diversity

MDPI

Article

A Hotspot of Subterranean Biodiversity on the Brink: Mo So Cave and the Hon Chong Karst of Vietnam

Louis Deharveng [1,*], Cong Kiet Le [2], Anne Bedos [1], Mark L. I. Judson [1], Cong Man Le [2], Marko Lukić [3,4], Hong Truong Luu [5,6], Ngoc Sam Ly [6,7], Tran Quoc Trung Nguyen [5], Quang Tam Truong [7] and Jaap Vermeulen [8]

1 Institut de Systématique, Évolution, Biodiversité (ISYEB), UMR 7205 CNRS, Muséum National d'Histoire Naturelle, Sorbonne Université, 57 rue Cuvier, 75005 Paris, France; bedosanne@yahoo.fr (A.B.); judson@mnhn.fr (M.L.I.J.)
2 Department of Ecology-Evolutionary Biology, Faculty of Biology-Biotechnology, University of Science, Vietnam National University Ho Chi Minh City, 227 Nguyen Van Cu Street, District 5, Ho Chi Minh City 749000, Vietnam; lecongkiet@gmail.com (C.K.L.); lecongman2202@gmail.com (C.M.L.)
3 Croatian Biospeleological Society, Rooseveltov trg 6, HR-10000 Zagreb, Croatia; lukic.mar@gmail.com
4 Department of Molecular Biology, Ruđer Bošković Institute, Bijenička cesta 54, HR-10000 Zagreb, Croatia
5 Southern Institute of Ecology, Institute of Applied Materials Science, Vietnam Academy of Science and Technology, 1D, TL 29 Street, Thanh Loc Ward, District 12, Ho Chi Minh City 729110, Vietnam; hongtruongluu@gmail.com (H.T.L.); ntqtrung@gmail.com (T.Q.T.N.)
6 Vietnam Academy of Science and Technology, Graduate University of Science and Technology, 18 Hoang Quoc Viet, Cau Giay District, Ha Noi 122000, Vietnam; lysamitb@gmail.com
7 Institute of Tropical Biology, Vietnam Academy of Science and Technology, 85 Tran Quoc Toan Street, Vo Thi Sau Ward, District 3, Ho Chi Minh City 722700, Vietnam; truongtam58@yahoo.com
8 JK Art and Science, Lauwerbes 8, 2318 AT Leiden, The Netherlands; jk.artandscience@gmail.com
* Correspondence: dehar.louis@wanadoo.fr

Abstract: The southern part of the Mekong Delta Limestones of Vietnam (MDL-HC or Hon Chong karst) comprises numerous small limestone hills. It is a hotspot of biodiversity for soil and cave invertebrates. Here, we synthesize the results of biological surveys carried out in Hang Mo So, the richest MDL-HC cave for troglobionts, and in surrounding karsts. Methodologies for the ecological characterization of species are discussed, with emphasis on parallel sampling (external soil plus cave). Hang Mo So has 27 troglobionts, including many still undescribed. An additional 40 cave-obligate species are known from other caves of MDL-HC. Among them, several are expected to be found in Hang Mo So. Most troglobionts of MDL-HC are endemic. Several relictual taxa without close relatives in Southeast Asia occur in Hang Mo So and in MDL-HC, reflecting an ancient origin of the fauna. The reasons for this richness are uncertain, but the cause of its current destruction—quarrying—is all too evident. Most of the original 4 km^2 of the MDL-HC karst has been destroyed or soon will be, ultimately leaving only 1.6 km^2 unquarried. Endemic species linked to karst habitats are, therefore, under clear threat of extinction. The Hon Chong karst (MDL-HC) was listed among the ten most endangered karsts on the planet 25 years ago. Today it would probably top the list.

Keywords: invertebrates; Mekong Delta; karst; species richness; stygobionts; troglobionts; quarrying; sampling; caves; species extinction

check for updates

Citation: Deharveng, L.; Le, C.K.; Bedos, A.; Judson, M.L.I.; Le, C.M.; Lukić, M.; Luu, H.T.; Ly, N.S.; Nguyen, T.Q.T.; Truong, Q.T.; et al. A Hotspot of Subterranean Biodiversity on the Brink: Mo So Cave and the Hon Chong Karst of Vietnam. *Diversity* **2023**, *15*, 1058. https://doi.org/10.3390/d15101058

Academic Editor: Michel Baguette

Received: 17 August 2023
Revised: 21 September 2023
Accepted: 25 September 2023
Published: 2 October 2023

1. Introduction

Vietnam has many large and famous karsts in its central and northern regions, in particular at Ke Bang and Ha Long Bay. However, further south (below 17° N), limestones are limited to small, sparse isolated outcrops in two regions: Da Nang where a few small limestone towers are located in the town itself, and a larger region straddling the border between Vietnam and Cambodia (the Mekong Delta Limestones or MDL). The latter is composed of numerous small limestone hills of Permian age, extending from the south-western part of the Mekong Delta to southern Cambodia. Along 70 km, from Hon Chong hill in the southeast to Laang hill in the west, limestone outcrops emerge above the Mekong plain. Many are grouped in loose clusters of small, karstified hills that rarely exceed a square kilometer in surface area. Those located southeast of the Giang Thanh River in Vietnam—collectively referred to as Hon Chong karst in the literature and as MDL-HC here—have highly dissected surfaces, deep dolines and numerous cave passages, remnants of larger cave systems.

Long caves with underground rivers are generally those richest in biodiversity [1], such as Mammoth Cave in USA [2], the Postojna-Planina Cave System in Slovenia [3], Ojo Guarena in Spain [4], Feihu Dong in China [5], the Towakkalak system in Sulawesi [6] or Agua Clara in Brazil [7]. The MDL caves are quite different: they are short and shallow, without active hydrological circulation, and are supplied with large amounts of nutrients (roots, guano, debris) due to surface proximity. The best-known and richest cave of the MDL karst is Hang Mo So (Hang = cave), in the Nui Bai Voi hill of MDL-HC. It is the focus of this work.

1.1. Karst and Caves of MDL

The MDL karst is spatially isolated from the other karst areas of the region: the Battambang karst in Cambodia is 250 km to the northwest; the small tower karst of Danang in Vietnam [8] is 700 km to the north; and the huge karst of Ke Bang-Khammouane is over 750 km to the north. No significant active system is known in the MDL karst, due to the small size of the limestone hills, their isolation, and the low level (0–2 m a.s.l.) of the alluvial plain in which they are situated. Nevertheless, numerous small, hydrologically unconnected caves are present. Many are of archeological, aesthetic, or historical interest, such as the old Khmer temples and monasteries in several caves of the Cambodian part of the karst [9], the cave-temple at Chua Hang, or the Mo So Cave in MDL-HC, which served as an important logistics base of Vietnamese liberation troops during the Vietnam war, with an arsenal and an army hospital. Shell impacts and bomb craters can still be seen, and munitions were still numerous in the underground passages 25 years ago [10]. Even today, ordnance is sometimes found in and around MDL caves.

The MDL karst is constituted of loose clusters of small limestone outcrops intermixed with non-limestone hills. The northwest part of MDL in Cambodia (MDL-C) includes two groups of hills: the Kampot group and the Tuk Meas group. The Ha Tien cluster straddles the border between Cambodia and Vietnam (Area 1 of [8]). Southeast of Ha Tien, in Vietnam, the Hon Chong karst (MDL-HC) is formed of four clusters (Figure 1): the Kien Luong group, between the Giang Thanh River and the Ba Hon canal (Area 2 of [8]); the northern Hon Chong group, between the Ba Hon canal and Nui Binh Tri (Area 3 of [8]); the southern Hon Chong group, south of Nui Binh Tri (Area 4 of [8]); and the minute, isolated karst of Hon Nghe island, 15 km southwest of Nui Hon Chong.

The MDL-HC karst landscape ranges from gentle hills to spectacular pinnacle formations on steep slopes and extremely rugged, impassable karst terrain (Figure 2). Caves are numerous, but all are short and hydrologically inactive [8]. They can be assigned to three categories:

(1) 'Tidal caves'. These are smooth-surfaced, horizontal, shallow caves at sea level, devoid of speleothems, associated with horizontal undercutting of the hill circumference. Undercuttings (notches) are often visible at two or three levels. They may have been caused by acids released from the sulphidic mangrove mud acting as a dissolving agent, since mangrove woodland probably surrounded most limestone hills [11]. They sometimes develop in deeper hill-foot caves (Figure 2C,D).

(2) 'Hill-foot caves'. These resemble "tidal caves" in their smooth-surfaced walls, horizontal development and lack of speleothems, but they penetrate deep into the hill (Figure 2E). They are frequent in tropical tower karsts on alluvial plains [12]. They are hydrologically inactive or filled with slow-moving water connected to surface swamp waters in the MDL karst.

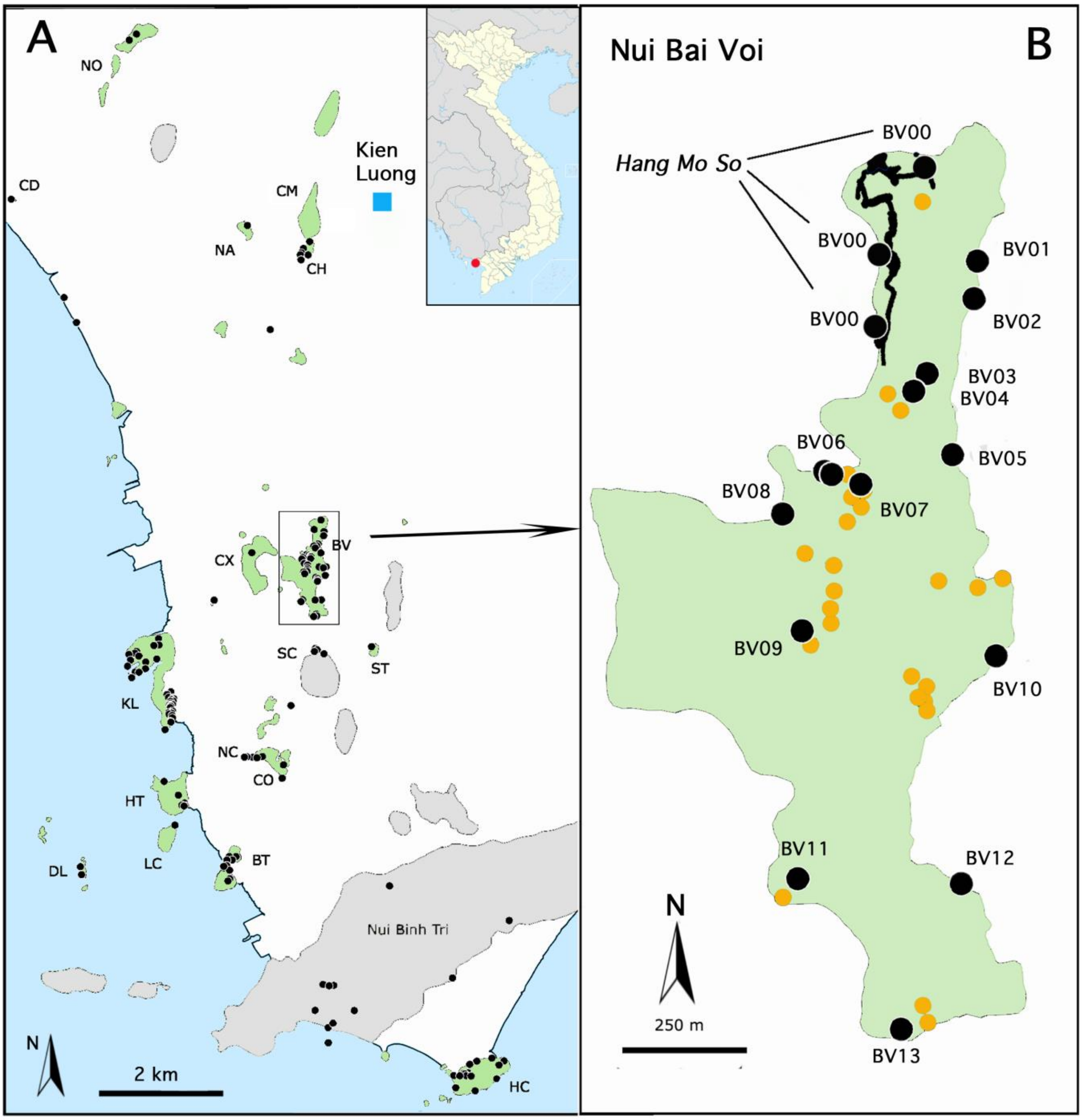

Figure 1. The MDL-HC karst. (**A**) Hills, islands and samples. Red dot on the inserted map, location of the MDLS-HC karst in Vietnam; blue square, the town of Kien Luong (Kien Giang Province); green, limestone hills; grey, non-limestone hills. Hill name abbreviations (Nui and Phnom mean hill, Hon means island, Hang means cave): BT, Nui Ba Tai; BV, Nui Bai Voi; CD, Nui Ca Danh; CH, Nui Chau Hang; CM, Nui Com; CO, Nui Hang Cay Ot; CX, Nui Cay Xoai; DL, Hon Da Lua; HC, Nui Hon Chong; HT, Nui Hang Tien; KL, Nui Khoe La; LC, Hon Lo Coc; LV, Nui Lo Voi; NA, Nui Nai; NC, Nui Coc; NO, Nui Ong; NT, Nui Trau; SC, Nui Son Cha; ST, Phnom Sray Toch. (**B**) Caves and samples in Nui Bai Voi. Black lines, main galleries of Hang Mo So; black circles, main entrances of sampled caves; orange circles, sites of soil and litter samples outside caves; one spot represents 1 to 20 samples. List of caves sampled in Nui Ba Voi: BV00, Hang Mo So, with its 3 main entrances; BV01, Guano Lake Cave; BV02, Roots Cave; BV03, Cliff Cave; BV04, Pass Cave; BV05, Hang Hei Truong; BV06, Old Man Caves; BV07, Feaellidae Cave; BV08, Hang Tai; BV09, French Man Cave; BV10, Cows Cave; BV11, Bai Voi SW cave 1; BV12, Hang Phat Man; BV13, Bai Voi SW cave 2.

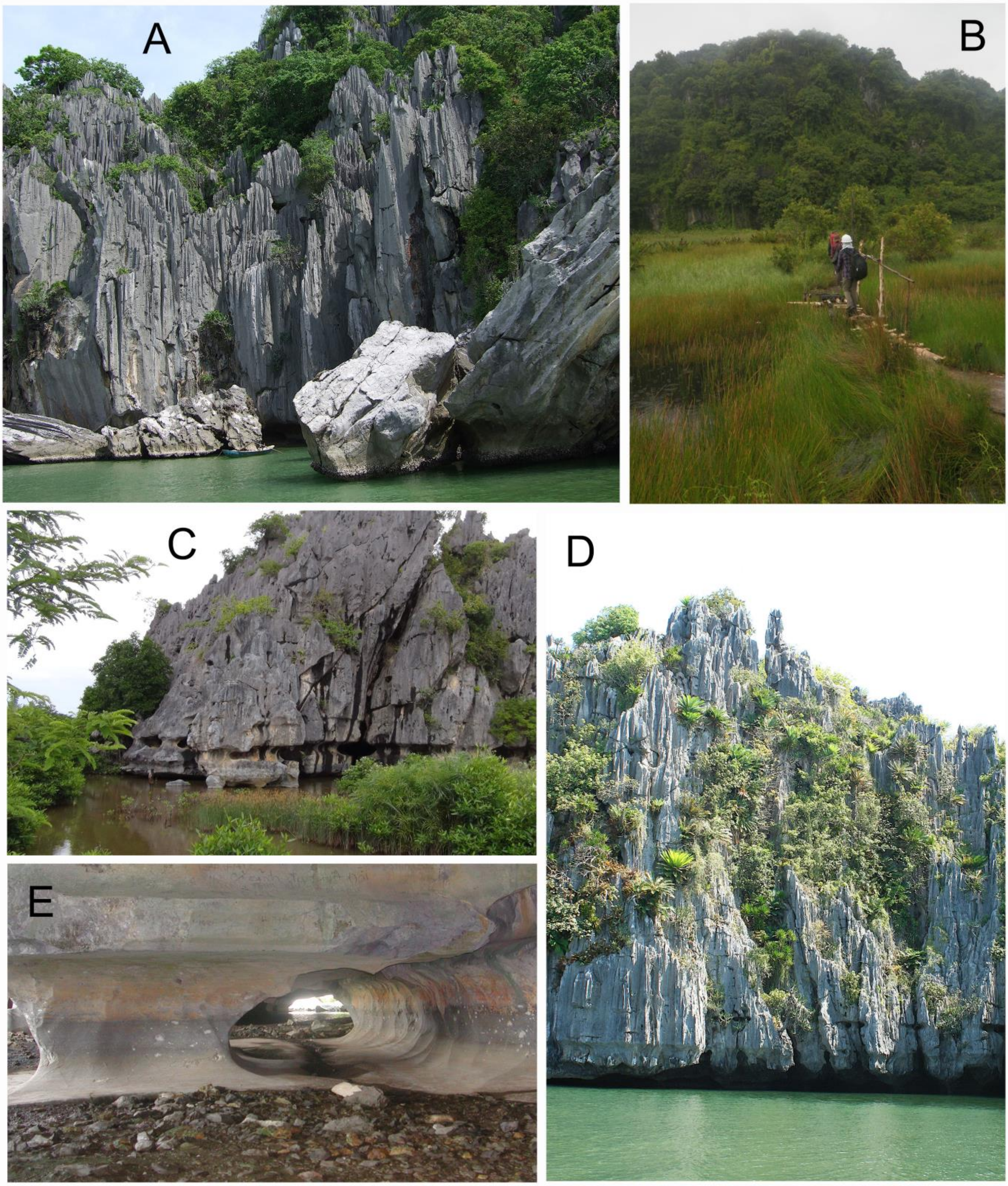

Figure 2. Karstic landscapes of Hon Chong hills: (**A**) sharp karstic relief along the coast of Nui Hon Chong; (**B**) southeast of Nui Bai Voi, access to the karst hill through marshes (ph. ML); (**C**) notches at Nui Hang Cay Ot; (**D**) a subvertical slope of Hon Da Lua with basal notches and specialized vegetation with *Cycas* on rocks; (**E**) network of galleries at entrance of Hang Mo So. Photos: Louis Deharveng (**A**,**C**–**E**), Marko Lukić (**B**).

