestry and involved them in ecotourism projects to generate income (GEF 2001). Government officials in Gunungkidul are equally concerned that karst quarries will ruin the landscape and affect tourism, which generated

US\$57,000 more than quarrying in 2002 (Bambang and Utomo 2003). In Malaysia, karsts that were preserved as aesthetic backdrops for a resort township (figure 1d) have not only attracted multimillion-dollar investments but also opened up job opportunities for local residents.

In most countries, karsts have been preserved on the basis of anthropocentric criteria (e.g., karsts with high tourist potential or those that are inaccessible to mining companies). While such an approach may seem pragmatic to conservation planners, the distinctiveness of a karst's biodiversity and geomorphology must not be neglected. To ensure that both these elements are considered during future environmental impact assessments (EIAs) of karsts, "terms of reference" were drawn up by the World Bank for consultants to follow (Vermeulen and Whitten 1999). During karst EIAs, high species richness and the presence of IUCN threatened species may function only as secondary indicators; the former does not reflect species rarity, and the latter often excludes uncharismatic organisms. Instead, endemism levels of range-restricted taxa (e.g., plants, land snails, and cave animals) could be used as the primary barometer for setting conservation priorities at karsts. If governments deem limestone quarrying to be necessary, groups of small and isolated karsts should not be selected, because these are more likely to harbor high numbers of endemic species; larger and more extensive karsts may instead be made open to quarrying prospects (Vermeulen and Whitten 1999).

About 13% of Southeast Asia's karst area has been nominally protected (Day and Urich 2000). This level of protection may appear satisfactory, given that a frequently cited goal of conservation scientists is to protect 10% of all habitat types globally (IUCN 1993). However, such percentages do not necessarily correspond to species representation (Rodrigues et al. 2004), and nominally protected habitats may be "paper parks" that are not properly managed because of insufficient resources. As karst protection in some countries is still absent or minimal (e.g., in Cambodia and Myanmar; table 2), regional governments and international agencies are still working to increase the percentage of protected karst area. For example, the state government of Sarawak has extended the coverage of the Gunung Mulu National Park by 250 km<sup>2</sup> to include other karsts (IUCN 2000), while organizations such as the World Bank and The Nature Conservancy have helped protect karst landscapes in Vietnam (e.g., Pu Luong-Cuc Phuong karsts) and Indonesia (e.g., Sangkulirang karsts) respectively. The IUCN has also set up a task force (Working Group on Cave and Karst Protection) to highlight additional karsts for protection. In 2001, the Asian Pacific Forum on Karst Ecosystems and World Heritage identified several karsts in this region for inscription into the World Heritage list. Karsts can now be found in 8 of the 12 World Heritage natural sites in Southeast Asia (UNESCO 2005). The impressive biodiversity at some of these sites (table 3) suggests that protected areas containing karsts may help reduce the number of gap species (species with distributions not covered by protected areas; Rodrigues et al. 2004) worldwide.

**Table 2. Protected status of karst areas in Southeast Asia.**

Country	Karst area (km <sup>2</sup> )	Protected karst area (km <sup>2</sup> )	Karst protected (percentage)
Cambodia	20,000	0	0
Indonesia	145,000	22,000	15
Laos	30,000	3000	10
Malaysia	18,000	8000	44
Myanmar	80,000	650	1
Philippines	35,000	10,000	29
Thailand	20,000	5000	25
Vietnam	60,000	4000	7
Total	408,000	52,650	13

km, kilometers.

Note: Figures should be treated cautiously, as they include information from protected areas that do not conform to United Nations criteria for recognition.

Source: Modified from Day and Ulrich (2000).

**Table 3. Taxonomic breakdown of species recorded in four of the eight World Heritage natural sites that contain karsts in Southeast Asia.**

World Heritage site	Country	Taxon				
		Plants	Mammals	Reptiles and amphibians	Birds	Fishes
Phong Nha-Ke Bang	Vietnam	876	113	81	302	72
Dong Phrayayen-Khao Yai	Thailand	2500	112	200	392	NA
Thungyai-Huai Kha Khaeng	Thailand	NA	120	139	400	113
Gunung Mulu	Malaysia	3500	81	131	270	48

NA, not available.

Source: UNESCO 2005.

