Chapter 14

The past vertebrate biodiversity of Southeast Asia and its relevance to ongoing environmental issues: current limitations and perspectives

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Abstract

The study of past faunal assemblages and of their evolution during the last millennia can enable us to describe the long-term modification of the fauna and to understand how, when, and why, it evolved. In Southeast Asia, such studies are rare which makes complex the understanding of the trajectories of the Human/Biodiversity interactions on the middle and long terms. Data regarding past wildlife faunas could also be extremely useful to document the original ecological niche of species later forced to adapt under human activity pressure. The lack of such information can have important consequences regarding biodiversity conservation/restauration policies implementation. This contribution, focused on Southeast Asian past vertebrate assemblages, present the current scientific knowledge regarding the Pleistocene and Holocene past biodiversity of this region and discuss what could be done to improve it. Such an improvement could be done by the excavation of additional sites presenting different depositional conditions, by the construction of appropriate paleontological and anatomical reference points, by informing open access databases, and by the training of more local scientists.

14.1 Introduction

The quantification of the modifications of a given ecological system varies with the initial reference point established for that system (Pauly, 1995). In the same way, the quantification of the effects of the current extinction crisis on ecosystems can strongly vary depending of what we estimate to be the "initial state" of the impacted ecosystems. This "initial state" is however difficult to define, is it of Pleistocene age or no older than the XXth century? In addition, independently of its age, can it be considered well known, as very few data exist regarding the quantification and description of the tropical biodiversity prior to the last one hundred years? In order to define this "initial stage", there is a need to establish anterior dynamics and to clearly disentangle human and natural determinants of diversity changes across historical and prehistoric times. Palaeontological and archaeological studies can provide information on these dynamics. In particular, it can allow to document the earliest evidence of environmental human perturbations, and to estimate the diachronic impact of societal and demographical changes on biodiversity. Defining a clear and precise temporal frame for these interaction is also necessary to produce correct scenarios and predictions.

The putative past environmental impact of the earliest human populations and its relation to the extinction of species is subject to much debate in the scientific literature. Regarding Southeast Asia, the earliest regional occurrences of humans (*Homo erectus*) are around 2 million years old in China (Boëda et al., 2011; Zhu et al., 2018) and Indonesia (Swisher et al. 1994), but the generally accepted date for its widespread presence in the region is around 1.5 million years (Huffmann et al., 2006). The potential impact of human populations could thus be very old in Southeast Asia. As an effect, since several decades, scientists argues in favor of the climatic or anthropic explanation for the extinction of the giant turtles, pangolins, and primates (Louys and Turner, 2012; Zhao et al., 2011) during the Middle Pleistocene (between 780 and 126 000 years) prior to the arrival of *Homo sapiens* in the region around 50 Ky B. P. (O Connel et al., 2018). The relevance of this debate is, however, questionable considering the poor quality of the paleontological data currently available in Southeast Asia and thus of our poor understanding of the broad environmental modifications taking place at the different periods. Such limitations were also pointed out in the discussion of Pleistocene megafaunal extinctions in China (Turvey et al., 2013) as well as in several other areas (Monjeau et al., 2017).

An important paradox is that the question of the past environmental human impact across the Holocene is even less documented which led conservation scientists to define 1950 as the starting point of human modification in several Southeast Asian areas, including Thailand. This datum was chosen because it is the start of a regional economic revolution manifested by a massive increase of populations as well as of agricultural and industrial productions. However, not all countries entered this revolution at the same time, and modern environmental disturbances strongly varies among Southeast Asian countries. Indeed, agricultural and deforestation practices as well as socio-economic models of goods consumption are subject to much differences. For example, while the ecological footprint per capita outpaced biocapacity in Thailand and Vietnam in the 80's, the biocapacity deficit balance started only recently in other countries such as Myanmar or Malaysia and earlier in Philippines (Global Footprint Network National Footprint and Biocapacity Accounts, 2021) (Figure 1). On the other hand, demographic trends vary among countries. While the population was multiplied by about 4.5 in the whole Southeast Asia over the last 70 years, some countries had slower demographic growth (Myanmar/Timor/Cambodia/Thailand population increase by 3 to 4 times in this time range) while other had faster growth (Malyasia and Philippines population increase by 5 to 6 times in the last 70 years). As a result, deforestation and natural habitats destruction are not synchronous among countries. Nonetheless, these environmental transitions contributed to make the rich Southeast Asian biodiversity one of the most threatened in the world (Sodhi et al., 2004, 2010). However, although starting the study of the effects of Human impact on biodiversity in 1950 seems to make sense, archaeological evidences clearly show that perturbations started thousands of years earlier (White et al., 2004). Unfortunately, the near absence of data regarding the Holocene biodiversity of Southeast Asia made the pre-modern human impact in this region arbitrarily defined as being null (Baker and Phongpaichit, 2014) without any scientific evidence to demonstrate it. This is damageable because predictions of future ecological changes only rely on a short term dynamic and do not take into account the background of ecosystem alterations produced by earlier generations. This problem might be inducing strong biases because past animal species distributions in the 50's or 60's are likely to not reflect a pristine state on which conservation policies can be based. This reasoning and the lack of paleontological data is problematic as it could potentially lead to bad decisions regarding conservation and restoration policies, for instance with the conservation and reintroduction of invasive taxa (Corlett, 2013).