(3) 'Phreatic or vadose caves'? These are formed by the dissolving action of rainwater seeping through rock fissures, or by flowing freshwater. They often have an uneven, tilted floor, and speleothems are common. In the MDL karst, phreatic caves are remnants of old cave systems dissected by surface erosion of the hills.

Eighteen caves of MDL-HC have been mapped [8,13], several others have been explored, and many remain to be discovered, especially shafts in almost impassable terrain. From 1993 to 2014, biologists and cavers extensively sampled many caves, particularly Hang Mo So (also called Hang Moi Chau in [8] and Grotte-hôpital in [13]). Hang Mo So, with 1 km of passages, is the longest cave of MDL (Figure 3).

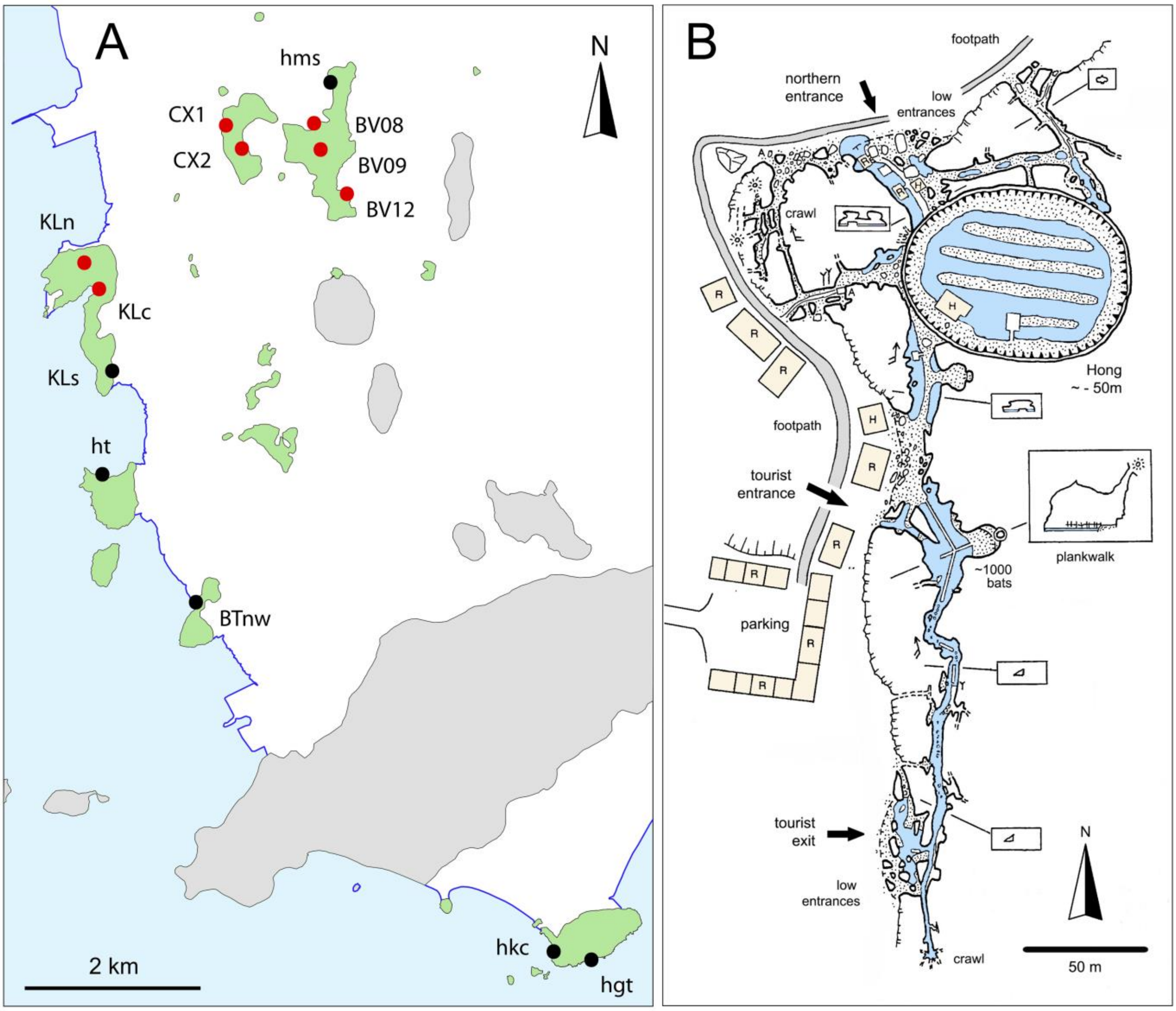

Figure 3. (**A**) Location of the MDL-HC caves cited in the text. Blue line, sea coastline; green, limestone hills; grey, non-limestone hills; black dots, richest caves in unquarried hills or parts of hills not planned to be quarried; red dots, caves of interest in hills quarried or planned to be quarried. BTnw, cave northwest of Nui Ba Tai; BV08, Hang Tai; BV09, French Man Cave; BV12, cave south of Nui Bai Voi; CX1, CX2, Nui Cay Xoai caves 1 and 2; hgt, Hang Gieng Tien; hkc, Hang Kim Cuong; hms, Hang Mo So; ht, Hang Tien; KLn, KLc, KLs, caves north, center and south of Nui Khoe La. (**B**) Map of Hang Mo So after Laumanns [8], modified; cave length 1003 m; survey dates, 6 and 8 July 2001. Blue, water; A, altar; H, house; R, restaurant.

Two other significant caves of MDL-HC penetrate almost perpendicularly into the hill, suggesting that larger systems existed in the past. These are Hang Gieng Tien in Nui Hon Chong, the southernmost hill of MDL-HC [8,13], and Hang Tien, a cave that runs through the northwestern arm of Nui Hang Tien (Figure 3A). Both contain a large array of oligotrophic habitats, unusual in the MDL karst, and host a rich fauna.

1.2. Description of Hang Mo So

Hang Mo So, the largest cave of Nui Bai Voi, extends 1003 m into the limestone. It was mapped and described in 1995 [13] and later, in more detail, in 2011 [8] (Figure 3B). Nui Bai Voi was formerly surrounded by mangroves and semi-natural wetlands, but these have been largely converted into commercial ponds. The main cement plant of MDL-HC is situated along the western side of Nui Bai Voi and most of the hill is currently being quarried (see Section 5.3). Hang Mo So is located at the northern tip of Nui Bai Voi, which is supposed to be left untouched (Figure 1B). Its main passages are horizontal and accessible to tourists. These include a large entrance hall, with a ceiling window and a lake, followed by a spacious (often over 3 $\times$ 3 m) phreatic gallery that leads to the southern entrances. This gallery often shows a keyhole cross-section, with its narrow lower cutting, more or less filled with brackish water or sediment. Brackish water is also present, at least seasonally, in most parts of the cave, flowing very slowly from south to north. The main hall is connected to a large central depression used for farming and fish ponds (annotated "hong" on the cave map). Several much smaller passages branch on each side of the main gallery, at the same level (Figure 2E). At the southernmost part of the cave, a low crawl has been followed for 30 m and might continue further. Calcite formations are small and rare throughout the cave.

Habitats in the cave are quite diverse. A colony of fruit bats that roosts in a large chimney near the entrance produces a big amount of guano. Impressive hanging root bundles are present near the entrance and further along the main gallery (Figure 4A). The limestone floor is covered with soil in the main hall, but often becomes exposed in the galleries, which are locally very damp, especially in short blind passages and in the southernmost low crawl. These passages have only sparse deposits of organic debris, approaching oligotrophic conditions. It is likely that most habitats at floor level are seasonally washed during flooding, with an unknown impact on the fauna. Human disturbance and pollution are obvious in most parts of the cave. Bags of concrete and sand are placed on the ground, a wooden walkway has been constructed along the entrance lake, and hanging roots have been cut (Figure 4). There are accumulations of rubbish in some recesses and numerous spots for religious offerings, with many incense sticks left along the main gallery [8].

1.3. History of Biological Studies

In 1970–1974 [14,15], Le Cong Kiet recognized two formations that characterize the unique vegetation of the MDL-HC karst:

(1) Cremnophyte and xerophilous shrub formations, dominated by *Cycas clivicola* subsp. *lutea*, *Euphorbia antiquorum*, and *Dracaena cambodiana*, which develop on patchy soil accumulated between exposed rocks and cliffs.

(2) Mesophilic tree formations, found in small patches on shallow soil, near the base of the hills and on low slopes. These may develop into a semi-deciduous forest dominated by *Tetrameles nudiflora*, *Diospyros crumenata*, *Sterculia foetida*, and *Ficus* spp. The most significant example was on Nui Com near Kien Luong, but the hill was totally erased by quarrying shortly after the publication of Le Cong Kiet's study. Roots of *Ficus* spp. host rich subterranean invertebrate communities in Hang Mo So and in several other caves of MDL-HC.

The MDL-HC flora is not species-rich, but several micro-endemic phanerogams that are strictly linked to limestone habitats have been described from there [16–18], providing additional evidence for the interest of this karst.

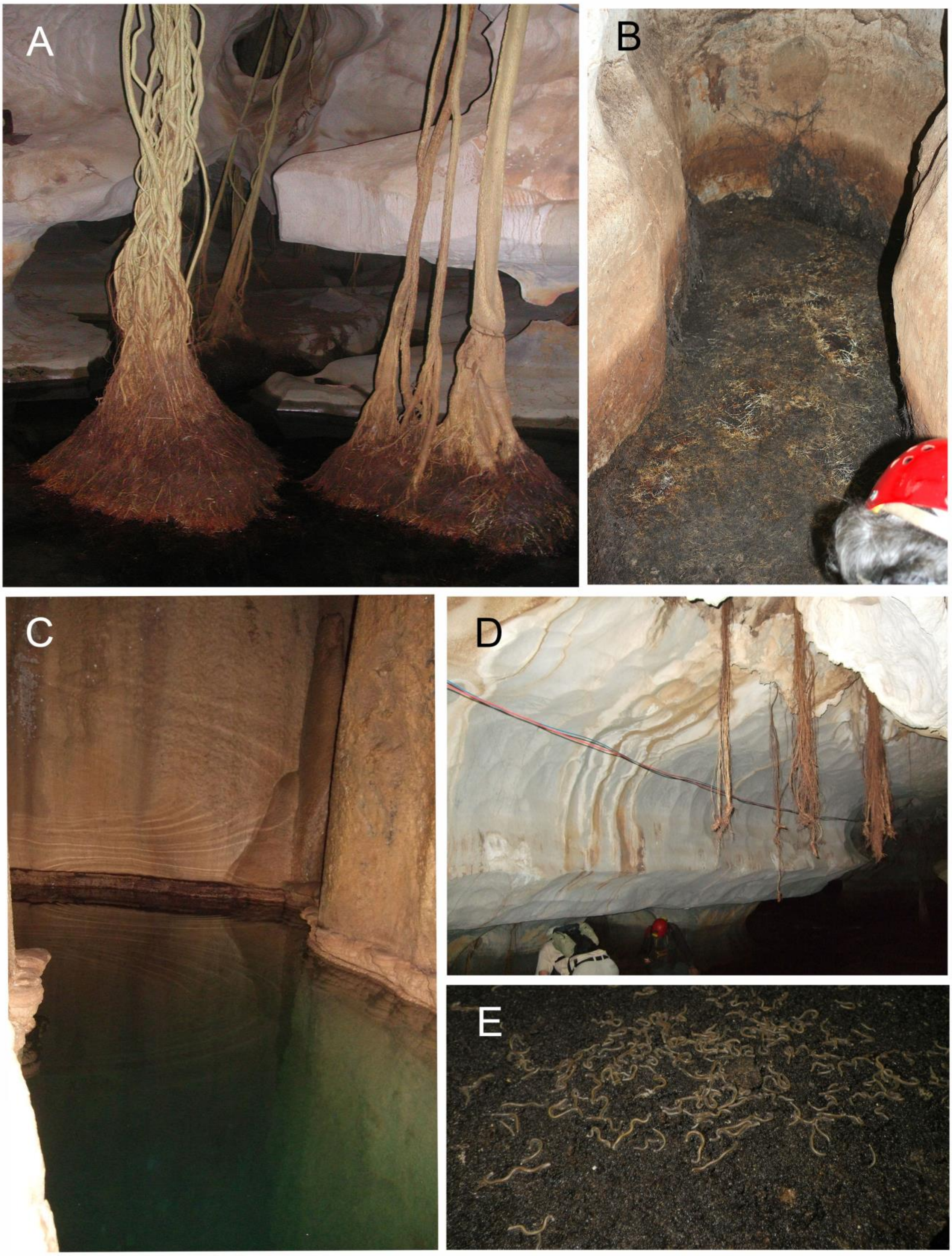

Figure 4. Cave habitats: (**A**) hanging roots in Hang Mo So; (**B**) root-mat in cave BV08 of Nui Bai Voi; (**C**) deep freshwater lake in Hang Gieng Tien (Nui Hon Chong); (**D**) hanging roots cut in the touristic gallery of Hang Mo So in 2008; (**E**) swarming of *Trachyjulus singularis* on guano in the cave of Hon Lo Coc. Photos: Louis Deharveng (**A**,**C**,**D**), Anne Bedos (**B**), Marko Lukić (**E**).

Research on the cave and soil fauna in MDL-HC started 20 years after the pioneering work of Le Cong Kiet, with two Franco-Vietnamese biological surveys in 1993 and 1994. These evaluated the invertebrate biodiversity value of selected caves and limestone hills, where drilling had just started as a prelude to quarrying. They discovered several cave endemics from various zoological groups. The first described species were two troglobionts: the springtail *Lepidonella lecongkieti* Deharveng & Bedos, 1995 and the beetle *Eustra honchongensis* Deuve, 1996. These results provided the impetus for a succession of biological excursions up to 2014, which yielded an exceptionally rich cave, soil and limestone associated fauna, including new endemic species and supra-specific taxa, especially among snails and soil beetles.

In 2001, Deharveng et al. [19] listed nine troglobionts for MDL-HC, seven of which were undescribed. At the same time, Boutin [20] reported four troglobionts for MDL-C, none of which were shared with MDL-HC. By 2009, the troglobiotic invertebrate richness had increased to 30 species for MDL-HC, while remaining unchanged for MDL-C [21]. Some additional troglophilic or guanobiotic taxa were later recorded by Steiner [22] from several caves of the MDL karst.

1.4. Threats and Focus

We focus on the MDL-HC karst for two reasons. Firstly, it is currently the best-known part of MDL. Many micro-endemic and relictual invertebrates have been discovered in these hills, whereas the MDL-C karst remains insufficiently investigated. Secondly, the threats to this karst are more acute than for any other karst in the world [21,23]. Quarrying on a massive scale since the 1990s has erased entire hills, critically endangering a greater number of species than in any other subterranean system, with the possible exception of the karstic groundwater fauna of the Dutch Caribbean island of Curaçao [24]. Several spots of high aesthetic and biological value (Nui Com, Nui Cay Xoai, and the natural cirque at the center of Nui Bai Voi) have been irreversibly lost to limestone exploitation, despite the international efforts led and coordinated by Tony Whitten [25] to curb the appetites of mining companies [26]. At present, many of the largest limestone hills have either been erased (Nui Trau, Nui Com, Nui Cay Xoai) or are undergoing destruction (most of Nui Bai Voi, Nui Khoe La, Nui Hang Cay Ot), thus increasing the risk of extinction for micro-endemic species. In addition, one remarkable landmark in the flat and densely populated Mekong Delta—Hang Mo So—is being degraded by an increasing flux of tourists.

In most parts of MDL-HC, the severity of conservation threats is obvious at a glance. We therefore analyse the cave fauna of Hang Mo So (the focus of the present paper) in the context of the hill in which it is situated, namely Nui Bai Voi (Figure 1B), and the wider Hon Chong cluster of hills (Figure 1A). This extended coverage provides an idea of the number of troglobionts that have not yet been collected and of the proportion of site endemics in the fauna, several of which are on the brink of extinction.

2. Materials and Methods

2.1. Assessment of the Ecological Status of Species

Many publications define, or refine, the concepts of troglophiles, stygophiles, troglobionts and stygobionts. However, the grounds on which the ecological status of a species is assessed are less frequently addressed (but see [27,28]), despite the importance of understanding the degree of dependence on the subterranean environment when evaluating cave biodiversity.

Caves in the MDL-HC karst are usually short and shallow, with frequent terrestrial and aquatic connections to the exterior, allowing constant inputs of nutrients. This results in cave communities dominated by troglophiles and tramp species, making the ecological category assessment of individual species hazardous. We have therefore adopted four approaches:

(1) Morphological inference, based on the presence or absence of troglomorphic traits. This approach is straightforward but raises two caveats. Firstly, depigmentation and

eye reduction are frequently considered troglomorphic, but they actually occur in most deep-soil species as well. Thus, a cave arthropod that has these two characteristics can only be qualified as troglomorphic if additional traits are present that have been established as cave-dependent [29], such as appendage elongation or larger body size. It is these additional traits that make the difference between troglomorphic species, which are almost always linked to subterranean life, and euedaphomorphic species, which dominate in the deep soil but are also present in caves. Secondly, troglomorphy is clearly linked to cave-restricted life, whereas euedaphomorphy can be linked to either cave or soil life. Since cave invertebrates are more often euedaphomorphic than troglomorphic, especially in lowland caves of the humid tropics like MDL-HC, morphological inference alone will not work for them.