Current laws that protect karsts in Southeast Asia, however, appear *ad hoc*, ineffective, or in some cases simply nonexistent. For example, many karsts in Malaysia receive protection only by virtue of being located within the boundaries of national parks (Kiew 1991). In Borneo, agricultural activities often proceed unchecked toward the bases of protected karsts, while localized bans on swiftlet nest harvesting have only served to divert poachers to other unprotected karsts (MacKinnon et al. 1996). Laws to protect karst species are severely lacking (Kiew 2001, Lim and Cranbrook 2002); the only known case is a cave fish from central Java, Indonesia (Vermeulen and Whitten 1999). Moreover, mining companies often exploit the uncertain demarcation of legal authority arising from the involvement of too many agencies. In Indonesia, laws that necessitate EIAs prior to quarrying are often circumvented (Bambang and Utomo 2003).

Evidently, additional legislative measures need to be formulated. For example, the retention of forested buffer zones around karsts (to prevent fires and maintain habitat integrity) should be made compulsory, and mining companies should be prohibited

from starting small-scale operations elsewhere if the karsts allocated to them have not been completely quarried. To curb unnecessary limestone quarrying (e.g., 14 million metric tons of cement in excess of domestic demand was produced in Malaysia during one year; Lock 1998), quarrying rates could perhaps be monitored and made more transparent. Existing wildlife laws must also be amended to protect certain key-stone species that can serve as umbrellas for the entire karst community (Vermeulen and Whitten 1999). For the above-mentioned laws and policies to work, however, governments must clamp down on corruption, resolve conflicting jurisdictions, and provide administrators with greater incentives (e.g., income from geotourism and fines from offenses) to ensure better enforcement and accountability.

The paucity of biological information on karsts ultimately weakens justifications for their conservation in the long run.

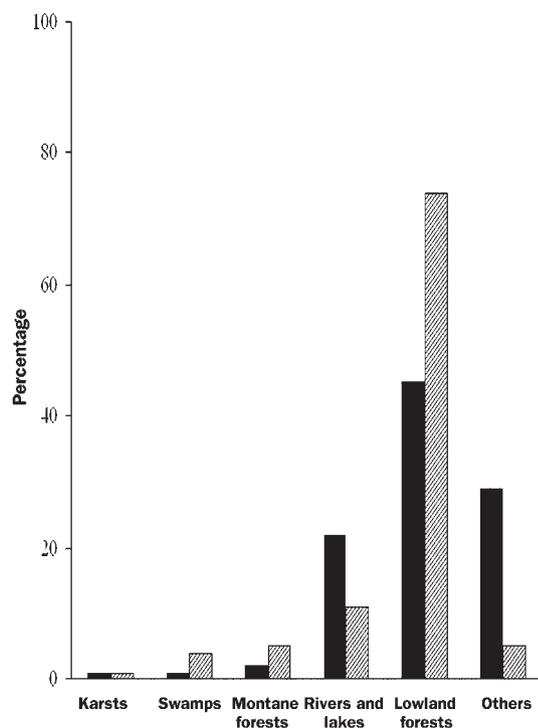
To support this argument, we screened internationally peer-reviewed articles from the Biological Abstracts database for biodiversity-related articles over a 20-year period (1985–2004). We found that karsts contribute just 1% of the global and regional biodiversity research output from terrestrial and freshwater ecosystems (figure 7). Given that karsts cover around 10% of the land area in Southeast Asia (Day and Ulrich 2000), more studies need to

be devoted to these ecosystems. For example, a paper by Chapman (1982) is the only known ecological study of karst caves from the region thus far (Deharveng and Bedos 2000). To promote research on karsts, governments must commit more funds for capacity building in biodiversity research, and regional institutions should form collaborative efforts with international scientific agencies. The ASEAN (Association of Southeast Asian Nations) Regional Centre for Biodiversity Conservation, or ARCBC, which facilitates institutional linkages between regional and European Union organizations, has already implemented eight karst-related research projects in six different Southeast Asian countries (table 4; ARCBC 2004). It is encouraging that community-based educational

**Table 4. Description of eight karst-related research projects funded by the ASEAN (Association of Southeast Asian Nations) Regional Centre for Biodiversity Conservation in six Southeast Asian countries.**

Karst study area	Country	Budget (euro)	Duration (months)	Research theme
Maros	Indonesia	115,102	24	Biological uses and values
Luangprabang	Laos	20,000	15	Biological uses and values
Sarawak	Malaysia	99,320	30	Biological uses and values
Southwestern Negros	Philippines	48,125	24	Ecological reconstruction
Northwest Panay	Philippines	100,000	36	Ecological reconstruction
Phang Nga Bay	Thailand	115,102	24	Biological uses and values
Ha Long Bay	Vietnam	58,605	24	Biological uses and values
Phong Nha-Ke Bang	Vietnam	94,500	24	Biological uses and values

Source: ARCBC 2004.