In this contribution, we present the currently available scientific knowledge regarding parts of the Pleistocene (large mammals) and Holocene (reptiles) past biodiversity of Southeast Asia. We then discuss the current limitations regarding the study of the past Southeast Asian biodiversity and propose ideas to push these studies further at a regional scale. The quantity of quality of the currently available data in Southeast Asia is still too limited to provide a clear and reliable image of the evolution of its biodiversity, and of the putative impact of past human populations across the millennia. This issue is, however, not impossible to overcome and we tried to propose several ideas to upgrade the available fossil record of Southeast Asia in order to enable the quantification of past human environmental impact and to make it relevant to the massive challenge these countries are currently facing for the preservation, and restoration of their rich biodiversity, one of the most diverse and threatened of our planet.

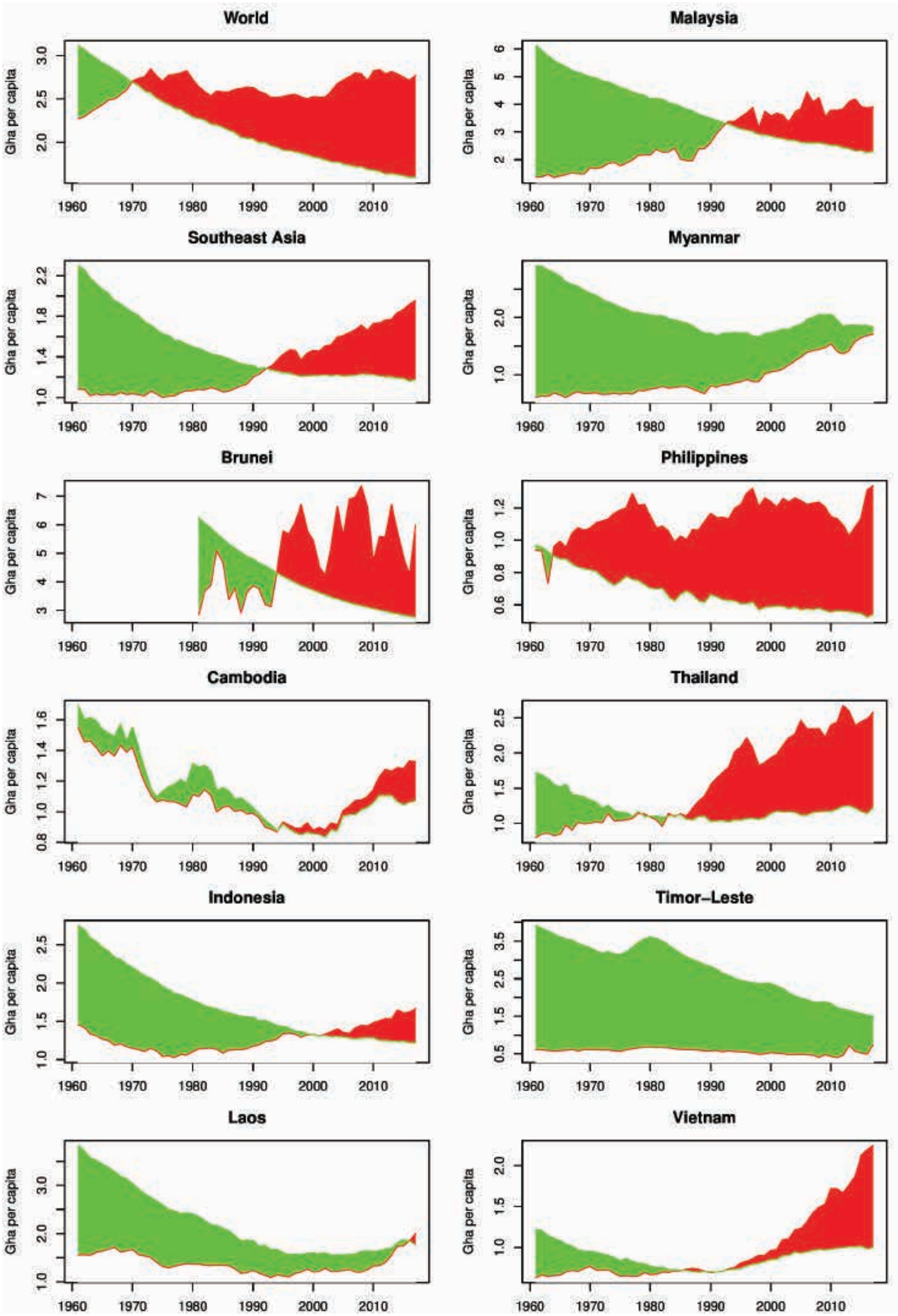

Figure 1. Evolution of evolution and ecological footprint per capita in the different South-Asian Countries. (data from Global Footprint Network National Footprint and Biocapacity Accounts (2021))

14.2 The Pleistocene large mammals of Southeast Asia

In order to address the current biodiversity extinction crisis it is important to understand the patterns and drivers of biodiversity loss across taxonomy, time and space. According to some authors, the disappearance of large mammals at the end of the Quaternary has strong implications for the structuration of the modern mammalian diversity (Faurby and Svenning, 2015) and for the extinction risk it currently faced (Fritz et al., 2009; Turvey and Fritz, 2011). Long-term archival data are therefore needed to provide a context for measuring changes in biodiversity over broad temporal and spatial scales (Crees et al., 2019). However, to obtain reliable paleobiodiversity data, taxonomic, taphonomic, spatio-temporal biases, as well as shifting baselines have to be taken into account. Previous studies were carried out on the Pleistocene fossil large mammal record of Southeast Asia to describe the taxonomic diversity, its relation to past climate as well as its interactions with humans (Bekken et al., 2004). However, the mechanisms at the origin of the Pleistocene large mammal extinctions are extremely challenging to uncover. A good example of this situation is the faunal complex *Ailuropoda-Pongo-Stegodon* whose definition, timing and causes of extinctions are still subject to many uncertainties. This faunal complex is a typical paleontological assemblage of Southeast Asia that includes taxa that are endemic or strongly associated with tropical environments, including: *Stegodon*, an Asian proboscidian, various species of rhinoceros, the large primates *Gigantopithecus* and *Pongo*, as well as numerous species of suidae, deer and bovidae. The most common carnivores are the hyena, tiger, panther, cuon and Tibetan bear, as well as the giant panda: *Ailuropoda*. This particular faunal complex was first