(2) Parallel-sampling inference, based on the occurrence of species outside subterranean habitats. Many species found in caves are described as troglobionts in the literature, even though they do not exhibit typical troglomorphic traits, or only show euedaphomorphic traits similar to those of many deep-soil species. The absence of a species outside caves can be a good indicator in such cases. This information is often available in the literature for well-investigated regions, but not for the tropics, where it is thus necessary to gather data both inside and outside caves in comparable microhabitats. Extensive parallel sampling in the MDL-HC karst, with 270 cave samples and 674 non-cave samples (including 322 in mineral soil), allows a reasonably reliable ecological status assessment. Because the strength of such inference depends on sampling effort and species frequency, it will be less reliable for species with low population densities or patchy distributions.

(3) Taxonomic inference, based on the ecological status of related taxa. Certain groups are particularly prone to diversify in subterranean habitats, even though the underlying biological mechanisms are not well understood [30–32]. This may cast suspicion on the putative troglobiont status of a species when it belongs to a group that is otherwise not known for having cave-obligate species.

(4) Barcoding inference, based on levels of genetic divergence between populations. Cryptic diversity poses problems for the recognition of species using morphological characters alone. Molecular barcoding often reveals lineages with identical morphologies that show divergence levels as high as those encountered between traditional morphospecies, as has been demonstrated for several Collembola [33]. Moreover, such cryptic lineages may differ in their degree of dependence on cave habitats [34]. Molecular sequencing can, therefore, provide greater accuracy in the delimitation and ecological characterization of species. Another advantage is that it can allow otherwise unidentifiable larval forms to be correlated with their adult stages, especially in insects.

Here, we classify as a troglobiont (TB) or stygobiont (STB) a species (or morphospecies) that has been collected exclusively in caves and exhibits unambiguous troglomorphic traits, or that has euedaphomorphic traits (reduced eyes or/and depigmentation) without being known from soil. We consider as a putative troglobiont ("TB?") or stygobiont ("STB?") a species (or morphospecies) that shows neither euedaphomorphic nor troglomorphic traits, but has been collected exclusively in caves (e.g., guano-associated species). In the latter case, the assessment is less reliable when the species is rare.

We classify as a troglophile or a stygophile a species (or morphospecies) that has been collected in both caves and non-cave habitats in significant numbers, or is numerous in subterranean communities even if much less so than in the outside (as is the case for several tramp species), or is mostly found in the twilight zone. Troglophiles in Hon Chong caves are either eutroglophiles or subtroglophiles [29]. It is noteworthy that parietal communities in the MDL-HC caves and in the tropics include both eutroglophiles and non-seasonal subtroglophiles, whereas seasonal subtroglophiles largely dominate in temperate caves.

2.2. Sampling

2.2.1. Sampled Habitats

Though limited in extent, the MDL-HC karst displays a wide range of surface habitats due to its rugged relief. Adjacent microhabitats may differ greatly in soil thickness, inclination, limestone denudation, drainage and vegetation. Within caves, we sampled soil, roots (root-mats and hanging roots), habitats rich in nutrients (guano piles, scattered bat feces, organic debris from outside, water rich in organic matter and human-generated debris), nutrient-poor (oligotrophic) habitats (clay, speleothem surface, lakes, puddles, dripping water and endogenic streamlets), screes and boulders, and habitats at the subterranean/epigean interface (entrance zone, walls, springs and soil/limestone bedrock interface) (Figure 4). Non-limestone hills and the alluvial plain were also sampled for comparison. Terrestrial habitats were extensively sampled, but aquatic habitats only occasionally.

Soils and roots, which are often neglected in biological surveys, received special attention. In the caves of MDL-HC, soils are often rich in organic matter and in fauna, due to the massive input of material from the outside, through karst windows or water movement across the swamp areas of the alluvial plain, and the frequent occurrence of bats. Roots of *Ficus* (12 species in the area [15]) are common in subterranean passages, due to the shallowness of the caves and the deeply dissected karst. These occur as isolated roots or in dense aggregates of finer, hanging roots (Figure 4A,B,D). Less frequently, rootlets form a dense carpet on the floor of some passages that are probably flooded during the rainy season. Cave roots may host a rich and characteristic fauna in both groundwater [35] and terrestrial habitats [36–38], as was the case in Hang Mo So and several MDL-HC caves (see below).

2.2.2. Parallel Sampling and Techniques

For the reasons explained in (Section 2.1), we systematically carried out parallel sampling during surveys, pairing inside cave and external sampling. Samples taken outside caves outnumbered those from inside caves, in order to cover the higher diversity of surface microhabitats and offset patchy distributions.

Sampling techniques used for the aquatic fauna were limited to netting and filtration of water from puddles or lakes. The terrestrial fauna was much more extensively sampled by means of various techniques both inside and outside caves, combining techniques traditionally used in soil and subterranean arthropod surveys [39,40] with other more rarely employed methods (5 and 6 below):

(1) Collection by sight (timed or not timed) using a fine brush or pooter in all visited caves
(2) Bulk extraction of arthropods on Berlese funnels from litter and soil cores of standardized volumes, associated with larger unstandardized samples for rare species
(3) Sieving litter and debris for arthropods and gastropods
(4) Baiting and pitfall trapping for arthropods active on the ground—this being the only technique that produces significant numbers of invertebrates in oligotrophic cave habitats
(5) Beating of hanging roots in caves
(6) Mineral soil washing to collect deep-soil arthropods by flotation
(7) Flotation of litter and debris for snails

3. Results

The cave-obligate species or morphospecies of Hang Mo So and other MDL-HC caves (Figures 1 and 3) are listed in Table 1. Here, we comment on them, explaining the rationale for their ecological status. We also place them in their wider taxonomic and ecological contexts, and provide basic information on the main troglophilic species in the area. Authorship of stygobiotic and troglobiotic species is given in Table 1 and not repeated in the text.

Table 1. List of stygobionts and troglobionts of MDL-HC, with emphasis on Hang Mo So. Columns: Ecol, ecological category of species (STB, stygobiont; TB, troglobiont; "?", when uncertain); RL, published IUCN category for red-listed species (CR, critically endangered; EN, endangered; NT, near threatened; VU, vulnerable); End: single hill endemic; HMS, number of samples that contained the species in Hang Mo So; NBV, caves of Nui Bai Voi (number of samples that contained the species in parentheses), cave numbers as in Figure 1B; MDL-HC: hills of MDL-HC (number of samples that contained the species in parentheses), hill abbreviations as in Figure 1A.

Taxon	Species	Ecol	RL	End	HMS	NBV	MDL-HC
Gastropoda: Pomatiopsidae							
	Pseudoiglica sp.	STB		x	0		HC (2)
Actinotrichida: Leeuwenhoekiidae							
	gen. sp.	TB			1	bv00 (1), bv10 (1), bv12 (2)	BV (4), HT (1), KL (1)
Anactinotrichida: Opilioacaridae							
	Siamacarus sp.	TB			0	bv12 (1)	BV (1), HC (2), KL (2), LC (1), NA (1)
Amblypygi: Charinidae							
	Weygoldtia sp.	TB?			3	bv00 (3), bv12 (2), bv13 (1)	BT (1), BV (6), HC (8), KL (1), LC (1), NA (1)
Araneae: Ctenidae							
	gen.sp. 1	TB		x	0		KL (1)
	gen. sp. 2	TB			5	bv00 (5), bv08 (1), bv11 (1), bv12 (1), bv13 (1)	BT (1), BV (9), CH (1), HC (1), HT (3), KL (3), NA (1), NO (1)
Araneae: Halonoproctidae							
	Latouchia schwendingeri Decae, 2019	TB		+	0		HT (1)
Araneae: Ochyroceratidae							
	gen. sp. 1	TB?		x	0		BT (1)
	gen. sp. 2	TB			0		BT (1), HC (3)
	gen. sp. 3	TB?			0	bv12 (2)	BT (2), BV (2), KL (2), NO (1)
Araneae: Oonopidae							
	gen. sp. 1	TB?		x	0	bv12 (1)	BV (1)
	gen. sp. 2	TB			3	bv00 (3), bv08 (1)	BV (4), KL (1)
	gen. sp. 3	TB?			0	bv13 (1)	BT (1), BV (1)
Araneae: Pholcidae							
	gen. sp. 1	TB?		x	0		NA (1)
	gen. sp. 2	TB			0	bv13 (1)	BT (2), BV (1), HC (1), LC (1), NA (1)
	gen. sp. 3	TB?			0		HC (1), NA (1)
	gen. sp. 4	TB?			1	bv00 (1), bv08 (1)	BV (2), HC (1), KL (1)
Araneae: Telemidae							
	gen. sp. 1	TB?		x	0		HC (1)
	gen. sp. 2	TB?		x	1	bv00 (1)	BV (1)
	gen. sp. 3	TB?		x	0	bv13 (1)	BV (1)
	gen. sp. 4	TB		x	0		KL (2)
	gen. sp. 5	TB?		x	0	bv13 (1)	BV (1)
Araneae: Tetrablemmidae							
	gen. sp.	TB?		x	1	bv00 (1)	BV (1)
Opiliones: Epedanidae							
	gen. sp. 1	TB			4	bv00 (4), bv09 (1)	BT (1), BV (5)
	gen. sp. 2	TB		x	0		HC (1)
Opiliones: family undet.							
	gen. sp.	TB?			0		BT (1)
Pseudoscorpiones: Chthoniidae							
	Lagynochthonius fragilis Judson, 2007	TB		x	5	bv00 (5)	BV (5)

Table 1. *Cont.*

Taxon	Species	Ecol	RL	End	HMS	NBV	MDL-HC
Diplopoda: Haplodesmidae							
	gen. sp.	TB?		x	1	bv00 (1)	BV (1)
Diplopoda: Pyrgodesmidae							
	gen. sp.	TB			0		HC (1), HT (1)
Diplopoda: Trichopolydesmidae							
	gen. sp.	TB?			0		HT (1)
Diplopoda: Siphonophoridae				x			
	gen. sp.	TB?		x	1	bv00 (1)	BV (1)
Diplopoda: Cambalopsidae							
	Glyphiulus sp.	TB?			0		BT (3), NC (1)
	Trachyjulus singularis Attems, 1938	TB?			14	bv00 (14), bv01 (3), bv05 (2), bv08 (3), bv09 (1), bv10 (1), bv11 (1), bv12 (3), bv13 (1)	BV (29), CH (2), HT (4), KL (6), LC (3), NA (3)
Diplopoda: Stemmiulidae							
	Eostemmiulus caecus Mauriès, Golovatch & Geoffroy, 2010	TB	CR	x	1	bv00 (1)	BV (1)
Amphipoda: Bogidiellidae							
	gen. sp.	STB		x	0		BT (1)
Isopoda Oniscidea: family undet.							
	gen. sp.	TB?		x	0		BT (1)
Isopoda Oniscidea: Armadillidae							
	Sumatrillo sp.	TB	VU		0		HC (1), HT (2)
Isopoda Oniscidea: Philosciidae							
	Burmoniscus sp.	TB	EN	x	3	bv00 (3), bv12 (2)	BV (5)
	gen. sp.	TB?		x	0		LC (1)
Isopoda Asellota: Stenasellidae							
	Stenasellus sp.	STB		x	0		HC (1)
Collembola: Hypogastruridae							
	Acherontiella sp.	TB?		x	0		NO (1)
	Ceratophysella sp.	TB	CR	x	0		HC (1)
Collembola: Tullbergiidae							
	gen. sp.	TB			0		BT (1), HT (1), LC (1), NC (1)
Collembola: Entomobryidae							
	Acrocyrtus (cf.) sp.	TB	VU	x	0		KL (1)
	Ascocyrtus sp.	TB?		x	1	bv00 (1)	BV (1)
	Coecobrya sp.	TB		x	1	bv00 (1), bv11 (1)	BV (2)
	Lepidocyrtinae gen. sp.	TB			0		BT (1), LC (1)
	Lepidosinella sp.	TB			2	bv00 (2)	BV (2), KL (1)
Collembola: Isotomidae							
	Folsomides anops Deharveng, Bedos & Lukić, 2020	TB	VU	x	0		BT (2)
	Folsomides whitteni Deharveng, Bedos & Lukić, 2020	TB		x	2	bv00 (2), bv08 (3)	BV (5)
Collembola: Paronellidae							
	Lepidonella lecongkieti Deharveng & & Bedos, 1995	TB	NT		7	bv00 (7), bv01 (2), bv08 (3), bv12 (2), bv13 (3)	BT (3), BV (17), CH (1), HC (6), HT (8), KL (9), NA (1), NO (2)
	Lepidonella sp.	TB?		x	1	bv00 (1)	BV (1)

Table 1. *Cont.*

Taxon	Species	Ecol	RL	End	HMS	NBV	MDL-HC
Collembola: Neelidae							
	Spinaethorax adamantis Schneider & Deharveng 2017	TB		x	0		HC (4)
	Spinaethorax sp. 1	TB		x	0	bv01 (1)	BV (1)
	Spinaethorax sp. 2	TB?		x	0		NC (1)
Diplura: Japygidae							
	gen. sp.	TB?		x	0	bv01 (1), bv12 (1)	BV (2)
Zygentoma: Family ind.							
	gen. sp.	TB			0	bv13 (1)	BV (1), HC (1)
Zygentoma: Nicoletiidae							
	gen. sp. 1	TB?		x	0		BT (1)
	gen. sp. 2	TB		x	1	bv00 (1)	BV (1)
Blattodea: Nocticolidae							
	Spelaeoblatta sp.	TB			4	bv00 (4), bv01 (1), bv08 (1), bv12 (1), bv13 (1)	BV (8), CH (1), KL (3), NA (1)
Coleoptera: Carabidae							
	Eustra honchongensis Deuve, 1996	TB	EN	x	4	bv00 (4), bv01 (1), bv12 (1), bv13 (1)	BV (7)
Coleoptera: Curculionidae							
	gen. sp.	TB			0		BT (1), KL (1)
Coleoptera: Tenebrionidae							
	Harvengia vietnamita Ferrer, 2004	TB	EN		0		BT (2), CO (1), HC (5), KL (1)
	Pseudochillus honchongensis Schawaller & Faille, 2023	TB		x	1	bv00 (1)	BV (1)
Heteroptera: Reduviidae: Harpactorinae							
	gen. sp.	TB?			0	bv12 (1)	BV (1), HC (1), NA (1), NC (1)
Heteroptera: Schizopteridae							
	gen. sp.	TB?		x	0		BT (1)
Homoptera: Cixiidae							
	gen. sp. 1	TB			2	bv00 (2), bv07 (1), bv08 (1), bv11 (1), bv12 (1), bv13 (2)	BT (1), BV (8), CO (1), KL (2)
	gen. sp. 2	TB		x	0		KL (2)
Homoptera: Delphacidae							
	gen. sp.	TB		x	1	bv00 (1), bv08 (2)	BV (3)
Homoptera: Kinnaridae: Kinnarini							
	gen. sp.	TB?		x	1	bv00 (1)	BV (1)
Total				**43**	**27**	**38**	**70**

3.1. Gastropoda (Snails)

The land snail fauna (including several introduced species) of the MDL-HC karst is an 'island fauna' [41] with relatively few species (only 87 recorded so far). Many species that are common and widespread in Indochina are notably absent. However, the rate of endemism (to MDL or parts of MDL) is staggering: 52 species or 60% of the fauna, with several groups still in need of investigation. Snail surveys in the MDL karst were aimed at collecting shells rather than the entire organisms. The resulting collection provides an adequate overview of the fauna, but it is biased against slugs and semi-slugs and does not allow the observation of adaptations to cave life. None of the collected species can be qualified as a troglobiont, but several are considered troglophiles here because they are also found in deep-soil samples [42], and one is a stygobiont.

Several genera found in soils and caves of MDL are of special interest. *Macrochlamys psyche* Vermeulen, Luu, Theary & Anker, 2019 (Ariophantidae) (Figure 5A) is endemic to Nui Bai Voi and nearby Nui Khoe La, and is frequent in Hang Mo So. The genus *Speleocyclotus* Vermeulen, Luu, Theary & Anker, 2019 (Cyclophoridae) was established to accommodate four endemic MDL species. Among these are *S. macrocoryphe* Vermeulen, Luu, Theary & Anker, 2019 (Figure 5B), from soil and nutrient-poor areas in a cave in Nui Hon Chong, and *S. microcoryphe* Vermeulen, Luu, Theary & Anker, 2019, from Hang Mo So and deep soil deposits in Nui Bai Voi, and three localities in Cambodia. Elsewhere, the genus occurs in the Malaysian Peninsula. The troglophilic genus *Notharinia* Vermeulen, Phung & Truong, 2007 (Diplommatinidae) is represented in MDL by 10 tiny (ca 2 mm long) species with partly overlapping ranges. Surprisingly, none have been reported yet from the most intensely sampled hill, Nui Bai Voi, although nearby Nui Khoe La is home to two site-endemic [43] species. Elsewhere, the genus is only known from two species, one from northern Laos and one from Sarawak. Finally, the cave Hang Gieng Tien in Nui Hon Chong has, at its end, a basin of a few cubic meters (Figure 4C), which is the only known locality of a site-endemic hydrobioid freshwater snail, probably of the genus *Pseudoiglica* Grego, 2018.