**Figure 7.** Percentage of global (black bars) and Southeast Asian (gray bars) biodiversity research conducted in major terrestrial and freshwater ecosystems over a 20-year period (1985–2004). These percentages suggest a paucity of biological information on karsts relative to other ecosystems. Data were obtained from article searches within the abstract, title, and keywords of citations in the Biological Abstracts database using hierarchically nested combinations of relevant keywords and wild cards (available from Reuben Clements upon request).

programs and workshops on karsts have been carried out with ARCBC and other conservation initiatives (e.g., at the Pu Luong–Cuc Phuong karsts; GEF 2001), but public awareness of karst conservation still needs to be heightened throughout the region.

We have shown that karsts are major foci for speciation and important biodiversity arks. Considering the immense financial returns from cement manufacturing, their continued exploitation for limestone cannot be stopped. In Southeast Asia, karsts warrant greater conservation attention, given the relatively high limestone quarrying rates. Furthermore, the region has the world's highest relative rates of deforestation and is expected to lose 42% of its biodiversity by the year 2100 (Sodhi and Brook 2006); this estimate does not even consider species extirpations that may result from quarrying activities. The question now is this: Can habitat loss at karsts be slowed down long enough for scientists to get a better handle on the challenges ahead? Unfortunately, given the lack of baseline data on karst biota and their extinction rates, this is a conservation battle we may well lose.

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## References cited

- Alcala EL, Paalan RB, Dolino CN, Alcala AC. 2004. Bat thought to be extinct rediscovered in southwestern Negros Island, Philippines. *ASEAN Biodiversity* 4: 54–55.
- Annandale N. 1918. Fish and fisheries of the Inlé Lake. *Records of the Indian Museum* 14: 33–64.
- [ARCBC] ASEAN (Association of Southeast Asian Nations) Regional Centre for Biodiversity Conservation. 2004. Research Programme. (28 June 2006; [www.arcbc.org.ph/research.htm](http://www.arcbc.org.ph/research.htm))
- Bambang M, Utomo GW. 2003. Limestone quarries ruin Gunungkidul's beauty. *Jakarta Post*. 17 May.
- Chapman P. 1982. The ecology of caves in the Mulu National Park, Sarawak. *Transactions of the British Cave Research Association* 9: 142–162.
- Chin SC. 1977. The limestone hill flora of Malaya: Part 1. *Gardens' Bulletin Singapore* 30: 165–220.
- [CIMA] Cement Industries of Malaysia Berhad. 2004. Company Annual Report. (23 June 2006; [www.cima.com.my/annual\\_reports.html](http://www.cima.com.my/annual_reports.html))
- Colwell RK. 2005. Estimates: Statistical Estimation of Species Richness and Shared Species from Samples. Version 7.5. (28 June 2006; <http://purl.oclc.org/estimates>)
- Culver DC, Master LL, Christman MC, Hobbs HH. 2000. Obligate cave fauna of the 48 contiguous United States. *Conservation Biology* 14: 386–401.
- Davison GWH. 1991. Terrestrial molluscs of Peninsular Malaysia. Pages 101–104 in Kiew R, ed. *The State of Nature Conservation in Malaysia*. Kuala Lumpur (Malaysia): Malayan Nature Society.
- . 2001. Limestone conservation: Options available to planners and users. In Schilthuizen M, ed. *The Evolution and Conservation of Biodiversity of Limestone Areas*. Kota Kinabalu (Malaysia): Universiti Malaysia Sabah. (23 June 2006; [www.schilthuizen.org/PDF/pdf\\_45.pdf](http://www.schilthuizen.org/PDF/pdf_45.pdf))
- Day MJ, Ulrich PB. 2000. An assessment of protected karst landscapes in Southeast Asia. *Cave and Karst Science* 27: 61–70.
- Deharveng L, Bedos A. 2000. The cave fauna of Southeast Asia: Origin, evolution and ecology. Pages 603–632 in Wilkens H, Culver DC, Humphreys WF, eds. *Ecosystems of the World 30: Subterranean Ecosystems*. Amsterdam: Elsevier.
- Dennis C, Aldhous P. 2004. Biodiversity: A tragedy with many players. *Nature* 430: 396–398.
- Dittmar K, Porter ML, Price L, Svenson G, Whiting MF. 2005. A brief survey of invertebrates in caves of Peninsular Malaysia. *Malayan Nature Journal* 57: 221–233.
- Farjon A, Nguyen TH, Harder DK, Phan KL, Aveyanov LV. 2002. A new genus and species in Cupressaceae (Coniferales) from northern Vietnam, *Xanthocyparis vietnamensis*. *Novon* 12: 179–189.
- [GEF] Global Environment Facility. 2001. Conservation of Pu Luong-Cuc Phuong Limestone Landscape. (23 June 2006; [www.gefweb.org/Documents/Medium-Sized\\_Project\\_Proposals/MSP\\_Proposals/VIETNAM-MSP.pdf](http://www.gefweb.org/Documents/Medium-Sized_Project_Proposals/MSP_Proposals/VIETNAM-MSP.pdf))