identified in southern China (Matthew and Granger, 1923) in association with tropical taxa such as *Hylobates* and *Tapirus* and was then found in Vietnam (Patte, 1928), Laos (Fromaget, 1936) and Myanmar (De Terra, 1938). Von Koenigswald (1938, 1939) originally described this faunal assemblage as "Sino-Malayan". Also discovered in Cambodia (Beden and Guérin, 1973) and Thailand (Pope et al., 1981; Ginsburg et al., 1982), it is associated with the so-called Indochinese biogeographical zone extending from the Yangtze River to the Kra Isthmus. This palaeontological assemblage considered as emblematic of the Middle Pleistocene (between 780,000 and 126,000 years ago) to the Upper Pleistocne (126,000 years to 11,700 years ago) of Southeast Asia by many authors has been used as a milestone to establish a regional biostratigraphy (Kahlke, 1961; Han and Xu, 1985; Tougard, 1998) and then as a tool to reconstruct evolutionary scenarios (Tougard and Montuire, 2006). However, this type of study was based on the hypothesis that the assemblages were homogeneous in terms of chronology and ecological niche, although several authors (Patte, 1928; Colbert, 1943; Pei, 1957; Kahlke, 1961; Orchiston and Siesser 1982; De Vos, 1984) had for long been reluctant to consider these Indochinese paleontological assemblages that are likely to be admixtures from different time periods and environments. This raises the question of the relevance of using those composite reference assemblages to test evolutionary, environmental or ecological hypotheses, but also to quantify precisely the evolution of biodiversity over a long period. The questions of the precise definition of the *Ailuropoda-Pongo-Stegodon* complex, as well as its evolution in time and space are in fact still open. Indeed, *Ailuropoda*, *Pongo* and *Stegodon* are not systematically present in each of the sites that are said to belong to this regional assemblage. Among the 29 Chinese sites described by Kahlke (1961), 7 provide only 2 taxa (Yenchingkuo, Hsiachungchiawan, Maba and Shaochin) or 3 taxa (Hoshantung cave, Hsinsuehchungtsun and Newshuishan) of this assemblage. *Pongo* is absent from Chinese sites such as Guanyindong, Xuetangliangzi, Longtandong, Gongwangling (Dong et al., 2000). At the Tham Wiman Nakin site in Thailand (Tougard,1998), *Stegodon* is missing. In Vietnam, *Ailuropoda* is missing from Tham Om and Tham Hai I and II (Cuong, 1992) and *Stegodon* is the only one from the assemblage at Ham Hum I when *Pongo* is the only species present from the assemblage at Ham Hum II. High precision in the taxonomic identification and stratigraphic/chronological context of the paleontological remains are essential factors for the assessment of the evolution of biodiversity, and the question of the baseline is essential. In the absence of good stratigraphic, chronological, and paleoenvironmental data in most fossil deposits in the region, the question of the role of humans in the extinction of this faunal assemblage remain open. In the next section we discuss more in deft the current issues preventing from reaching a satisfactory conclusion to this question.