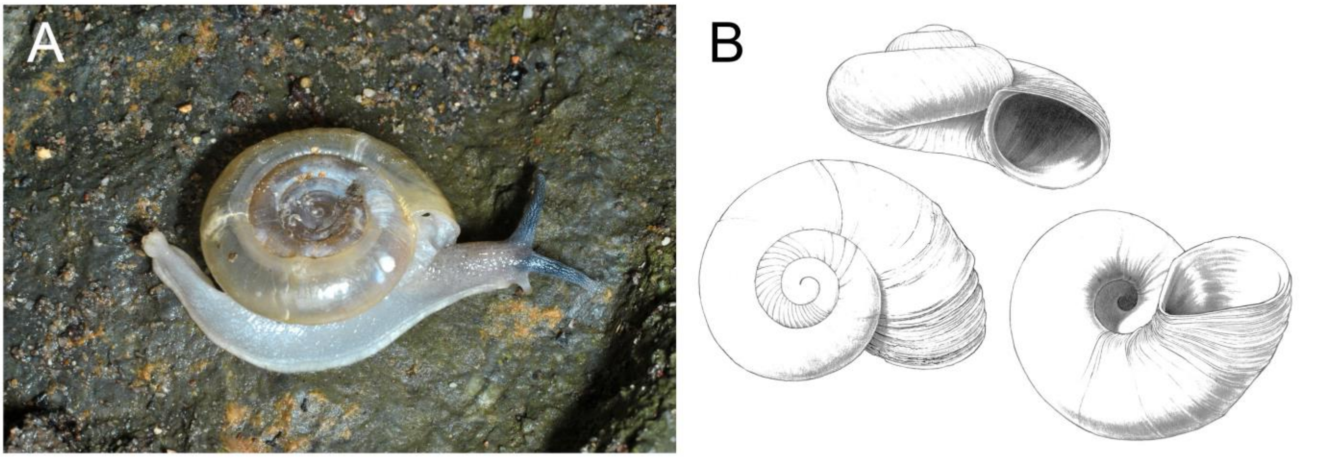

Figure 5. Gastropoda: (**A**) *Macrochlamys psyche*; (**B**) *Speleocyclotus macrocoryphe.* Photo and drawings: Jaap Vermeulen.

3.2. Arachnida

- Anactinotrichida (parasitiform mites)

An opilioacarid of the genus *Siamacarus* Leclerc, 1989 is remarkable for its extremely elongated legs (Figure 6A). It has only been collected in caves, mostly under loose rocks. It was not found in Hang Mo So, but it occurred in cave BV12 of Nui Bai Voi and in six other MDL-HC caves. Otherwise, *Siamacarus* is only known from two cave species in southern Thailand [44].

- Actinotrichida (acariform mites)

Very few cave mites have been identified from Southeast Asia [45]. The numerous small mites associated with guano have not been analyzed in the present study, but a large obligate cave species collected in Hang Mo So belongs to Leeuwenhoekiidae (Figure 6B), a family of Trombidioidea that occurs frequently in caves of Southeast Asia.

Caecothrombium deharvengi Makol & Gabrys, 2005 is only known from deep soil in the twilight zone near an entrance of Hang Tien in Nui Hang Tien. It is one of the three species of the monogeneric subfamily Caecothrombiinae (Eutrombidiidae). The species is small (body length about 1 mm), eyeless, and clearly euedaphomorphic, but it is not possible to reliably determine its ecological status because most mites in our samples remain unidentified.

Figure 6. Arachnida: (**A**) *Siamacarus* sp. from a cave of Nui Nai; (**B**) *Leeuwenhoekiidae* sp. from Hang Tien (Nui Hang Tien); (**C**) *Ctenidae* sp. 2 from cave BV08 of Nui Bai Voi; (**D**) *Telemidae* sp. 5 from cave BV13 of Nui Bai Voi; (**E**) *Ochyroceratidae* sp. 2 from Hang Kim Cuong (Nui Hon Chong); (**F**) *Epedanidae* sp. 1 from cave BV09 of Nui Bai Voi; (**G**) *Gnomulus bedoharvengorum* from cave BV12 of Nui Bai Voi; (**H**) *Isometrus (Reddyanus) deharvengi* from Hang Gieng Tien (Nui Hon Chong); (**I**) *Lagynochthonius fragilis* from Hang Mo So. Photos: Louis Deharveng (**B**–**F**), Marko Lukić (**A**,**G**,**I**), Elise-Anne Leguin from the Museum national d'Histoire naturelle, Paris (**H**).

- Amblypygi (whip spiders)

Three species of Amblypygi are present in MDL, but only one, *Weygoldtia* sp. (probably the same as "cf. *Sarax*" in [22] and *Stygophrynus* sp. in [19]), has been found in MDL-HC, including Hang Mo So. Elsewhere, three species of *Weygoldtia* are known from surface habitats and under stones in Southeast Asia [46–48]. However, Zhu et al. [49] found another species in Hainan, China, in karst crevices—a habitat that has not been sampled intensively in MDL-HC. Therefore, we consider the Hon Chong *Weygoldtia* a questionable troglobiont, even though it is currently only known from caves.

- Araneae (spiders)

With the possible exception of mites, spiders are the most diverse terrestrial invertebrates in the caves of MDL-HC. Many of the species collected are troglophiles or trogloxenes, and several are probably troglobionts (Figure 6C–E). They have yet to be studied taxonomically. Interpreting a spider as a troglobiont or troglophile can be difficult, even in temperate lineages [50]. In MDL-HC, the diversity and euedaphomorphic morphology of the many small species from soil or caves makes the task particularly complicated, even with parallel sampling. A number of these species, which are rather similar in appearance, are not included in our list since they were mostly obtained from soil samples and are often immature.

Anapidae. One species, probably *Pseudanapis paroculus* (Simon, 1899), was collected twice in Hang Mo So. It is also present in the nearby cave of Son Cha. In the Kien Luong karst, it was found outside caves on Nui Chau Hang. It is known from soils elsewhere in SE Asia [51].

Ctenidae. A rather large species, possessing eyes but devoid of pigment, is the most common troglobiotic spider in the caves of MDL-HC. It was not found outside caves. A similar, but eyeless, species was found only in the southern cave of Nui Khoe La.

Mygalomorphae. Three troglophilic mygalomorphs have been recorded in caves of MDL-HC: a species of Ctenizidae, found in six caves of MDL-HC, including Hang Mo So, and in a single litter sample on Nui Ba Tai; *Latouchia schwendingeri* (Halonoproctidae), a small species known only from the type locality, Hang Tien in Nui Hang Tien [52]; and a relatively large species found in soil on Nui Bai Voi and Nui Hon Chong, and in caves at Nui Ba Tai and Nui Chau Hang.

Ochyroceratidae and Telemidae occur rather frequently in the Hon Chong caves and soils. They are small (less than 2 mm), with reduced pigmentation and eyes. Six morphospecies belong to Telemidae: five are rare troglobionts (including one in Hang Mo So) and the sixth is frequent in caves of MDL-HC, but also present in the soil. Three cave morphospecies belong to Ochyroceratidae, of which one, from some Nui Ba Tai and Nui Hon Chong caves, probably belongs to the speciose genus *Speocera*, known from caves and soil in Southeast Asia [53].

Oonopidae. Five morphospecies of this family are restricted to caves of MDL-HC. That from BV12 in Nui Bai Voi has a reduced number of unpigmented eyes. The other two, from Bai Voi Hill, have well-developed eyes; one, with a small dorsal plate on the abdomen, occurs in three caves, including Hang Mo So. Surprisingly, the only blind morphospecies of Oonopidae encountered in MDL-HC was collected more frequently from soil than from caves.

Pholcidae. Five morphospecies of Pholcidae occur in the MDL-HC caves. All have eyes, but their bodies are, at most, feebly pigmented. One, with pale patches of pigment on the abdomen, was found in several caves but never outside; three others are potential troglobionts, but, because of the rarity of adult specimens in our samples, we cannot now confirm their ecological status.

Sparassidae. Steiner [22] recorded *Heteropoda* sp. in only one cave of MDL-HC while citing it as present in several caves in the nearby mountain of Da Dung, close to Ha Tien. We confirm this unusual rarity of huntsman spiders, which are otherwise very common in most Southeast Asian caves.

Tetrablemmidae. Few cave species were known in the 1980s [54], but several have since been described, particularly from southern China [55]. A single species occurs in Hang Mo So and seems to be limited to this cave. Elsewhere in MDL-HC, two widespread eyed morphospecies are troglophiles. Another blind species, found in two caves and in the outside soil, is also present in MDL-C.

- Opiliones (harvestmen)

Harvestmen (Laniatores) are rare but diverse in caves of MDL-HC (Figure 6F,G). *Gnomulus bedoharvengorum* Schwendinger & Martens, 2006 (Sandakanidae) is a robust troglophile from Hang Mo So, Hang Tien, and the soils of Nui Bai Voi and Nui Hon Chong [56]. Later, it was also collected on Nui Khoe La. A long-legged, unpigmented but eyed Epedanidae, resembling morphospecies from several caves of Southeast Asia, was found as isolated individuals in oligotrophic habitats in two caves of Nui Bai Voi and one cave of Nui Ba Tai, on walls and on the floor. In the latter cave, it co-occurs with another troglobiont harvestman, unidentified to family. In Hang Gieng Tien cave (Nui Hon Chong), a cave-adapted Epedanidae and a less modified Tithaeidae occur. Interestingly, a small, unpigmented Petrobunidae with reduced eyes is common in soil and litter, but rare inside caves (only in Nui Ba Tai).

- Palpigradi

Palpigradi are common in soils, but were only collected in six MDL-HC caves, including Hang Mo So. Two genera occur in soil: *Eukoenenia* (Börner, 1901) and *Prokoenenia* Börner, 1901 [21]. The cave specimens, not identified to genus, are provisionally classified as troglophiles. The two caves in Southeast Asia where Palpigradi have been studied, Tham Chiang Dao in Thailand and Towakkalak in Sulawesi, each hosted two different species [6,57–59]. Cave species can, therefore, be expected in our unidentified MDL-HC material.

- Pseudoscorpiones

One species, the chthoniid *Lagynochthonius fragilis* (Figure 6I), is a troglobiont restricted to Hang Mo So [60]. An undescribed species of *Cryptocheiridium* (Chamberlin, 1931) (Cheiridiidae) has been found in deep soil at the entrance of cave BV03 on Nui Bai Voi. Two Feaellidae are known in the MDL karstic hills: *Cybella deharvengi* Judson, 2017 from Nui Bai Voi (in the small cavity BV07) and near Hang Mo So (in soil), and *Cybella bedosae* Judson, 2017 from a shallow cave of MDL-C. The subfamily Cybellinae was erected for the new genus *Cybella* and *Protofeaella* Henderickx, 2016, a fossil genus from Burmese amber [61]. Later, two additional *Cybella* species were described from caves in Malaysia [62]. These records are of biogeographical interest because Feaellidae were previously unknown from Southeast Asia. More troglobionts and troglophiles might be found among the numerous Chernetidae, Chthoniidae and Ideoroncidae in our material from MDL.

- Schizomida

Schizomida of the family Hubbardiidae are not uncommon in the MDL-HC caves and soil. They are absent in Hang Mo So, but were collected on several occasions in cave BV13 of the same hill (Nui Bai Voi). They are also present in several caves of Nui Ba Tai, Nui Khoe La and Nui Hon Chong. Schizomida are under-studied in Southeast Asia, but their high diversification in Australasia [63] might prefigure a similar richness in Southeast Asia caves.

- Scorpiones

Isometrus (*Reddyanus*) *deharvengi* Lourenço & Duhem, 2010 (Figure 6H) is an elegant buthid scorpion [64,65], collected as isolated specimens in Nui Bai Voi caves (Hang Mo So and BV07), Nui Khoe La (one cave) and Nui Hon Chong (one cave). We list it as troglophile because it also occurred in a deep crevice of Nui Cay Ot.

3.3. Diplopoda (Millipedes)

Compared with central Indochina or China [66,67], the MDL-HC caves, including Hang Mo So, are poor in millipedes. Typically, one troglobiotic Cambalopsidae and one troglophilic Haplodesmidae occur in a cave. The tramp species *Orthomorpha coarctata* (de Saussure, 1860) is locally present in caves and soils.

As elsewhere in Southeast Asia, Cambalopsidae occur in dense monospecific populations on guano (Figure 4E) in many MDL caves and more rarely in soils. They include four troglobionts (*Trachyjulus singularis*, *Plusioglyphiulus boutini* Mauriès, 1970, *Plusioglyphiulus biserratus* Likhitrakarn et al., 2020 and *Glyphiulus* sp.) and two epigean species (*Plusioglyphiulus khmer* Likhitrakarn et al., 2020 and an undescribed species from Nui Ong). *Plusioglyphiulus boutini, P. biserratus* and *P. khmer* are only known from MDL-C [68]. *Trachyjulus singularis* (Figure 7A) is the only Cambalopsidae in Hang Mo So. It also occurs in several other MDL-HC caves. The undescribed *Glyphiulus* sp. is limited to Nui Ba Tai and Nui Coc caves. All Cambalopsidae species show mutually exclusive distributions. For instance, *Glyphiulus* sp. replaces *T. singularis* on the hills mentioned, notwithstanding the short distance between the distribution areas of the two species, their high abundance where present, and the relatively large range of *T. singularis* (southeast Vietnam and southeastern Thailand). In MDL-HC and in Thailand, *T. singularis* occurs exclusively in caves, but the population at its type locality (“Pulau Condor” = Con Son Island), 270 km to the southeast, is epigean [69]. The MDL-HC populations are here considered as a troglobiont lineage of *T. singularis* of uncertain taxonomic status, as is also suggested by unpublished barcode studies. Interestingly, no Cambalopsidae have ever been found in Nui Hon Chong caves or soils. This is quite unusual in southeast Asian karsts and may reflect a long isolation.

Eostemmiulus caecus, the only species of the genus, is known from Hang Mo So (Figure 7B). Geographically, it is isolated from other Stemmiulida; the nearest species occur in Sri Lanka, 2600 km to the west, and in Maluku (Indonesia), 2800 km to the southeast [70]. Morphologically, *E. caecus* is blind—a trait only shared with the non-cave African *Stemmiulus oculiscaptus* Demange & Mauriès, 1975 among Stemmiulida. *Eostemmiulus caecus* was only found in a small oligotrophic recess of Hang Mo So, but we assume that it persists in the other narrow under-sampled southern passages of the cave.

Among Haplodesmidae, *Eutrichodesmus griseus*, described from soil and rather widespread in MDL-HC, is more frequent inside than outside caves in our samples. Its closest relative, *E. cambodiensis* Srisonchai & Panha, 2020, endemic to the Tuk Meas karst, occurs outside caves [71]. Another Haplodesmidae unique to Hang Mo So might be a troglobiont. The related family Pyrgodesmidae is absent from Hang Mo So but represented by a rare cave species in oligotrophic habitats of Hang Tien (Nui Hang Tien) and Hang Kim Cuong (Nui Hon Chong). A slightly troglomorphic Trichopolydesmidae has also been found in oligotrophic Hang Tien habitats, while epigean representatives of this family are frequent and diversified in soil and litter of MDL [72].

Hang Mo So hosts at least one Siphonophorida with slightly elongated antennae, unknown elsewhere, which could, therefore, be a troglobiont.

3.4. Malacostracea: Isopoda

- Oniscidea (woodlice) (Figure 7C–E)

The oniscid fauna of MDL-HC is characterized by (i) the absence of Trichoniscidae and Styloniscidae and the dominance of Armadillidae and Philosciidae, and (ii) diverse and abundant troglophilic species. Troglobionts include four rare species.

Most remarkable is an undescribed *Sumatrillo* Taiti, Paoli & Ferrara, 1998, white and eyeless, from oligotrophic habitats of two caves (Hang Tien in Nui Hang Tien and Hang Gieng Tien in Nui Hon Chong). Another species of unidentified family, also white and eyeless, is a putative troglobiont in a cave of Nui Ba Tai. The third troglobiont is a *Burmoniscus* Collinge, 1914 with an unmistakable colour pattern, only found in hanging roots of Hang Mo So and in BV12. The fourth is a small Philosciidae with reduced eyes and pigment from a cave in Hon Lo Coc.

Figure 7. Diplopoda and Crustacea: (**A**) *Trachyjulus singularis* from a cave of Nui Nai; (**B**) *Eostemmiulus caecus* from Hang Mo So; (**C**) *Sumatrillo* sp. from Hang Gieng Tien (Nui Hon Chong); (**D**) *Troglodillo* sp. from a cave entrance in Phnom Sray Toch; (**E**) *Burmoniscus* sp. from Hang Mo So; (**F**) *Stenasellus* sp. from Hang Gieng Tien (Nui Hon Chong). Photos: Louis Deharveng (**B**,**D**,**E**), Marko Lukić (**A**,**C**,**F**).

Troglophiles are much more abundant than troglobionts in the MDL-HC caves. Two Philosciidae, a *Burmoniscus* and *Pseudotyphloscia alba* (Dollfus, 1898), are often swarming over hanging roots at Hang Mo So. In and around guano piles, Philosciidae are replaced by various species of Armadillidae, Platyarthridae and Trachelipodidae, which sometimes occur in large colonies. Several have a wide distribution, such as *Cubaris murina* Brandt, 1833, a very common species in Hang Mo So. *Nagurus pallidipennis* (Dollfus, 1898), only recorded from caves in MDL-HC, is reported from epigean habitats in southern Asia [73]. A large *Troglodillo* Jackson, 1937, showing an attractive colour pattern, is often found in large numbers at entrances of several MDL-HC caves and less frequently in litter and soil. The soil inside the caves of MDL-HC often hosts a small blind species of *Hybodillo* Taiti, Paoli & Ferrara, 1998, which occurs rarely in deep soils outside caves. It is absent from Hang Mo So.

- Asellota (Figure 7F)

Stenasellus cambodianus Boutin & Magniez, 1985 was described from a cave of the Tuk Meas karst in MDL-C. We discovered another large species in the freshwater lake of Hang Gieng Tien (Nui Hon Chong) (Figure 4C) at the extreme south of MDL-HC. The genus likely occurs in between these localities, but it has not been found in Hang Mo So, where accessible waters are slightly brackish.