- Gibert J, Deharveng L. 2002. Subterranean ecosystems: A truncated functional biodiversity. *BioScience* 52: 473–481.
- Graveland J, Van Der Wal R, Van Balen JH, Van Noordwijk AJ. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature* 368: 446–448.
- Hill JE. 1974. A new family, genus, and species of bat (Mammalia: Chiroptera) from Thailand. *Bulletin of the British Museum (Natural History)*, Zoology 27: 301–336.
- Holloway JD. 1986. Origins of lepidopteran faunas in high mountains of the Indo-Australian tropics. Pages 533–566 in Monasterio M, Vuilleumier F, eds. *High Altitude Tropical Biogeography*. Oxford (United Kingdom): Oxford University Press.
- Hutson AM, Mickleburgh SP, Racey PA. 2001. *Microchiropteran Bats: Global Status Survey and Conservation Action Plan*. Gland (Switzerland): Species Survival Commission Chiroptera Specialist Group, IUCN.
- [IUCN] The World Conservation Union. 1993. *Parks for Life: Report of the IVth World Congress on National Parks and Protected Areas*. Gland (Switzerland): IUCN.
- . 2000. World Heritage Nomination—IUCN Technical Evaluation, Gunung Mulu National Park (Sarawak, Malaysia). (23 June 2006; [whc.unesco.org/archive/advisory\\_body\\_evaluation/1013.pdf](http://whc.unesco.org/archive/advisory_body_evaluation/1013.pdf))
- Jenkins PD, Kilpatrick CW, Robinson MF, Timmins RJ. 2005. Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. *Systematics and Biodiversity* 2: 419–454.
- Juberthie C, Decu V, eds. 2001. *Encyclopedia Biospeologica*, vol. 3. Moulis (France): Société Internationale de Biospéologie.
- Kiew R. 1991. The limestone flora. Pages 42–50 in Kiew R, ed. *The State of Nature Conservation in Malaysia*. Kuala Lumpur (Malaysia): Malayan Nature Society.
- . 2001. Towards a limestone flora of Sabah. *Malayan Nature Journal* 55: 77–93.
- Kottelat M. 1988. Two species of cavefishes from northern Thailand in the genera *Nemacheilus* and *Homaloptera* (Osteichthyes: Homalopteridae). *Records of the Australian Museum* 40: 225–231.
- Kruckeberg AR, Rabinowitz D. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16: 447–480.
- Lim CL, Cranbrook G. 2002. *Swiftlets of Borneo: Builders of Edible Nests*. Kota Kinabalu (Malaysia): Natural History Publications (Borneo).
- Lock SN. 1998. Boosting country's cement industry. *New Straits Times*. 7 July.
- MacKinnon J, MacKinnon K. 1986. *Review of the Protected Areas System in the Indo-Malayan Realm*. Cambridge (United Kingdom): IUCN/United Nations Environment Programme.
- MacKinnon K, Hatta G, Halim H, Mangalik A. 1996. *The Ecology of Kalimantan. The Ecology of Indonesia Series*, vol. 3. Singapore: Periplus Editions.
- Mohamed H, Yong KT, Damanhuri A, Latiff QA. 2005. Moss diversity of Langkawi Islands, Peninsular Malaysia. *Malayan Nature Journal* 57: 243–254.
- Morwood MJ, et al. 2004. Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* 431: 1087–1091.
- Musser GG, Smith AL, Robinson MF, Lunde DP. 2005. Description of a new genus and species of rodent (Murinae, Muridae, Rodentia) from the Khammouan Limestone National Biodiversity Conservation Area in Lao PDR. *American Museum Novitates* 497: 1–31.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Ng PKL. 1991. *Cancrocaeca xenomorpha*, new genus and species, a blind troglobitic freshwater hymenostomatid (Crustacea: Decapoda: Brachyura) from Sulawesi, Indonesia. *Raffles Bulletin of Zoology* 39: 59–73.