14.2.1 The lack of good reference points and the mixture of paleontological collections

When dealing with Chinese or Southeast Asian fossil material from collections more than 30 years old, authors are generally expected to be aware of the limitations inherent in the constitution of such assemblages. However, although these limitations have been mentioned and discussed on numerous occasions (e.g., Allen, 1991; Bouteaux et al., 2007; Chen et al., 2013; De Vos, 1983, 1984; Huffman et al., 2010; Orchiston and Siesser, 1982; Rink et al., 2008; Saegusa et al., 2005; Van den Bergh, 1999; Ibrahim et al., 2013; Turvey et al., 2013; Zeitoun et al., 2010, 2019), several authors still use these collections to build or discuss paleoenvironmental or palaeogeographic models. For example, the Yenchingkuo (now Yanjinggou) collection described in detail by Colbert and Hill (1953) includes the localities of Yenchingkuo I and II and the upper cave of Pingba. Similarly, the Koloshan collection, often also used as a reference, includes the cavities of Kanchuantung, Wuchiatatung (locality 51 and 52), Lungkutung, Kuayintung and Hoshangtung. These heterogeneous historical collections mixing different origins (localities, stratigraphic layers etc.) cannot constitute a useful and reliable milestone and, their use as reference can only disrupt the interpretation and hide the biostratigraphic value of newly discovered and better documented sites (Zeitoun et al., 2019).

14.2.2 Taphonomic biases

Different levels of paleontological data quality coexist in the literature in relation to the detail of the information provided by the authors and the nature of the described material. In some cases, authors fail to provide taphonomic information that precludes assessing the constitution biases of the assemblages. Sometimes, it is even unclear whether different fossils belong to the same site, locality, area, or stratigraphic unit. In such cases, the data cannot be used to establish any biostratigraphic reference, to construct any palaeoecological model, or to describe biodiversity changes. The inclusion of such data including questionable dates and/or associations between dated samples in database may have strong implication for the description of relevant paleontological phenomena (Saegusa, 2001; Pettitt et al., 2003). Due to different taphonomic processes, fossils are often sorted by various natural parameters (e. g. fluvial, volcanic, sedimentary events…) including faunal accumulator agents such as the Porcupine, which is very common in Southeast Asia (Pei, 1938; Zeitoun et al., 2005; Lenoble et al., 2008). There are natural traps in pit caves, in which the bones suffer from mostly in situ modification, but in most cases, in karstic areas, bones are transported and altered by internal river systems. However, most of the Southeat Asian accumulations are created by porcupines that opportunistically collect portions of the carcasses of large animals from their close environment to gnaw them in their resting site. They then bury the remaining elements (isolated teeth and small faceted cubes of bone) in their dens. These accumulation processes result in the distorted representation of the past biodiversity provided by the Southeast Asian fossil record in which small fauna are mostly absent.

The taphonomic information, which is the only way to obtain information regarding the constitution conditions of a fossil assemblage, may be lost due to brecciation or erosion, but alteration of deposits and fossils may also affect the results of dating directly applied to fossil remains. Therefore, the resolution of the chronological signal recorded in the deposits provides different levels of accuracy. The scientific literature must therefore systematically account for all of these limiting factors in order to enable the evaluation of the reliability of the primary data. While natural mixtures of different faunal assemblages due to several taphonomical phenomena are known to be intrinsic biases for fossils in breccia in Southeast Asia, authors often continue to artificially mix data from different sources (localities, chambers, layers, etc.), leading to artificial faunal lists of limited relevance to address biodiversity issues. Significant progress could be made through more rigorous excavation and interpretation protocoles of new sites (Bakken, 1997; Ibrahim et al., 2013; Schepartz et al., 2001, 2003; Zeitoun et al., 2005, 2010, 2019).