3.5. Collembola (Springtails)

Springtails form an abundant and diverse component of cave faunas worldwide [31]. In MDL-HC, 15 troglobiont or probable troglobiont species occur. Troglophilic species also abound, encompassing both regional species and pantropical "tramp" species. The most common springtails of eutrophic MDL caves are tramps, such as *Xenylla yucatana* Mills, 1938, a bisexual, pigmented and oculate Hypogastruridae, and five species of Isotomidae, all parthenogenetic, pantropical, and with reduced eyes and pigment. They also colonize a wide range of surface habitats in the tropics, especially in disturbed areas.

- Poduromorpha

Hypogastruridae. Two troglobionts occur in MDL-HC. In Hang Kim Cuong (Nui Hon Chong), we found an undescribed relictual species of the large Holarctic genus *Ceratophysella* Börner, 1932, which has very few representatives in southern Asia, none of which was cave-restricted so far. The second is a putative troglobiont from a cave in Nui Ong. Two troglophilic Hypogastruridae are also present in MDL-HC caves. *Willemia* cf. *buddenbrocki*, a species of euedaphomorphic facies, was found in several caves and in deep soil outside. The tramp species *Xenylla yucatana* is often the dominant springtail in guano and is also common in soils.

Tullbergiidae. A new genus occurs in the soils of several hills. One species so far is cave-restricted.

- Entomobryomorpha (Figure 8A,B)

Isotomidae. This large family is abundant and diversified in surface habitats. Soil cores taken inside caves of MDL-HC produced the first troglobiotic Isotomidae for South-east Asia, *Folsomides anops* and *F. whitteni*. Both are rare and exhibit euedaphomorphic characters: minute size and regression of the pigment, eyes and furca. Other Isotomidae that are common in Hang Mo So and in many MDL-HC caves are pantropical tramp species. They are often the most abundant springtails in surface soils and subterranean habitats: *Folsomides centralis* (Denis, 1931), *F. parvulus* Stach, 1922, *Folsomina onychiurina* Denis, 1931, *Isotomiella nummulifer* Deharveng & Oliveira, 1990 and *I. symetrimucronata* Najt & Thibaud, 1987.

Entomobryidae: Entomobryinae. *Coecobrya* Yosii, 1956 is represented by several eyeless or microphthalmic morphospecies in soils and caves of MDL [21]. The only described species in MDL, *C. tukmeas* Zhang, Deharveng, & Chen, 2009, occurs in a cave at Tuk Meas. Among the blind morphospecies, one with slightly elongated antennae, found in two caves of Nui Bai Voi, is listed as a troglobiont here.

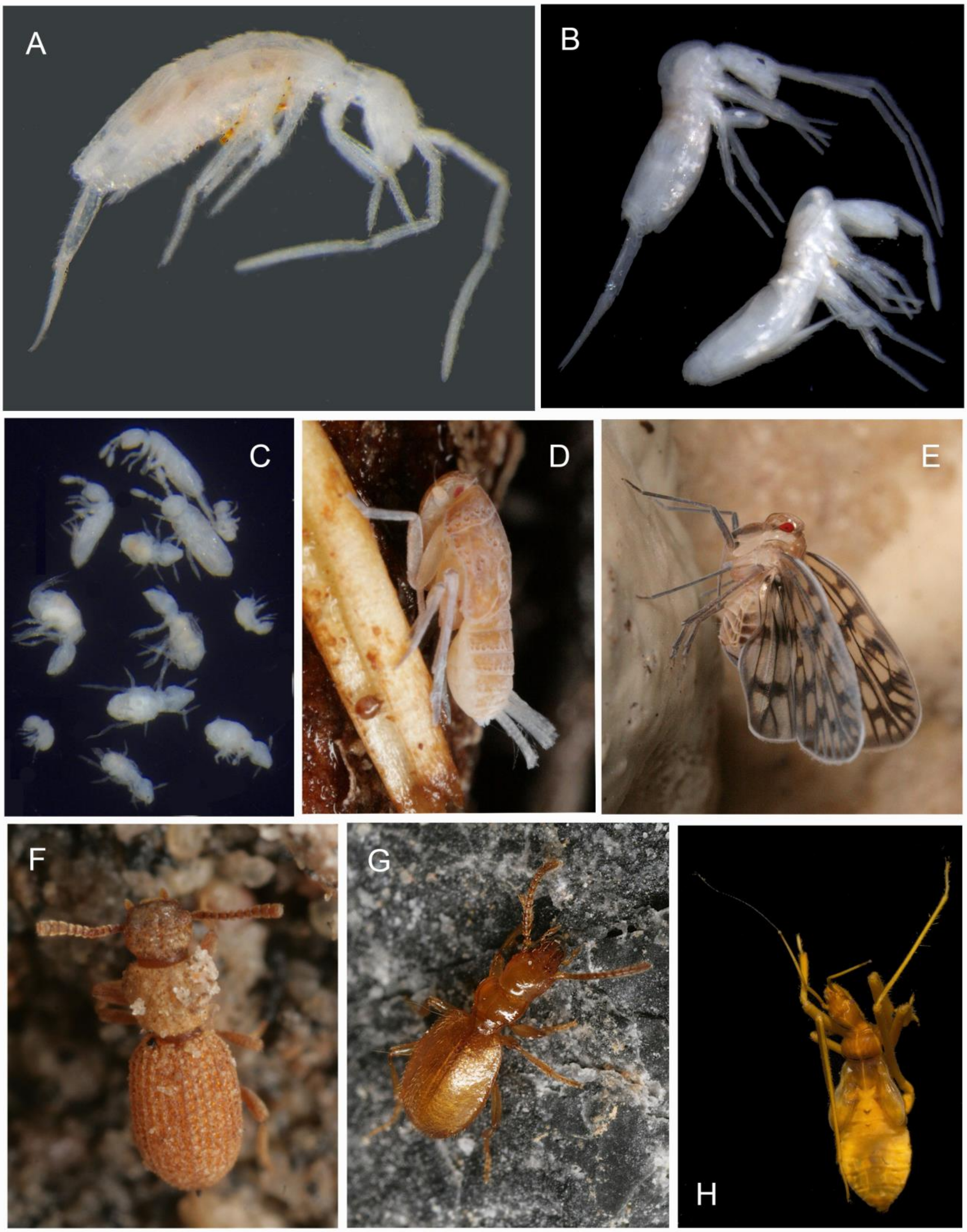

Figure 8. Hexapoda: (**A**) *Lepidosinella* sp. from Hang Mo So; (**B**) *Lepidonella lecongkieti* and *Acrocyrtus* (cf.) sp. from cave KLs of Nui Khoe La; (**C**) *Spinaethorax adamantis* and two troglophilic species, *Megalothorax laevis* and a blind *Rambutsinella* from Hang Kim Cuong (Nui Hon Chong); (**D**) larva of *Cixiidae* sp. 1 from cave BTnw of Nui Ba Tai; (**E**) *Borysthenes* sp. from a cave of Nui Khoe La; (**F**) *Harvengia vietnamita* from a cave of Nui Hon Chong; (**G**) *Eustra honchongensis* from cave BV12 of Nui Bai Voi; (**H**) Harpactorinae sp. from a cave of Nui Coc. Photos: Louis Deharveng (**A**–**C**,**H**), Marko Lukić (**D**–**G**).

Entomobryidae: Lepidocyrtinae. This subfamily is rich in troglobionts in temperate regions, but not in the tropics. Two MDL-HC species are listed as troglobionts: one eyeless species of an undescribed genus resembling *Acrocyrtus* (Yosii, 1959) occurs in the southern cave of Nui Khoe La; the second is an oculate species of uncertain generic assignment that lives in cave guano of two hills (Nui Ba Tai and Hon Lo Coc). A species of the genus *Ascocyrtus* Yosii, 1963 is abundant in hanging roots of Hang Mo So and might be troglobiotic. Another MDL-HC *Ascocyrtus*, also common in hanging roots of Hang Mo So, is found occasionally in humid litter on Nui Bai Voi and nearby hills, and can be considered a troglophile. In Southeast Asian soils, the genus *Rambutsinella* Deharveng & Bedos, 1996 is among the dominant springtails [74]. The species have a reduced number of eyes and are usually faintly pigmented. The most common in MDL-HC is *R. honchongensis* Deharveng & Bedos, 1996, from soils of Nui Ba Tai and Nui Bai Voi. In line with its euedaphomorphic morphology, it is frequent in deep soils but also occurs in litter and caves. Another undescribed, white, blind *Rambutsinella* is common in caves and deep soils, but restricted to Nui Hon Chong. *Pseudosinella* is the Collembolan genus with the highest number of troglobionts in temperate regions. It includes a few cave-obligate species in Southeast Asia (Thailand [75], Halmahera [76], Sulawesi [77]). The single *Pseudosinella* that occurs in the MDL-HC caves is a small, white, eyeless species which is one of the commonest troglophilic springtails.

Entomobryidae: Willowsiinae. The most remarkable springtail of Hang Mo So belongs to the genus *Lepidosinella* Handschin, 1920, previously known from a single termitophilous species, *L. armata* Handschin, 1920, in East Java [78]. *Lepidosinella* sp. occurs in Hang Mo So as rare, isolated specimens, not associated with termites or ants. It is a troglomorphic species, white and eyeless like *L. armata*, with significantly elongated appendages. *Hawinella* Bellinger & Christiansen, 1974 (with two species from Hawaii) and *Lepidosinella* are the only genera of the large subfamily Willowsiinae that have colonized subterranean habitats.

Paronellidae. This mainly tropical family includes epigean, soil, and many cave species. *Lepidonella*, the only genus present in the MDL-HC caves, includes numerous undescribed species from soils and caves in Vietnam, from Hon Chong to Ha Long Bay, in peninsular Malaysia and on Sumatra. Most cave species are clearly troglomorphic, showing reduced eyes and depigmentation, and having longer appendages and a larger size than epigean species. *Lepidonella lecongkieti*, the first troglobiotic invertebrate to be described from MDL-HC [79], and *L. doveri* (Carpenter, 1933) from the Batu Caves of Malaysia are the only troglomorphic species described in the genus [80]. *Lepidonella lecongkieti* is widespread in oligotrophic habitats of the MDL-HC caves. Another putative troglobiont, *Lepidonella* sp., is more similar to surface species and has only been found in Hang Mo So.

Cyphoderidae. Widespread across the world, this family includes many eyeless and unpigmented myrmecophilous or termitophilous species. Species resembling the temperate, strictly myrmecophilous *Cyphoderus albinus* Nicolet, 1842 form a major component of cave communities in Hang Mo So and other MDL-HC caves. As in Thailand [81], they are not associated with ants or termites in caves, and are rarely present in soils.

- Symphypleona

Sminthuridae. In most tropical regions, *Pararrhopalites* Bonet & Tellez, 1947 replaces the temperate Arrhopalitidae genera *Arrhopalites* Börner, 1906 and *Pygmarrhopalites* Vargovitsh, 2009. All three are diversified in caves and soils, and generally have reduced pigment and eyes. An unpigmented and microphthalmic *Pararrhopalites* species is present in soils and several caves of MDL-HC, including Hang Mo So.

- Neelipleona (Figure 8C)

Neelidae. The genera *Neelus* (Folsom, 1896), *Megalothorax* (Willem, 1900) and *Spinaethorax* Papáč & Palacios-Vargas, 2016 are present in several MDL-HC caves. The latter two occur in Hang Mo So. *Spinaethorax*, known from two cave-restricted species in Mexico [82], was unexpectedly discovered in the MDL-HC caves. *Spinaethorax adamantis* was described from Hang Kim Cuong (Nui Hon Chong) [83], and other undescribed and possibly troglobiotic species occur on Nui Bai Voi and Nui Coc (Table 1), as well as in Thailand (Surat Thani Province; Deharveng and Bedos, personal unpublished data). *Megalothorax*, which includes the smallest species of Collembola, is very common in all cave habitats and in soils. Several species occur in caves of MDL-HC, including Hang Mo So, but their taxonomic status needs to be updated following the new standards of Schneider [84].

3.6. Diplura

Campodeidae are frequent in caves and soils of MDL-HC. *Lepidocampa* cf. *weberi*, widespread in Southeast Asia, occurs in Hang Mo So and in soils of Nui Bai Voi, Nui Ba Tai and Nui Khoe La. Japygidae are not infrequent in the MDL-HC soils and caves. Large individuals with elongated antennae are possible troglobionts in Nui Bai Voi caves.

3.7. Zygentoma

Zygentoma are extremely rare in caves of Southeast Asia. Three potentially troglobiotic species were found as isolated specimens in a few MDL-HC caves, including a Nicoletiidae at Hang Mo So.

3.8. Pterygota

- Blattodea (cockroaches)

Nocticolidae are among the most common troglobionts of Southeast Asia [29] but remain largely unstudied [85]. An unpigmented and microphthalmic *Spelaeoblatta* Bolivar, 1897 occurs in oligotrophic habitats of several caves of MDL-HC (especially in Nui Bai Voi, including Hang Mo So). The genus has four species in Thailand and Myanmar, and is probably present elsewhere in caves of Indochina. Other cockroaches of the MDL-HC caves are troglophiles living at cave entrances or in guano. Larger cockroaches, such as *Pycnoscelus* spp. or *Periplaneta* spp., which often swarm in hot and disturbed caves elsewhere in Southern Asia, are exceptional in MDL-HC [19,22].

- Orthoptera (crickets)

Rhaphidophoridae are very common in caves of MDL-HC [21,22], as elsewhere in Southeast Asian caves. They have never been recorded outside. However, given their pigmentation, large eyes, and the biology of other species of the family, which can leave caves at night to feed outside, they are probably subtroglophiles, rather than troglobionts as assumed in [21]. The MDL-HC species seems to be undescribed.

- Heteroptera (Figure 8H)

Large Harpactorinae nymphs (Reduviidae), yellowish and with slightly reduced eyes, occur in some MDL-HC caves [19]. Similar species of uncertain taxonomic status and unknown biology are present in caves of China, Southeast Asia and Australia [29,86]. A Schizopteridae from a cave of Nui Ba Tai, which has reduced eyes, reduced pigment and slightly elongated appendages, is a possible troglobiont. Species of this family are otherwise frequent in MDL-HC litter.

- Homoptera (Figure 8D,E)

Root-sucking bugs are frequent in many MDL-HC caves, in hanging roots, or in the ground root-mat of cave BV08 in Nui Bai Voi. They belong to several genera of the families Kinnaridae (rare), Cixiidae (probably two species, one frequent) and Delphacidae (one species). One Cixiidae, only known from the southern cave of Nui Khoe La, is eyeless; the other species is frequent as nymphs and has reduced eyes. Adults of *Borysthenes* sp. also occur in hanging roots and may be the adult phase of these nymphs. We consider them probable troglobionts, by analogy with similarly eyed species from Hawaii [87] and Sulawesi [88]. The mealybug *Ripersiella ficaria* (Williams, 2004) was described from hanging roots in Hang Mo So. It is probably this species that is sometimes found in dense populations in root habitats of other caves of MDL-HC. Since no mealybug is known to be cave-restricted, we provisionally consider this species to be a troglophile.

- Coleoptera (beetles) (Figure 8F,G)

In lowland tropical caves, troglobionts are exceptional among beetles [29,89]. The only troglobiotic carabid of MDL-HC is *Eustra honchongensis*, restricted to oligotrophic habitats in four caves of Nui Bai Voi, including Hang Mo So [90]. Being unpigmented, with very reduced eyes and slightly elongated appendages, it resembles cave and soil species of the same genus from northern Thailand [90]. Tenebrionidae are much more frequent than Carabidae in the MDL-HC caves. A remarkable guanobiont-troglobiont, *Harvengia vietnamita*, the sole species of its genus, was discovered in four hills close to Nui Bai Voi, but never in Nui Bai Voi itself. It forms large populations on relatively dry guano. Placed in a new subtribe, Harvengina [91], it was at that time the only blind species known in the tribe Stenosini. Another Stenosini, *Pseudochillus honchongensis*, occurs in guano in Hang Mo So. Although dark-coloured and lacking troglomorphic traits, it has never been found outside this cave. A morphologically similar species, *Dichillus kuschstaberi* Kaszab, 1980, is known from a guano cave in Thailand [92]. We assume the Hang Mo So species is a guanobiont-troglobiont. A very rare, blind Curculionidae is only known from two specimens collected in caves of two MDL-HC hills, and in a cave of Phnom Ang in MDL-C. A second curculionid is a troglophilic Entiminae, common in Hang Mo So and several other MDL-HC caves, and occasionally found in soil samples. It is characteristic of root invertebrate communities. Other beetles of various families are encountered in cave guano or debris in MDL-HC, such as Histeridae and Ptiliidae, but none are troglobionts. Dark and eyed Ptiliidae are frequent in caves, whereas blind and pale species are well represented in soil, but absent from caves.

- Lepidoptera (moths)

Adult moths are regular components of cave-wall assemblages in temperate regions. MDL-HC cave-wall assemblages generally do not include moths, but larvae are abundant in two high-energy habitats: guano (Tineidae) and roots (Erebidae). In terms of biomass, Tineidae caterpillars, in their characteristic cases, are often the most important invertebrates of guano. Except for one species with reduced eyes in the Philippines, authors usually qualify cave-dwelling Tineidae as troglophiles [93]. The MDL-HC caves host several species of tineids, unstudied so far, that we provisionally consider troglophiles.

Caterpillars of the genus *Schrankia* (Erebidae), of which one species is probably a troglobiont, are numerous in the invertebrate root communities of Hawaiian caves [94]. Similarly, erebid caterpillars of an undetermined genus were abundant in subterranean root habitats of MDL-HC, particularly in the hanging roots that once flourished in Hang Mo So. Interestingly, erebid moths have rarely been reported from cave roots in other tropical regions.