- Ng PKL, Guinot D, Iffle TM. 1996. Revision of the anchialine varunine crabs of the genus *Orcovita* Ng & Tomascik, 1994 (Crustacea: Decapoda: Brachyura: Grapsidae), with descriptions of four new species. *Raffles Bulletin of Zoology* 44: 109–134.
- Peck SB, Finston TL. 1993. Galapagos Islands troglobites: The questions of tropical troglobites, parapatric distributions with eyed-sister species, and their origin by parapatric speciation. *Mémoires de Biospéologie* 20: 19–37.
- Proctor J, Anderson JM, Fogden SCL, Vallack HW. 1982. Ecological studies of four forest types. *Sarawak Museum Journal* 51: 207–224.
- Robinson MF, Webber M. 2000. Survey of bats (Mammalia: Chiroptera) in the Khammouan Limestone National Biodiversity Conservation Area, Lao P.D.R. *Natural History Bulletin of the Siam Society* 48: 21–45.
- Rodrigues ASL, et al. 2004. Global gap analysis: Priority regions for expanding the global protected-area network. *BioScience* 54: 1092–1100.
- Ross P. 1997. Opportunities for Commercially Under-exploited Tropical Fruits, Vegetables and Nuts. Barton (Australia): Rural Industries Research and Development Corporation. (23 June 2006; [www.rirdc.gov.au/reports/NPP/DAQ-W5967-19.doc](http://www.rirdc.gov.au/reports/NPP/DAQ-W5967-19.doc))
- Schilthuisen M. 2000. The evolution and conservation of limestone biotas in Malaysia, with special reference to land snails. Pages 358–362 in Leigh M, ed. *Borneo 2000: Environment, Conservation, and Land*. Proceedings of the Sixth Biennial Borneo Research Conference. Kuching (Malaysia): Borneo Research Bureau, Universiti Malaysia Sarawak.
- . 2004. Land snail conservation in Borneo: Limestone outcrops act as arks. *Journal of Conchology Special Publication* 3: 149–154.
- Schilthuisen M, Vermeulen JJ, Davison GWH, Gittenberger E. 1999. Population structure in a snail species from isolated Malaysian limestone hills, inferred from ribosomal DNA sequences. *Malacologia* 41: 283–296.
- Schilthuisen M, Liew TS, Bin Elahan B, Lackman-Ancrenaz I. 2005a. Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. *Conservation Biology* 19: 949–954.
- Schilthuisen M, Cabanban AS, Haase M. 2005b. Possible speciation with gene flow in tropical cave snails. *Journal of Zoological Systematics and Evolutionary Research* 43: 133–138.
- Sodhi NS, Brook BW. 2006. *Southeast Asian Biodiversity in Crisis*. Cambridge (United Kingdom): Cambridge University Press.
- [UNESCO] United Nations Educational, Scientific and Cultural Organization. 2005. Natural Properties on the World Heritage List. (14 July 2006; <http://whc.unesco.org/sites/natural.htm>)
- [UNFPA] United Nations Population Fund. 2004. *The State of World Population 2004*. (28 June 2006; [www.unfpa.org/swp/2004/english/ch1/index.htm](http://www.unfpa.org/swp/2004/english/ch1/index.htm))
- Vermeulen JJ. 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, Whitten T. 1999. *Biodiversity and Cultural Property in the Management of Limestone Resources—Lessons from East Asia*. Washington (DC): World Bank.
- Yong HS, Ng FSP, Lee EYE, eds. 2004. *Sarawak Bau Limestone Biodiversity*. Sarawak Museum Journal 59, Special Issue No. 6. Kuching (Malaysia): Sarawak Biodiversity Centre.