14.2.3 Chronological uncertainties and discrepancies

Despite recent advances in geochronology with direct fossil dating methods applied in Southeast Asia (Chen et al., 1987; Chen and Yuan, 1988; Duval et al., 2019; Jones et al., 2004; Rink et al., 2008; Shao et al., 2014, 20177; Wang et al., 2007; Ibrahim et al., 2013; Zeitoun et al., 2010, 2019), in most cases, the age of the faunal remains is given by dating the matrix containing the fossils. However, for such an approach to be relevant the precise stratigraphic context of each fossil should be clearly described and, different layers or areas of a single site should not be mixed. In a karst context, a preliminary requirement for testing palaeoenvironmental hypotheses or quantifying paleobiodiversity is to consider each locality separately, as well as each layer separately in a single site (Saegusa, 2001). An additional condition for a proper consideration of the evolution of faunas in respect to climate modifications is that the period of formation of the considered bone assemblage should not overlap several global climate fluctuations episodes (MIS time scale). This is an important limitation, as the presumed age of the *Ailuropoda-Pongo-Stegodon* complex sometimes shows a rather large chronological range. For example, in Thailand, at the Tham Wiman Nakin site, the dates of the faunal assemblage extend from 350 ka to 8 ka (Esposito et al., 2002). In China, the Wuyun site also extends over a fairly long period, as Wang et al. (2007) indicate that this fossil assemblage is dated between 287.6 ± 60.0 ka and 14.19 ± 4.2 ka. Ma and Tang (1992) provide a date around 8 ka for *Stegodon* in the Jinhua site in Zhejiang suggesting that the *Ailuropoda-Pongo-Stegodon* complex continues until the Holocene, whereas in the Huanglong cave (Hubei), the dates provide an age between 103±1.6 ka and 44 ±12.5 ka (Wu et al., 2006). According to the work of Bekken et al. (2004), in Guanyindong *Ailuropoda* and *Stegodon* are both present within a chronological range spending between 240 ka and 57±3 ka. In Tongzi, *Pongo*, *Ailuropoda* and *Stegodon* heve been dated between 113±11 ka and 181.11±9 ka, and in Maba between 135 ka and 129 ka (Han and Xu, 1989). According to Dong et al (2000), *Stegodon* and *Ailuropoda* were dated at Longtandong between 150 ka and 190 ka (Figure 2).

The significance of synchronicity of the faunal assemblages is not identical depending on whether it is based on individualized stratigraphic assemblages or on an assemblage that covers several stratigraphic entities without being able to distinguish them. Are the three taxa naturally grouped or separated by ecological causes or by the artificial constitution of distinct sets? The level of resolution of the observation is essential to decide for an ecological or chronological signature. While no Ailuropoda is known in the Southeast Asian islands, *Pongo* has been found on the continent up to the south of China (Bekken et al., 2004). In addition, the fossil record indicates the replacement of *Stegodon* by *Elephas* around 128 ka in Indonesia (Westaway et al., 2007) but elsewhere, between 600 and 200 ka, in India (Mishra et al., 2010). In Indonesia or southern China, these replacements are used as chronological milestones

(Van den Bergh, 1999; Wang et al., 2007). However, a general review of the co-existence of these two proboscidians throughout Southeast Asia (Zeitoun et al., 2016) showed that the quality of the available data greatly influenced the significance or even the reality of such a replacement. A detailed study demonstrated that *Elephas* replaced *Stegodon* and *Stegodon* replaced *Elephas* alternatively during the Late Pleistocene in Northern Thailand (Zeitoun et al., 2010). This replacement would thus reflect environmental modifications and thus cannot be used as a clear chronological milestone. Inspired by the studies undertaken by Van den Bergh (1999) for Flores and Sulawesi or by Huffman et al. (2010) for Ngandong, a complete reassessment of field data reports is necessary before using former paleontological data (historical benchmarks) to quantify the erosion of the biodiversity. Unfortunately, as these authors point out, primary field reports or data are not always available, making it difficult to assess the quality of the existing data. Therefore, one of the keys for the future is to carry out new geochronological works on already known and still existing sites (Jin et al., 2014; Sun et al., 2014), or to excavate new deposits using up to date excavation and dating protocols. Indeed, the chronological resolution must be precise enough to establish new paleontological benchmarks useful to describe the evolution of the biodiversity in its chronological and climatic framework.

14.2.4 Bias regarding paleo-environmental data

Recognition of paleoenvironmental or paleoecological changes can only be made if differences are observable in the taxonomical composition of assemblages over time, which is only possible if assemblages, whose integrity and dating are guaranted, are recognized. The use of actualistic and/or isotopic models for the interpretation of the data cannot allow to by-pass this prerequisite. In the context of the lack of well-contextualized data, there is a need to re-examine the causes and consequences of environmental change on fauna, at the finest scale and if possible with sufficient depth of time. One of the explanation for variations of biodiversity is the change in available suitable environment for species to survive. The natural tropical environment, which is generally forested, can be characterized by wetter or drier forests, but can also be interrupted by portions of savannah or localy and regionally decimated by sporadic volcanic events (Sémah et al., 2002; Semah and Semah, 2012; Williams et al., 2009). However, past data regarding palaeoenvironmental changes are still scanty in Southeast Asia making difficult their interpretation at the regional geographical and temporal scale.