4. Discussion

4.1. Species Richness

The richness of Hang Mo So in troglobionts is comparable to that of the Towakkalak system in Indonesia (27 versus 26 species), but it does not include a single stygobiont, as opposed to the 10 in Towakkalak [6]. This similarity in the number of troglobionts is surprising since Hang Mo So is a shallow cave, rich in organic debris and bats, which lacks active karstic water circulation, whereas Towakkalak is large and deep, with a wider array of habitats and is active hydrogeologically. Both caves share faunal characteristics typical of tropical lowland terrestrial caves [29], such as the prevalence of arachnids over insects, high diversity of guano species, rarity of troglobiotic beetles, and a low number of troglomorphic species. Cave species richness is often linked to the regional stock of epigean (especially edaphic) species, which may be potential colonizers [95]. This only partly holds true for the MDL-HC cave fauna, which is less rich than could be expected from the exceptional diversity of deep-soil invertebrates, while at the same time being richer than might be expected from the low biodiversity observed so far in other external habitats [21].

How complete is the current species list for Hang Mo So? The high proportion of troglobionts collected only once (14 out of 27) suggests that other rare species remain to be discovered. From a nested perspective (cave > hill > karst), it appears that, of the 38 troglobionts present in the caves of Nui Bai Voi, 11 have not yet been found in Hang Mo So (Table 1). With all caves of the hill being close to each other (Figure 1B) and likely interconnected by fissures, several of these 'missing' species might yet be found in Hang Mo So.

At the MDL-HC level, 29 cave-obligate species are absent in Nui Bai Voi. It is unlikely that many of these will be found in Hang Mo So, because species dispersion between MDL-HC hills is more difficult than between caves of Nui Bai Voi. Nevertheless, the configuration of the MDL-HC karst makes the exchanges of cave-restricted fauna between hills conceivable, provided that they are not too distant from one another. The potential dispersal vector is water, which sometimes floods large parts of the plain and flows slowly in various directions during the rainy season. The limestone hills near Nui Bai Voi also share the same limestone stratum underground, so it is possible that they once had, or even still have, subterranean connections. This is not the case for Nui Hon Chong because it is separated from this cluster of hills by the sandstone hill of Nui Binh Tri (Figure 1A), which might explain why its cave fauna is rather different.

Another limitation of the Hang Mo So species list is the uncertain ecological status of several species (those marked '?' in Table 1), despite the parallel-sampling strategy employed and the extensive sampling that was carried out in MDL-HC. However, the same is true for most surveys carried out in under-sampled karsts of the world.

4.2. Endemism

Endemism rates are very high among karst-dependent invertebrates of MDL-HC, i.e., snails [42], soil arthropods and cave invertebrates [21], as in many tropical karst areas. This endemism is particularly narrow, with single-hill endemics on most surveyed hills of MDL-HC (Table 1). A number of generic or suprageneric taxa have been erected, reflecting an exceptional level of phyletic and geographic isolation among this fauna, probably caused by a long isolation of the MDL karst—these can be provisionally qualified as relicts.

Deep-soil species include several endemics at the supra-specific level, notably among mites [96], beetles [91,97,98] and springtails [21]. Snail endemism rates in MDL-HC are also high, while several species widespread in Indochina are absent [42]. Most MDL-HC troglobionts are endemic, many to a single cave (Table 1). Among these are two taxonomically isolated genera: the millipede *Eostemmiulus* from Hang Mo So, basal to the order Stemmiulida [99], and the tenebrionid *Harvengia*, type genus of the subtribe Harvengina [91]; the pseudoscorpion genus *Cybella*, type of the subfamily Cybellinae, was described from two troglophilic endemics of the MDL karsts [61]. Altogether, the levels of endemism and relictuality among the MDL-HC fauna are currently unmatched in other karst areas of Asia.

Other less studied caves of MDL-HC are known to host some remarkable endemic troglobionts, so they may ultimately prove to have levels of biodiversity similar to that of Hang Mo So. Examples are the southern cave of Nui Khoe La, Hang Tien in Nui Hang Tien, Hang Gieng Tien in Nui Hon Chong, and a cave NW of Nui Ba Tai (Figure 3A). The same might also have been true of several MDL-HC caves now destroyed by quarrying, such as BV08 (Hang Tai) and BV09 in Nui Bai Voi (Figure 1B), a large cave of central Nui Khoe La, believed to have been the longest of the MDL-HC karst, a cave in northern Nui Khoe La, and two caves of Nui Cay Xoai (Figure 3A).

4.3. Gaps

Our sampling largely neglected the aquatic fauna, leaving a major gap in the data set (Table 1). Marine or anchialine habitats were only sampled once, in Hang Tien (Nui Hang Tien), but are presumably developed along the kilometers of highly karstified coasts of MDL-HC (Figure 2A,D). No stygobiont has been found in Hang Mo So itself. This might be due to the scarcity of phreatic waters, since the water in the cave (Figure 3B) is directly connected to the slightly brackish surface waters of the alluvial plain. The few freshwater stygobionts in our list mostly come from Hang Gieng Tien (Nui Hon Chong), the only cave with deep karstic water (Figure 4C). Besides *Pseudoiglica* (Gastropoda) and *Stenasellus* (Isopoda), these include Copepoda and Ostracoda. Two unstudied freshwater samples from caves BV08 and BV09 of Nui Bai Voi, taken before their destruction by quarrying, contained Gastropoda, Hydracari, Copepoda and Ostracoda. The presence of stygobionts is therefore highly probable in other MDL-HC caves.

Among terrestrial groups, sampling has been much more extensive, but highly diverse cave-dwellers collected in large numbers, such as spiders, mites and woodlice, have been only identified as morphospecies.

Geographical gaps, in addition to those mentioned for aquatic fauna, are due to access restrictions to some hills being quarried, or managed by the military. Hills that are inaccessible due to rugged terrain are likely to be rich in unexplored shafts, deep crevices and caves.

4.4. Causes of Species Richness

Overall, the richness in troglobionts of MDL-HC is high for a tropical karst by current standards [1]. Several factors have been advanced to explain the similarly high richness of the Towakkalak system, a hotspot of subterranean diversity in Southeast Asia [100]. These were seasonal climate, proximity to the sea, intensive sampling effort, and location at the foot of mountains, all of which, except for the last, apply to MDL-HC. Other well-sampled caves in Southeast Asia are Tham Chiang Dao (Thailand [76]), the Batu Caves (Western Malaysia [101]), the Clearwater Cave System in Mulu (Sarawak [86]), and Niah Cave (Sarawak [102]). Tham Chiang Dao's richness in troglobionts is comparable to that of Towakkalak or Hang Mo So. These three caves are under a seasonal tropical climate (category Am or Aw of Köppen-Geiger [103]). Interestingly, the three other caves, in Western Malaysia and Sarawak, are under a permanent non-seasonal tropical climate (category Af); they are noticeably less rich than the caves listed above.

Differences in species richness are often best explained by unequal sampling effort [104]. The main drivers of diversity are climate and geological history, but their impact may only become apparent after standardized sampling. Quaternary sea-level fluctuations, linked to glaciation periods, are considered to have had a strong influence on faunal diversification in Southeast Asia, through habitat fragmentation [105]. For instance, the sea was 120 m below its current level 21,000 BP [106], and the Mekong Delta extended more than 220 km southwards into the South China Sea 8000 BP [107,108]. Slight faunal differences between adjacent hills could be the result of past isolation by higher sea levels. Differences at higher taxonomic levels probably result from more ancient events that are not yet decipherable in the absence of phylogenies and information on past changes in the karst environment.

5. Conservation Issues

In 1997, the Karst Water Institute (USA) listed Hon Chong among the 10 most endangered karsts worldwide based on threats to its fauna [109]. Since then, existing quarries have been expanded and new ones opened, leaving unaffected an ever smaller surface of the original karst and severely impacting the surroundings (Figure 9). Of the original karst surface of about 4.01 km^2, 1.71 km^2 had already been quarried by 2018, and this is set to rise to 2.41 km^2 within a few years, leaving, at best, only 1.60 km^2 unquarried. In terms of the number of hills, 13 had been erased by 2018, a further two will disappear in the coming years, and the two largest will be erased over most of their surface (Figure 10). Hang Mo So and a small part of Nui Bai Voi around it will be spared, along with a few other hills, provided that the present quarrying plans are not expanded again.

Figure 9. Evolution of limestone quarrying in the MDL-HC karst from 1985 to 2018. Year 1985: before quarrying; abbreviations of hills as in Figure 1A. Photos Google Earth.

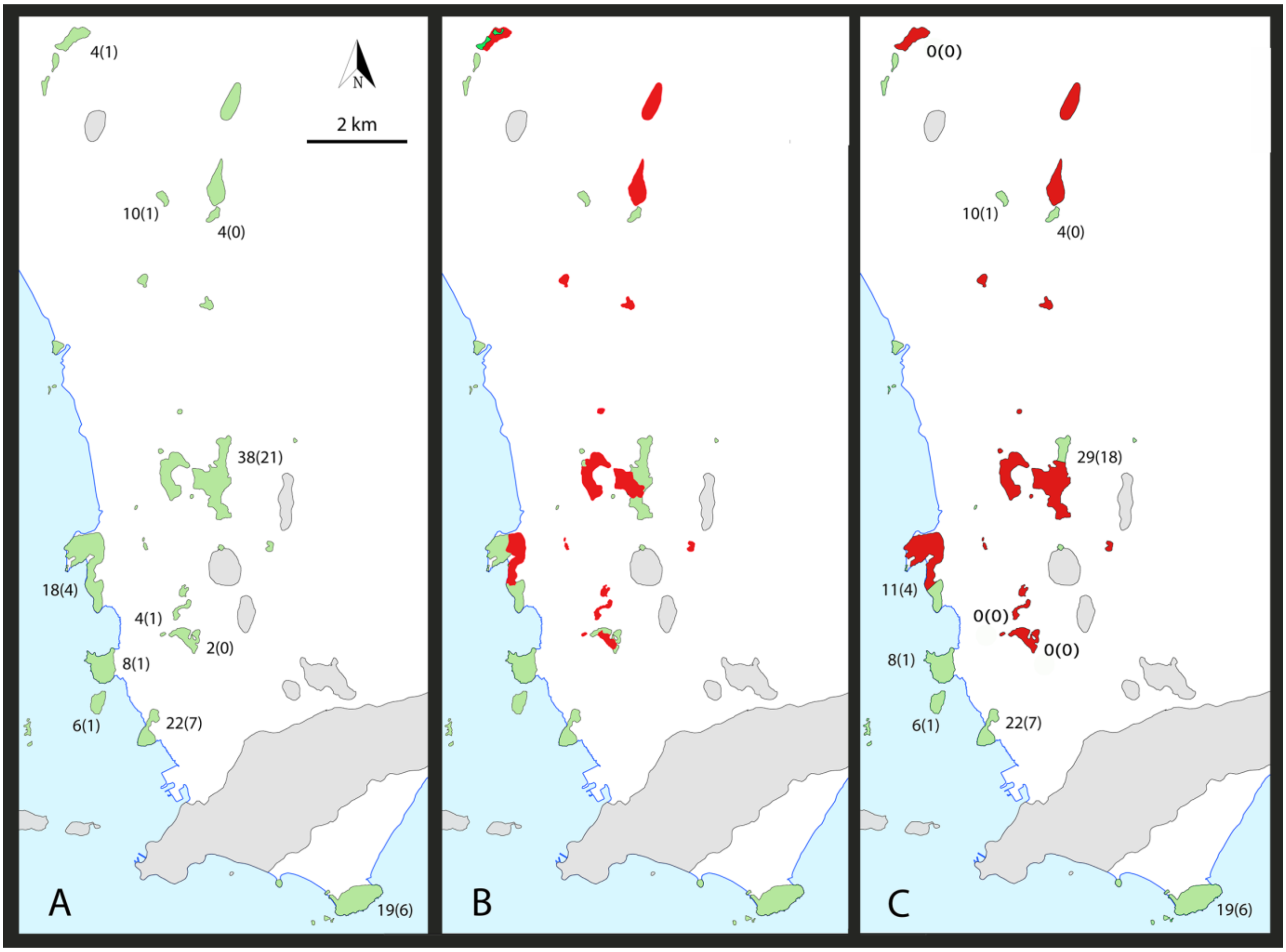

Figure 10. The MDL-HC karst. Blue line, sea coastline; green and red, limestone hills; grey, non-limestone hills; species numbers per hill are extracted from Table 1. (**A**) Limestone hills in the 1980s, before quarrying, in green; numbers are total numbers of troglobionts, with number of single-hill endemics in parentheses, recognized in 2023. (**B**) In 2018: green, limestone hills or parts of hills not quarried; red, limestone hills or parts of hills quarried. (**C**) Scenario for the future: green, limestone hills or parts of hills that will not be quarried; red, limestone hills or parts of hills already quarried or planned to be quarried; numbers are total numbers of troglobionts, with number of single-hill endemics that would remain in parentheses; hills in red without annotations were destroyed before they could be sampled.

Quarrying is also causing severe disturbance to non-karst habitats of MDL-HC, linked to the infrastructure of limestone exploitation (harbour, roads, buildings, mud dispersal, and non-limestone quarrying). The attendant increase in the local population also has adverse effects (water pollution, shrimp ponds, mangrove destruction, and huge pressure on remaining forests of sandstone hills). The ravages caused are obvious on the ground and from satellite imagery (Figure 9).

5.1. How Did We Get Here?

MDL-HC is the only limestone resource in southern Vietnam. In 1993, several hills had already been quarried to elimination by Vietnamese companies, but Nui Bai Voi, including Hang Mo So, was still pristine. The history of limestone exploitation from this time onwards is summarized in a leaflet of the International Finance Corporation (IFC) [110] and various unpublished reports.

In 1993, regional cement supply was falling short of demand in the rapidly growing Vietnamese economy. The companies Ha Tien I and Holderbank approached IFC for a loan to establish a cement plant in the MDL-HC region, called Morning Star Cement (MSC), which would produce 1.4 M tonnes of cement per year. Limestone was to be extracted initially from Nui Bai Voi and Nui Cay Xoai. Later, a large part of Nui Khoe La was added to the concession in order to 'compensate' for the designation of a small part of Nui Bai Voi as a cultural monument.

The tourist potential of the local karst landscape was recognized as significant in the otherwise monotonous Mekong Delta plains, but it did not meet IFC's natural habitat standard [110] and was therefore not taken into consideration as a reason to curtail the MSC project. A first Environmental Impact Assessment (EIA), required by IFC, was carried out in 1995. It focused on technical aspects and neglected karst-dependent biodiversity issues. Just before the board took its decision, IFC received a letter from biologists who happened to be surveying the area at the time, pointing out the risk of serious biodiversity loss. In response, the IFC, following their consultant's advice, considered that these biologists had overstated this risk and failed to "recognize Vietnam's critical need for cement" [110]. It is at least true that no MDL-HC species were on the IUCN Red List at that time. But the second assertion ignored the fact that the large limestone outcrops of central Vietnam could be exploited with much less damage to biodiversity than the small hills of MDL-HC, as was pointed out to IFC in the letter. It was too late to question such a large project and, even though IFC acknowledged the weakness of the EIA, its board approved a $97 M loan for the project [110].

Nevertheless, at the start of the quarrying operations in 1999, after consulting Tony Whitten, Senior Biodiversity Specialist for the East Asia and Pacific Region at the World Bank, IFC commissioned a new EIA from Sinclair Knight Merz (SKM) from Australia and a team of the Vietnamese Sub-Institute of Ecology Resources and Environmental Studies (SIERES) of the Institute of Tropical Biology (ITB) in Ho Chi Minh City. This second EIA [111] provided information on plants and vertebrates, and recognized that the conservation of biodiversity in small, fragmented karst landscapes required a tailored approach.

In 2004, the board of Holcim Vietnam (formerly MSC) agreed to launch a new biodiversity study focusing on Nui Bai Voi. The resulting report highlighted the critical impact that quarrying would have on the local population of langur monkeys, but little else [110].

In 2008, a workshop was organized in Rach Gia by the Center for Biodiversity and Development (CBD) of the Institute of Tropical Biology (ITB) of Ho Chi Minh City, which was attended by Kien Giang Province authorities, Holcim staff, and several biologists. Serious concerns were expressed at this meeting about the increasing risks of species extinction due to the rapid destruction of local karst habitats [112] (Figure 11). In 2009, Holcim and IUCN entered a 4-year partnership to prepare a Biodiversity Action Plan. This partnership was later extended to 2015, with a view to establishing a Nature Reserve at Kien Luong. In 2016–2017, the Hon Chong cement plant was acquired by the Siam City Cement Company (SCCC). In 2018 and 2021, successive 3-year MOUs were signed between IUCN and SCCC, with the same objectives. Despite this long partnership, quarrying has continued unabated and the proposed nature reserve has yet to be implemented.

5.2. Species at Risk

At present, many subterranean and soil invertebrates in the MDL-HC karst, along with several plants, are at great risk of extinction due to quarrying. Figure 10 gives the current number of troglobionts and single-hill endemics per hill, and the number of those anticipated to remain at the end of the planned quarrying operations, under the most favourable scenario (i.e. without enlargement of current concession). The true numbers of threatened or possibly extinct endemics will, however, be even higher. This is because (a) several large hills have been destroyed without ever being surveyed (Nui Com, Nui Trau, Nui Cay Xoai); (b) our survey methods were less effective for certain species-rich groups, such as worms and microcrustaceans; and (c) other species-rich groups collected in large numbers have yet to be studied taxonomically, either entirely or in part.

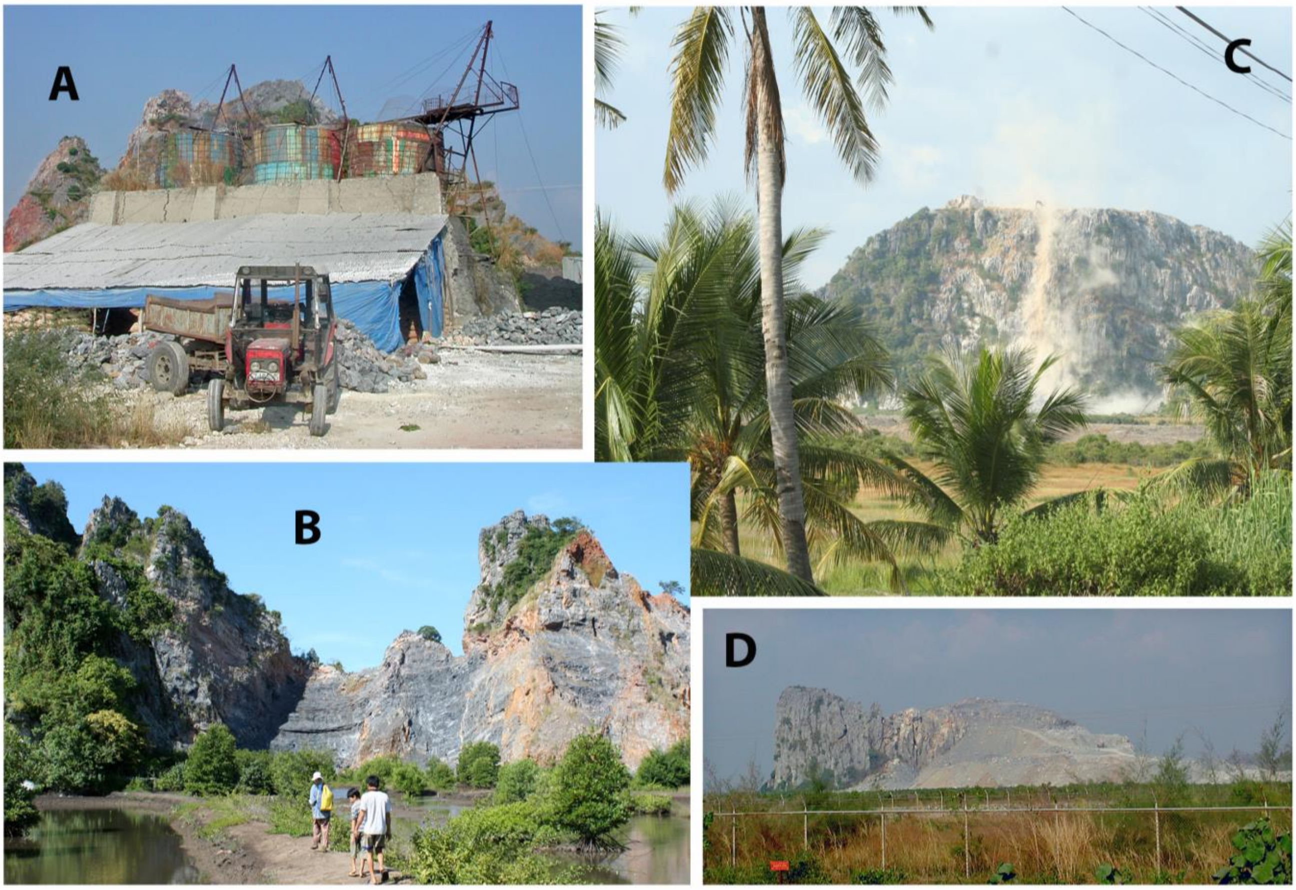

Figure 11. The MDL-HC karst under quarry: (**A**) artisanal limestone quarrying in Xom Lo Voi; (**B**) Nui Khoe La, in 2005; (**C**) part of Nui Bai Voi, southwest of Hang Mo So, at the beginning of quarrying in 2006; (**D**) Nui Cay Xoai, in 2003. Photos: Louis Deharveng.

Range reduction through site destruction is the most immediate threat for narrow endemics. For instance, the planned quarrying of Nui Bai Voi will reduce the known range of 10 troglobionts to a single locality (Table 1). Of course, these might also occur in other caves, but the extensive sampling and ongoing quarrying make this increasingly improbable. In the MDL-HC karst as a whole, five troglobiotic species are due to lose the only site where they have been found and thus likely become extinct. These numbers only include cave-obligate species, representing a small proportion of the total biodiversity [21].

5.3. Conservation Actions

As faunal data accumulated and the situation became increasingly critical, relevant information was disseminated in concert with Tony Whitten. Thus, international media [26,113], IUCN, and Fauna & Flora International (FFI) were informed of developments in the discovery of remarkable taxa, additions to the IUCN Red Lists, the situation at the MDL-HC karst, and proposed actions for conserving the most biologically significant sites. Moreover, Tony Whitten tirelessly led discussions of the situation with the IFC, official authorities, and mining companies.

Over the course of these efforts, it became evident that IUCN red-listing of endangered species represented the only means to impress the companies and financial institutions involved. A special project was therefore initiated, aimed at red-listing selected MDL-HC species. In 2015 and 2016, 9 troglobiotic and 3 troglophilic arthropods were assessed as CR

(2 species), EN (6), VU (4) and NT (1) (Table 1). We also red-listed non-cave invertebrates and plants from MDL-HC: 4 edaphic arthropods (1 CR, 2 VU, 2 NT), 13 gastropods (3 CR, 4 EN, 5 VU, 1 NT) and 3 plants (1 CR, 2 VU). Several other MDL-HC invertebrates, notably at Hang Mo So, match the IUCN categories of CR or EN and will be assessed in the future.

In this context, Hang Mo So is particularly important because it represents a rich pocket of endemism within the small part of Nui Bai Voi (about 0.11 km^2) that is expected to escape quarrying. It is also the last refuge for other species that previously occurred on parts of Nui Bai Voi that have since been destroyed (Figure 11C). However, Hang Mo So itself is at risk from other pressures. As a major local tourist attraction, it is suffering from growing disturbance. Concrete has already been poured in some passages of the cave, hanging root bundles have been cut to make way for electrical wires, rubbish accumulates in recesses, and new settlements near the cave entrance add to the disturbance. If not properly managed, this human impact will accelerate habitat destruction [10] and could thus lead to further species extinctions. Regulation of tourist visits to Hang Mo So will therefore be a prerequisite for the success of a future nature reserve in the MDL-HC karst.

It should be evident from this brief account that the tiny karst of Hong Chong (MDL-HC) faces a greater and more imminent threat than any other karst in the world. It is home to a diverse cave fauna and its deep-soil fauna is probably the richest in the tropics, hence we risk losing a major hotspot of karstic biodiversity in Asia. The only hope for saving part of this unique fauna is the rapid implementation (as opposed to endless discussion) of an action plan for conserving the small portions of the karst that remain.

Author Contributions: Conceptualization, L.D., J.V. and M.L.; data acquisition: M.L., J.V., C.M.L., M.L.I.J., N.S.L. and Q.T.T.; methodology, A.B., C.M.L., Q.T.T. and T.Q.T.N.; writing—original draft preparation, L.D., A.B. and J.V.; writing—review and editing, L.D., J.V., M.L.I.J., C.K.L., N.S.L., M.L. and H.T.L. All authors have read and agreed to the published version of the manuscript.

Funding: Funding was provided in 2014 by IUCN Vietnam for the project "Baseline survey of biodiversity in Kien Giang Province", which included a cave invertebrate survey in the Hon Chong karst (project number PO1221).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Katja Anker, Quan Mai, Sibyle Moulin, Jean-Christophe Levet, Pham Van Giau, Nguyen Thanh Hai, Phan Van Hung, and other staff of local authorities for their contributions to and help with fieldwork. We are grateful to Thierry Bourgoin, Henri Dalens, Thierry Deuve, Arnaud Faille, Nestor Fernandez, Julio Ferrer, Sergei Golovatch, Adriano Kury, Elise-Anne Leguin, Wilson Lourenço, Joanna Makol, Jean-Paul Mauriès, Christine Rollard, Wolfgang Schawaller, Clément Schneider, Peter Schwendinger, Stefano Taiti, Lubomir Vidlicka, Douglas Williams and Feng Zhang for identifications and information. We owe a particular debt to the late Tony Whitten, who enthusiastically encouraged our work over many years and fought tirelessly to save the unique invertebrate fauna of the Hon Chong hills.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Culver, D.C.; Deharveng, L.; Pipan, T.; Bedos, A. An Overview of Subterranean Biodiversity Hotspots. *Diversity* **2021**, *13*, 487. [CrossRef]
2. Niemiller, M.L.; Helf, K.; Toomey, R.S. Mammoth Cave: A Hotspot of Subterranean Biodiversity in the United States. *Diversity* **2021**, *13*, 373. [CrossRef]
3. Zagmajster, M.; Polak, S.; Fišer, C. Postojna-Planina Cave System in Slovenia, a Hotspot of Subterranean Biodiversity and a Cradle of Speleobiology. *Diversity* **2021**, *13*, 271. [CrossRef]
4. Camacho, A.I.; Puch, C. Ojo Guareña: A Hotspot of Subterranean Biodiversity in Spain. *Diversity* **2021**, *13*, 199. [CrossRef]
5. Huang, S.; Zhao, M.; Luo, X.; Bedos, A.; Wang, Y.; Chocat, M.; Tian, M.; Liu, W. Feihu Dong, a New Hotspot Cave of Subterranean Biodiversity from China. *Diversity* **2023**, *15*, 902. [CrossRef]
6. Deharveng, L.; Rahmadi, C.; Suhardjono, Y.R.; Bedos, A. The Towakkalak System, a Hotspot of Subterranean Biodiversity in Sulawesi, Indonesia. *Diversity* **2021**, *13*, 392. [CrossRef]

7. Ferreira, R.L.; Berbert-Born, M.; Souza-Silva, M. The Água Clara Cave System in Northeastern Brazil: The Richest Hotspot of Subterranean Biodiversity in South America. *Diversity* **2023**, *15*, 761. [CrossRef]
8. Laumanns, M. Karsts and Caves of South Vietnam, Part 1: Provinces of Kien Giang, An Giang and Da Nang. *Berl. Höhlenkundliche Berichte* **2011**, *43*, 1–73.
9. Denneborg, M.; Laumanns, M.; Schnadwinkel, M.; Vogt, S. German Speleological Campaign, Cambodia 95/96. *Berl. Höhlenkundliche Berichte* **2002**, *6*, 1–92.
10. Kiernan, K. Human impacts on geodiversity and associated natural values of bedrock hills in the Mekong Delta. *Geoheritage* **2010**, *2*, 101–122. [CrossRef]
11. Pirazzoli, P.A. Marine notches. In *Sea-Level Research: A Manual for the Collection and Evaluation of Data*; van de Plassche, O., Ed.; Geo Books: Norwich, UK, 1986; pp. 361–400.
12. Salomon, J. Les influences climatiques sur la géomorphologie karstique: Exemple des milieux tropicaux et arides. *Quaternaire* **1997**, *8*, 107–117. [CrossRef]
13. Deharveng, L.; Truong, Q.T.; Duong, T.D. Explorations au centre et au sud du Vietnam. *Spelunca* **1995**, *59*, 8–10.
14. Le, C.K. La végétation des collines calcaires de la région de Kien-Luong—Ha Tien. *Nien-San* **1970**, *3*, 121–200.
15. Le, C.K. La végétation des collines calcaires de la région de Kien-Luong—Ha Tien (suite). *Nien-San* **1974**, *4*, 11–90.
16. Truong, Q.T.; Kiew, R.; Vermeulen, J.J. *Begonia bataiensis* Kiew, a new species in section Leprosae (Begoniaceae) from Vietnam. *Gard. Bull. Singap.* **2005**, *57*, 119–123.
17. Middleton, D.J.; Ly, N.S. A new species of *Ornithoboea* (Gesneriaceae) from Vietnam. *Edinb. J. Bot.* **2008**, *65*, 353–357. [CrossRef]
18. Nguyen, V.D.; Luu, H.T.; Nguyen, Q.D.; Hetterscheid, W.L.A. *Amorphophallus kienluongensis* (Araceae), a new species from the Mekong Delta, Southern Vietnam. *Blumea* **2016**, *61*, 1–3. [CrossRef]
19. Deharveng, L.; Le, C.K.; Bedos, A. Vietnam. In *Encyclopaedia Biospeologica Tome III*; Juberthie, C., Decu, V., Eds.; Société Internationale de Biospéologie: Moulis, France; Bucarest, Romania, 2001; pp. 2027–2037.
20. Boutin, C. Cambodge. In *Encyclopaedia Biospeologica Tome III*; Juberthie, C., Decu, V., Eds.; Société Internationale de Biospéologie: Moulis, France; Bucarest, Romania, 2001; pp. 1755–1762.
21. Deharveng, L.; Bedos, A.; Le, C.K.; Le, C.M.; Truong, Q.T. Endemic arthropods of the Hon Chong hills (Kien Giang), an unrivaled biodiversity heritage in Southeast Asia. In *Beleaguered Hills: Managing the Biodiversity of the Remaining Karst Hills of Kien Giang, Vietnam*; Le, C.K., Truong, Q.T., Ly, N.S., Eds.; Nha Xuat Ban Nong Nghiep: Ho Chi Minh, Vietnam, 2009; pp. 31–57.
22. Steiner, H. Karsts and Caves of South Vietnam, Part 1: Provinces of Kien Giang, An Giang and Da Nang. Biospeleology of southern Vietnam. *Berl. Höhlenkundliche Berichte* **2011**, *43*, 53–73.
23. Deharveng, L.; Le, C.K.; Le, C.M.; Bedos, A. Hot issues in karst conservation: The biodiversity of Hon Chong hills (southern Vietnam), with emphasis on invertebrate endemism. In *Trans-KARST 2004, Proceedings of the International Transdisciplinary Conference on Development and Conservation of Karst Regions, Hanoi, Vietnam, 13–18 September 2004*; Batelaan, O., Dusar, M., Masschelein, J., Vu, T.T., Tran, T.V., Nguyen, X.K., Eds.; Research Institute of Geology and Mineral Resources: Hanoi, Vietnam, 2005; p. 40.
24. Humphreys, W.F. Community extinction: The groundwater (stygo-) fauna of Curaçao, Netherlands Antilles. *Hydrobiologia* **2022**, *849*, 4605–4611. [CrossRef]
25. Ng, P.K.L.; Kottelat, M.; Deharveng, L. Tony Whitten and biodiversity: Personal recollections. *Raffles Bull. Zool.* **2020**, *35*, 11–13.
26. Ives, M. *The Big Story. Threatened Vietnam Cave Bugs Draw Little Sympathy*; Associated Press: New York, NY, USA, 2012.
27. Santos, A.J.; Ferreira, R.L.; Buzatto, B.A. Two New Cave-Dwelling Species of the Short-Tailed Whipscorpion Genus *Rowlandius* (Arachnida: Schizomida: Hubbardiidae) from Northeastern Brazil, with Comments on Male Dimorphism. *PLoS ONE* **2013**, *8*, e63616. [CrossRef] [PubMed]
28. Eberhard, S.M.; Howarth, F.G. Undara lava cave fauna in tropical Queensland with an annotated list of Australian subterranean biodiversity hotspots. *Diversity* **2021**, *13*, 326. [CrossRef]
29. Deharveng, L.; Bedos, A. Diversity of Terrestrial Invertebrates in Subterranean Habitats. In *Cave Ecology, Ecological Studies 235*; Moldovan, O.T., Kovác, L., Halse, S., Eds.; Springer Nature: Cham, Switzerland, 2018; pp. 107–172.
30. Faille, A. Beetles. In *Encyclopedia of Caves*; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: New York, NY, USA, 2019; pp. 102–108.
31. Lukić, M. Collembola. In *Encyclopedia of Caves*; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: New York, NY, USA, 2019; pp. 308–319.
32. Fišer, C. Niphargus—A model system for evolution and ecology. In *Encyclopedia of Caves*; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: New York, NY, USA, 2019; pp. 746–755.
33. Porco, D.; Bedos, A.; Greenslade, P.; Janion, C.; Skarzynski, D.; Stevens, M.I.; Jansen van Vuuren, B.; Deharveng, L. Challenging species delimitation in Collembola: Cryptic diversity among common springtails unveiled by DNA barcoding. *Invertebr. Syst.* **2012**, *26*, 470–477. [CrossRef]
34. Lukić, M.; Delic, T.; Pavlek, M.; Deharveng, L.; Zagmajster, M. Distribution pattern and radiation of the European subterranean genus *Verhoeffiella* (Collembola, Entomobryidae). *Zool. Scr.* **2020**, *49*, 86–100. [CrossRef]
35. Jasinska, E.J.; Knott, B.; McComb, A.J. Root mats in ground water: A fauna-rich cave habitat. *J. N. Am. Benthol. Soc.* **1996**, *15*, 508–519. [CrossRef]
36. Howarth, F.G. Ecology of cave Arthropods. *Annu. Rev. Entomol.* **1983**, *28*, 365–389. [CrossRef]