Based on works regarding vegetation cover in peninsular and island Southeast Asia and by an association of low eustatic events with seasonal forest and savannah expansion, Heaney (1991) proposed that a low rainfall corridor existed on the Sunda Plateau along an arc extending from southern Thailand to eastern Java. The hypothesis of the occurrence of large rivers with gallery forest,

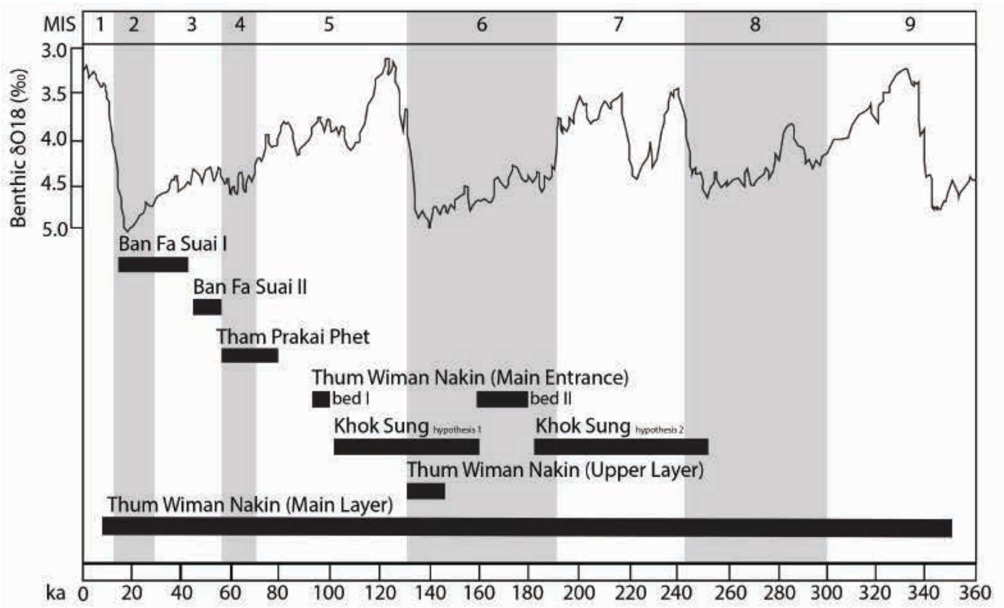

Figure 2. Dating of the Ailuropoda-Pongo-Stegodon faunal complex in Thailand : Ban Fa Suai I (Zeitoun et al. 2010); Ban Fa Suai II (Zeitoun et al. 2019); Tham Prakai Phet (Duval et al. 2019); Khok Sung (Duval et al 2019); Thum Wiman Nakin (Esposito et al. 1998; Esposito et al. 2002).

of high canopy forest habitat on higher ground, and of savannah, constituting a mosaic panorama is based on only a few coastal or island sites paleobotanical data (Bird et al., 2005; Morley and Flenley, 1987; Hope et al., 2004; Würster et al., 2010). Most of the fossil deposits that would be relevant to demonstrate this hypothesis are currently underwater.

This continuous past alternation between savannahs and tropical forests, as well as the fragmentation of the landmass by eustatic rise, would likely have been a major factor contributing to the distribution range reduction and/or the extinction of fauna in Southeast Asia. Cannon et al. (2009) proposed several palaeoenvironmental hypotheses, two of which simulate the separation of the lowland evergreen rainforest blocks of East Borneo and West Central Sumatra, while the other two simulate a narrow evergreen rainforest corridor from Central Sumatra, Banka, and Belitung through the Kalimatan Strait to West Borneo. Despise being based on a limited amont of data, these models and hypotheses have been largely used in the scientific community, especially because they were also coherent with the XXth century idea that savannah provides a wide array of selective factors that could help to explain the divergence of hominins from other primates. However, recent reconstructions of the environments where early hominins lived seem to cast doubt on the degree to which these biomes played a meaningful role in the emergence of the human lineage (Dominguez-Rodrigo, 2014) and shows that the past mosaic landscapes may only be the reflection of mixed paleoenvironmental data. Thus, in their reconstruction of the habitat types of 25 Pleistocene sites in Southeast Asia using a synecological method, Louys and Meijaard (2010), advocated that the Monk's Cave was one of only two sites, along with Tam Hang, that could be attributed with certainty to a "mixed habitat". This "mixed habitat" is, however, most certainly the result of an admixture of the two ecological components of the fauna, which alternate over several thousand years (Zeitoun et al., 2010). In Tham Hang, the image of a so-called "mixed habitat" may be an effect of the admixture of fauna from three localities which may reflect different environments. In addition, the mismatch between chronological data and faunal assemblages, the lack of taphonomy work, and the absence of recording of the position of remains in the sediments preclude to clearly demonstrating the existence of this type of environment.