37. Novak, T.; Perc, M.; Lipovšek, S.; Janžekovič, F. Duality of terrestrial subterranean fauna. *Int. J. Speleol.* **2012**, *41*, 181–188. [CrossRef]
38. Oromí, P.; Socorro, S. Biodiversity in the Cueva del Viento lava tube system (Tenerife, Canary Islands). *Diversity* **2021**, *13*, 226. [CrossRef]
39. Vandel, A. *Biospéologie. La Biologie des Animaux Cavernicoles*; Gauthier-Villars: Paris, France, 1964; pp. 1–619.
40. Wynne, J.J.; Howarth, F.G.; Sommer, S.; Dickson, B.G. Fifty years of cave arthropod sampling: Techniques and best practices. *Int. J. Speleol.* **2019**, *48*, 33–48. [CrossRef]
41. Vermeulen, J.J.; Phung, L.C.; Truong, Q.T. New species of terrestrial molluscs (Caenogastropoda, Pupinidae & Pulmonata, Vertiginidae) of the Hon Chong-Ha Tien limestone hills, Southern Vietnam. *Basteria* **2007**, *71*, 81–92.
42. Vermeulen, J.J.; Luu, H.T.; Theary, K.; Anker, K. New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong Delta limestone hills (Cambodia, Vietnam). *Folia Malacol.* **2019**, *27*, 7–41. [CrossRef]
43. Vermeulen, J.; Whitten, T. *Biodiversity and Cultural Property in the Management of Limestone Resources. Lessons from East Asia*; Directions in Development Series; The World Bank: Washington, DC, UAS, 1999; pp. 1–120.
44. Leclerc, P. Considérations paléogéographiques à propos de la découverte en Thaïlande d'Opilioacariens nouveaux (Acari-Notostigmata). *C. R. Soc. Biogéogr.* **1989**, *65*, 162–174.
45. Beron, P. Comparative study of the invertebrate cave faunas of Southeast Asia and New Guinea. *Hist. Nat. Bulg.* **2015**, *21*, 169–210.
46. Fage, L. Scorpions et pédipalpes de l'Indochine française. *Ann. Soc. Entomol. Fr.* **1946**, *113*, 71–81.
47. Miranda, G.S.; Giupponi, A.P.; Prendini, L.; Scharff, N. Systematic revision of the pantropical whip spider family Charinidae Quintero, 1986 (Arachnida, Amblypygi). *Eur. J. Taxon.* **2021**, *772*, 1–409. [CrossRef]
48. Nguyen, T.T.A.; Phung, T.H.L. A new species of the whip spider genus *Weygoldtia* (Arachnida: Amblypygi: Charinidae) from Con Dao National Park, Vietnam. *Acad. J. Biol.* **2022**, *44*, 67–76.
49. Zhu, X.Y.; Wu, S.Y.; Liu, Y.J.; Reardon, C.R.; Roman-Palacios, C.; Li, Z.; He, Z.Q. A new species of whip spider, *Weygoldtia hainanensis* sp. nov., from Hainan, China (Arachnida: Amblypygi: Charinidae). *Zootaxa* **2021**, *5082*, 65–76. [CrossRef]
50. Mammola, S.; Cardoso, P.; Ribera, C.; Pavlek, M.; Isaia, M. A synthesis on cave-dwelling spiders in Europe. *J. Zool. Syst. Evol. Res.* **2018**, *56*, 301–316. [CrossRef]
51. Brignoli, P.M. New or interesting Anapidae (Arachnida, Araneae). *Rev. Suisse Zool.* **1981**, *88*, 109–134. [CrossRef]
52. Decae, A.E. Three new species in the genus *Latouchia* Pocock, 1901 (Araneae, Mygalomorphae, Halonoproctidae) from Vietnam. *Rev. Suisse Zool.* **2019**, *126*, 275–289.
53. Tong, Y.; Li, F.; Song, Y.; Chen, H.; Li, S. Thirty-two new species of the genus *Speocera* Berland, 1914 (Araneae: Ochyroceratidae) from China, Madagascar and Southeast Asia. *Zool. Syst.* **2019**, *44*, 1–75.
54. Lehtinen, P.T. Spiders of the Oriental-Australian region III. Tetrablemmidae, with a world revision. *Acta Zool. Fenn.* **1981**, *162*, 1–151.
55. Lin, Y.; Li, S. New cave-dwelling armored spiders (Araneae, Tetrablemmidae) from Southwest China. *Zookeys* **2014**, *388*, 35–67.
56. Schwendinger, P.; Martens, J. A taxonomic revision of the family Oncopodidae V. *Gnomulus* from Vietnam and China, with the description of five new species (Opiliones, Laniatores). *Rev. Suisse Zool.* **2006**, *113*, 595–615. [CrossRef]
57. Condé, B. Nouveaux palpigrades de Trieste, de Slovénie, de Malte, du Paraguay, de Thaïlande et de Bornéo. *Rev. Suisse Zool.* **1988**, *95*, 723–750. [CrossRef]
58. Condé, B. Palpigrades cavernicoles et endogés de Thaïlande et des Célèbes (première note). *Rev. Suisse Zool.* **1992**, *99*, 655–672. [CrossRef]
59. Condé, B. Palpigrades cavernicoles et endogés de Thaïlande et de Célèbes (2e note). *Rev. Suisse Zool.* **1994**, *101*, 233–263. [CrossRef]
60. Judson, M.L.I. A new and endangered species of the pseudoscorpion genus *Lagynochthonius* from a cave in Vietnam, with notes on chelal morphology and the composition of the Tyrannochthoniini (Arachnida, Chelonethi, Chthoniidae). *Zootaxa* **2007**, *1627*, 53–68. [CrossRef]
61. Judson, M.L.I. A new subfamily of Feaellidae (Arachnida, Chelonethi, Feaelloidea) from Southeast Asia. *Zootaxa* **2017**, *4258*, 1–33. [CrossRef]
62. Harvey, M.S. Two new species of the pseudoscorpion genus *Cybella* (Pseudoscorpiones: Feaellidae) from Malaysian caves. *Zool. Anz.* **2018**, *273*, 124–132. [CrossRef]
63. Harvey, M.S.; Berry, O.; Edward, K.L.; Humphreys, G. Molecular and morphological systematics of hypogean schizomids (Schizomida: Hubbardiidae) in semiarid Australia. *Invertebr. Syst.* **2008**, *22*, 167–194. [CrossRef]
64. Lourenço, W.R.; Duhem, B. Buthid scorpions found in caves; a new species of *Isometrus* Ehrenberg, 1828 (Scorpiones, Buthidae) from southern Vietnam. *C. R. Biol.* **2010**, *333*, 631–636. [CrossRef] [PubMed]
65. Lourenço, W.R.; Leguin, E.A. A new species of *Isometrus* Ehrenberg 1828 (Scorpiones: Buthidae) from Laos. *Acta Arachnol.* **2012**, *61*, 71–76.
66. Golovatch, S.I. Cave Diplopoda of southern China with reference to millipede diversity in Southeast Asia. *Zookeys* **2015**, *510*, 79–94. [CrossRef] [PubMed]
67. Golovatch, S.I.; Liu, W.X. Diversity, distribution patterns, and fauno-genesis of the millipedes (Diplopoda) of mainland China. *Zookeys* **2020**, *930*, 153–198. [CrossRef]

68. Likhitrakarn, N.; Golovatch, S.I.; Thach, P.; Chhuoy, S.; Ngor, P.B.; Srisonchai, R.; Sutcharit, C.; Panha, S. Two new species of the millipede genus *Plusioglyphiulus* Silvestri, 1923 from Cambodia (Diplopoda, Spirostreptida). *Zookeys* **2020**, *938*, 137–151. [CrossRef]
69. Golovatch, S.I.; Geoffroy, J.J.; Mauriès, J.P.; VandenSpiegel, D. New or poorly-known species of the millipede genus *Trachyjulus* Peters, 1864 (Diplopoda: Spirostreptida: Cambalopsidae). *Arthropoda Sel.* **2012**, *21*, 103–129. [CrossRef]
70. Mauriès, J.P.; Golovatch, S.I. *Stemmiulus deharvengi* sp.n., le premier Stemmiulida signalé en Indonésie (Diplopoda: Stemmiulida). *Arthropoda Sel.* **2006**, *15*, 91–98.
71. Srisonchai, R.; Likhitrakarn, N.; Sutcharit, C.; Jeratthitikul, E.; Siriwut, W.; Thrach, P.; Chhuoy, S.; Ngor, P.B.; Panha, S. A new micropolydesmoid millipede of the genus *Eutrichodesmus* Silvestri, 1910 from Cambodia, with a key to species in mainland Southeast Asia (Diplopoda, Polydesmida, Haplodesmidae). *Zookeys* **2020**, *996*, 59–91. [CrossRef]
72. Golovatch, S.I.; Geoffroy, J.J.; VandenSpiegel, D. Review of the millipede family Trichopolydesmidae in the Oriental realm (Diplopoda, Polydesmida), with descriptions of new genera and species. *Zookeys* **2014**, *414*, 19–65. [CrossRef]
73. Schmalfuss, H. World catalog of terrestrial isopods (Isopoda: Oniscidea). *Stuttg. Beitr. Naturk.* **2003**, *(A) 654*, 1–341.
74. Deharveng, L.; Bedos, A. *Rambutsinella*, a new genus of Entomobryidae (Insecta: Collembola) from Southeast Asia. *Raffles Bull. Zool.* **1996**, *44*, 279–285.
75. Deharveng, L. Fauna of Thai caves. II. New Entomobryoidea Collembola from Chiang Dao Cave, Thailand. *Bish. Mus. Occas. Pap.* **1990**, *30*, 279–287.
76. Deharveng, L.; Bedos, A. The cave fauna of southeast Asia. Origin, evolution and ecology. In *Ecosystems of the World 30. Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphreys, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 603–632.
77. Deharveng, L.; Suhardjono, Y.R. *Pseudosinella maros* sp. n., a troglobitic Entomobryidae (Collembola) from Sulawesi Selatan, Indonesia. *Rev. Suisse Zool.* **2004**, *111*, 979–984. [CrossRef]
78. Yoshii, R. Finding of *Lepidosinella armata* Handschin from East Java. In Proceedings of the 3rd International Seminar on Apterygota, Siena, Italy, 21–26 August 1989; Dallai, R., Ed.; 1989; pp. 89–91.
79. Deharveng, L.; Bedos, A. *Lepidonella lecongkieti* n.sp., premier Collembole cavernicole du Vietnam (Collembola, Insecta). *Bull. Soc. Entomol. Fr.* **1995**, *100*, 21–24. [CrossRef]
80. Deharveng, L.; Jantarit, S.; Bedos, A. Revisiting *Lepidonella* Yosii (Collembola: Paronellidae): Character overview, checklist of world species and reassessment of *Pseudoparonella doveri* Carpenter. *Ann. Soc. Entomol. Fr.* **2018**, *54*, 381–400. [CrossRef]
81. Jantarit, S.; Satasook, C.; Deharveng, L. *Cyphoderus* (Cyphoderidae) as a major component of collembolan cave fauna in Thailand, with description of two new species. *Zookeys* **2014**, *368*, 1–21.
82. Papáč, V.; Palacios-Vargas, J.G. A new genus of Neelidae (Collembola) from Mexican caves. *Zookeys* **2016**, *569*, 37–51.
83. Schneider, C.; Deharveng, L. First record of the genus *Spinaethorax* Papác & Palacios Vargas, 2016 (Collembola, Neelipleona, Neelidae) in Asia, with a new species from a Vietnamese cave. *Eur. J. Taxon.* **2017**, *363*, 1–20.
84. Schneider, C. Morphological review of the order Neelipleona (Collembola) through the redescription of the type species of *Acanthoneelidus*, *Neelides* and *Neelus*. *Zootaxa* **2017**, *4308*, 1–94. [CrossRef]
85. Lucañas, C.C.; Bláha, M.; Rahmadi, C.; Patoka, J. The first *Nocticola* Bolivar 1892 (Blattodea: Nocticolidae) from New Guinea. *Zootaxa* **2021**, *5082*, 294–300. [CrossRef] [PubMed]
86. Moulds, T.; Anderson, J.; Anderson, R.; Nykiel, P. Preliminary Survey of Cave Fauna in the Gunung Mulu World Heritage Area, Sarawak, Malaysia. **2013**, *unpublished*.
87. Hoch, H.; Howarth, F.G. Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zool. J. Linn. Soc.* **1999**, *127*, 453–475. [CrossRef]
88. Hoch, H.; Mühlethaler, R.; Wachmann, E.; Stelbrink, B.; Wessel, A. *Celebenna thomarosa* gen. n., sp. n. (Hemiptera, Fulgoromorpha, Cixiidae, Bennini) from Indonesia: Sulawesi with notes on its ecology and behaviour. *Dtsch. Entomol. Z.* **2011**, *58*, 241–250. [CrossRef]
89. Casale, A.; Taglianti, A.V.; Juberthie, C.; Decu, V. Coleoptera Carabidae. In *Encyclopaedia Biospeologica Tome II*; Juberthie, C., Decu, V., Eds.; Société Internationale de Biospéologie: Moulis, France; Bucarest, Romania, 1998; pp. 1047–1081.
90. Deuve, T. Description d'un Coléoptère troglobie du genre *Eustra*, découvert dans un karst du Vietnam méridional. *Rev. Fr. Entomol.* **1996**, *18*, 23–26.
91. Ferrer, J. Description d'un nouveau genre de Stenosini troglobie du Vietnam (Coleoptera, Tenebrionidae). *Nouv. Rev. Entomol.* **2004**, *20*, 367–371.
92. Kaszab, Z. Eine neue höhlenbewohnende *Dichillus*-Art aus Thailand (Coleoptera: Tenebrionidae). *Ann. Nat. Hist. Mus. Wien* **1980**, *83*, 585–588.
93. Robinson, G.S. Cave-dwelling Tineid moths: A taxonomic review of the world species (Lepidoptera: Tineidae). *Trans. Br. Cave Res. Assoc.* **1980**, *7*, 83–120.
94. Howarth, F.G.; James, S.A.; Preston, D.J.; Imada, C.T. Identification of roots in lava tube caves using molecular techniques: Implications for conservation of cave arthropod faunas. *J. Insect Conserv.* **2007**, *11*, 251–261. [CrossRef]
95. Trajano, E.; Bichuette, M.E. Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa. *Subterr. Biol.* **2010**, *7*, 1–16.

96. Fernandez, N.; Theron, P.; Rollard, C.; Castillo, E.R. Oribatid mites from deep soils of Hòn Chông limestone hills, Vietnam: The family Lohmanniidae (Acari: Oribatida), with the descriptions of *Bedoslohmannia anneae* n. gen., n. sp., and *Paulianacarus vietnamese* n. sp. *Zoosystema* **2014**, *36*, 771–787. [CrossRef]
97. Meregalli, M.; Osella, G. Studies on Oriental Molytinae. IV. *Anonyxmolytes lilliput* new genus and new species from Vietnam (Coleoptera, Curculionidae). *Ital. J. Zool.* **2007**, *74*, 381–388. [CrossRef]
98. Jaloszynski, P. Subterranean Scydmaeninae of Southeast Asia (Coleoptera: Staphylinidae). *Ann. Zool.* **2017**, *67*, 713–723. [CrossRef]
99. Mauriès, J.P.; Golovatch, S.I.; Geoffroy, J.J. Un nouveau genre et une nouvelle espèce de l'ordre Stemmiulida du Viet-Nam (Diplopoda). *Arthropoda Sel.* **2010**, *19*, 73–80. [CrossRef]
100. Deharveng, L.; Bedos, A. Chapter 18—Diversity Patterns in the Tropics. In *Encyclopedia of Caves*; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: Cambridge, MA, USA, 2019; pp. 146–162.
101. Moseley, M.; Lim, T.W.; Lim, T.T. Fauna reported from Batu caves, Selangor, Malaysia: Annotated checklist and bibliography. *Cave Karst Sci.* **2012**, *39*, 77–92.
102. Chapman, P. Invertebrates in Niah Great Cave, Batu Niah National Park, Sarawak. *Cave Sci.* **1984**, *11*, 89–91.
103. Beck, H.E.; Zimmermann, N.E.; McVicar, T.R.; Vergopolan, N.; Berg, A.; Wood, E.F. Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Sci. Data* **2018**, *5*, 180214. [CrossRef]
104. Isaac, N.J.B.; Pocock, M.J.O. Bias and information in biological records. *Biol. J. Linn. Soc.* **2015**, *115*, 522–531. [CrossRef]
105. Li, F.; Li, S. Paleocene–Eocene and Plio–Pleistocene sea-level changes as "species T pumps" in Southeast Asia: Evidence from *Althepus* spiders. *Mol. Phylogenet. Evol.* **2018**, *127*, 545–555. [CrossRef]
106. Voris, H.K. Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *J. Biogeogr.* **2001**, *27*, 1153–1167. [CrossRef]
107. Tamura, T.; Saito, Y.; Sieng, S.; Ben, B.; Kong, M.; Sim, I.; Choup, S.; Akiba, F. Initiation of the Mekong River delta at 8 ka: Evidence from the sedimentary succession in the Cambodian lowland. *Quat. Sci. Rev.* **2009**, *28*, 327–344. [CrossRef]
108. Liu, J.P.; DeMaster, D.J.; Nguyen, T.T.; Saito, Y.; Nguyen, V.L.; Ta, T.K.O.; Li, X. Stratigraphic formation of the Mekong River Delta and its recent shoreline changes. *Oceanography* **2017**, *30*, 72–83. [CrossRef]
109. Mylroie, J.; Tronvig, K. Karst Waters Institute creates Top Ten List of endangered karst ecosystem. *NSS News* **1998**, *56*, 41–43.
110. IFC. *Cement Manufacturing in a Critical Ecosystem. A Guide to Biodiversity for the Private Sector*; Holcim Vietnam Ltd.: Ho Chi Minh City, Vietnam, 2005; pp. 1–3.
111. Sinclair Knight Merz (Australia). *Limestone Biodiversity Study, Hon Chong (EIA Report)*; Sinclair Knight Merz (Australia): St. Leonards, Australia, 2002; (Unpublished report).
112. Le, C.K.; Truong, Q.T.; Ly, N.S. (Eds.) *Beleaguered Hills: Managing the Biodiversity of the Remaining Karst Hills of Kien Giang, Vietnam, Proceedings of the International Workshop on Biodiversity of Kien Giang Karst, Rach Gia, Vietnam, 5–6 June 2008*; Nha Xuat Ban Nong Nghiep: Ho Chi Minh, Vietnam, 2009; pp. 1–199.
113. Lang, C. Vietnam: Unique biodiversity threatened by World Bank-funded cement plant. *World Rainfor. Mov. Bull.* **2003**, *71*, 1–3.