For the moment, the mismatch between chronological data and faunal assemblages precludes any possibility of demonstrating the existence or absence of a savannah corridor between mainland Southeast Asia and the rest of the Pleistocene Sundaland. Similar reservations can be made regarding the ecological effects of the Toba eruption on the structure of the mammalian community of the Late Pleistocene Southeast Asian fossil. The mobilization of isotope data is undoubtedly a good approach to answer these questions (Suraprasit et al., 2019) but only on the condition that the contextual information of the fossil on which it is applied are precise and well-documented, i.e. the stratigraphic position of the identified fossil remains and its dating. Recently, an interesting new hypothesis has emerged from the use of isotope analyses (Bocherens et al., 2017), that of the flexibility diet, which assume that some taxa have the possibility to adapt their diet to a certain extent. This new concept, should it be applied on relevant fossil material, would make possible to monitor the impact of changes in the tropical environment on different taxa in time and space, in parallel with a study of the evolution of biodiversity.

14.2.5 The extinction of the megafauna

Ideas and arguments about the extinction of megafauna were summarized by Martin and Klein (1984) as a "prehistoric revolution". The study of megafaunal extinction aims to quantify biodiversity loss and can potentially provide a possible model to predict the impacts of ongoing environmental disturbances on large mammal fauna, particularly in the tropics. Regarding Southeast Asia, Corlett (2010) proposed that the lack of a clear extinction peak at the arrival of modern humans in Southeast Asia could be related to an earlier impact of other human populations such as *Homo erectus* while Louys (2012) considered open habitat loss to be the predominant factor. However, as long as the question on the extinction of megafauna will be based on faunal assemblages of dubious nature (see above) solving this question will probably remain out of reach. Good fossil and paleoenvironmental data are still too scant to detect the expected impacts of megafaunal extinctions. In consequence, much of the literature regarding these impacts is based on analogy with the modern large fauna and its interaction with Humans. Overall, the question of the past human or climatic impact on Southeast Asian megafauna remains open because, as we have previously pointed out, inacurracies resulting from field and publication practices, and incomplete primary data do not yet allow to address the issue properly. Without prior critical analysis of the data such as the one provided by Turvey et al. (2013), discussing the extinction of the megafauna during the late Pleistocene and Holocene, remains impossible.

Despite the numerous limitations that make it challenging to establish a relationship between global climate changes and cultural evolution or adaptation in the tropics—due to constraints, errors, lack of data (particularly isotopic), and even poor practices, as discussed by Zeitoun et al. (2023)—recent studies provide promising insights. For instance, the analysis of different types of tooth wear in Javanese cervids and bovids from the Late Pleistocene successfully demonstrated a certain seasonality in well-defined chronological contexts during the LGM (Amano et al., 2016a, b). In addition, using sequential sampling of teeth for $\delta^{13}C$ and $\delta^{18}O$ analyses on tooth enamel from faunal assemblages in the successive archaeological layers of the Tham Lod rock shelter in Northern Thailand, Suraprasit et al. (2021) provided evidence for the existence of synchronous mosaic landscapes. Moreover, Suraprasit et al. (2024) identified an ecological shift associated with the Younger Dryas event.

14.3 The case of past reptile faunas

As discussed above, several locks still limit our understanding of the evolution of the ancient mammalian biodiversity of Southeast Asia, but these limitations are even more prevalent for other taxa and time periods. For instance, the data currently available for Late Pleistocene and Holocene reptilian fauna is still extremely limited (e.g., Auetrakulvit, 2004; Piper and Rabett, 2009, 2009; Conrad, 2015; Conrad et al., 2016; Frère et al., 2018). This currently prevents to study the origins of the current extinction crisis and its future evolution. This overall lack of data could be explained by several factors that are detailed below along with the actions needed to undertake in order to solve them.

14.3.1 Paleontological data and its bias regarding past biodiversity

The current vertebrate biodiversity of Southeast Asia is composed of hundreds of species, of which large mammals represent only a small fraction. For example, Thailand has only 68 species of large mammals compared to 185 species of small mammals (Table 1), 352 species of reptiles, and 1,050 species of birds (Figure 3). However, this abundant tropical diversity of small animals is very poorly represented in the known palaeontological sites that document overwhelmingly large mammal taxa, and only few representatives of other zoological groups (Figure 3, Table 1). This could be explained by the fact that paleontological sites are mostly accumulations of bones collected by porcupines. Indeed, porcupines only collect bones of large animals that they feed on; in consequence, bones of all smaller taxa are excluded from such bone assemblages. A similar remark could be made concerning archaeological sites where the accumulated bone remains corresponds to the large animals hunted and consumed by human groups. In both cases, the composition of the assemblage of bones reflects the strong choices made by a predator (the accumulator agent), and does not provide a relevant picture of the past biodiversity. These problems of representativeness are well known by specialists studying ancient biodiversity throughout the world and are usually corrected by the study of different types of accumulation (e.g., natural Vs archaeological). This documentation bias was driven by decades of quaternary paleontological research motivated by the potential discovery of human remains and by the limited development of zooarchaeological approach for the study of archaeological Holocene deposits. Regarding paleontological researches, less studies have been devoted to small karst infilling or terrace deposits compare to deep cave accumulation of large bones. This is damaging as, for instance, small karst infilling can help to document microvertebrate fauna accumulated by small predators, while terrace and river deposits can enable the documentation of aquatic fauna. As an effect of the lack of interest regarding the recovery of Pleistocene and Holocene small vertebrate bone samples the study of these animals remained poorly developed in Southeast Asia. The documentation of the small vertebrate fauna of Southeast Asia and Thailand is however not out of reach. Indeed, small bone remains accumulations are, however, very well represented in karst areas and sometimes even in already known archaeological sites, as we observed it during recent paleontological surveys. An increased scientific interest in this type of accumulation of small animal bones could therefore help to solve the problem of representativeness of the past biodiversity

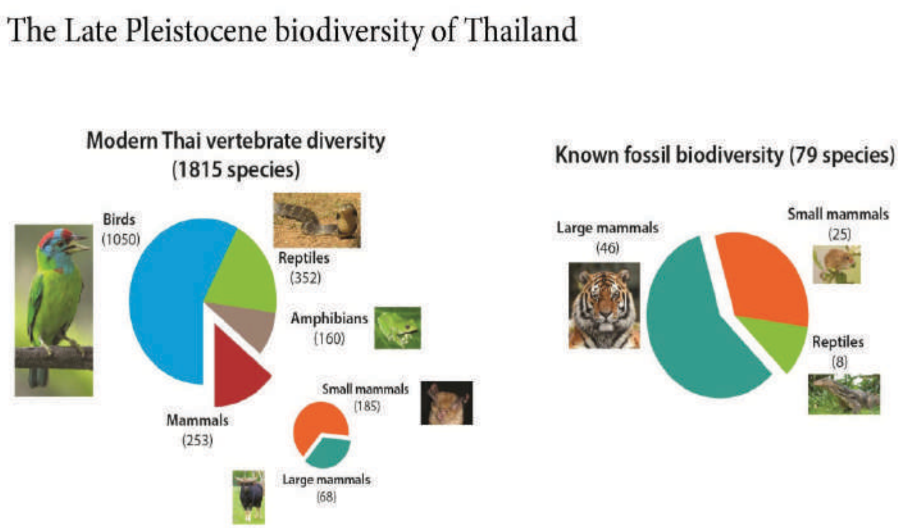

Figure 3. Comparison between the modern biodiversity of Thailand, and what is known of its Pleistocene biodiversity.

Table 1. Mammals of Thailand from Pleistocene to Present based on major palaeontological sites. According to Lekaguk et McNeely (1979) ; Pope et al. (1981) ; Chaimanee (1998) ; Suraprasit et al. (2016) ; Zeitoun et al. (2010, 2019)

	Thailand 1979	Ban Fa Suai I mixed	Ban Fa Suai II mixed	Tham Phrakai Phet	Khok Sung	TWN mixed	Khao Panam
Tupaiidae	4	0	0	0	0	0	0
Erinaceidae	2	0	0	0	0	0	0
Talpidae	1	0	0	0	0	0	0
Soricidae	9	0	0	0	0	0	0
Dermoptera	1	0	0	0	0	0	0
Chiroptera							
Chiroptera indet.		0	1	0	0	0	0
Pteropodidae	15	0	0	0	0	0	0
Rhinopomatidae	1	0	0	0	0	0	0
Emballonuridae	5	0	0	0	0	0	0
Craseonycteridae	5	0	0	0	0	0	0
Rhinolophidae	18	0	0	0	0	0	0
Hipposideridae	13	0	0	0	0	0	0
Vespertilionidae	32	0	0	0	0	0	0
Molossidae	2	0	0	0	0	0	0
Primates							
Primates indet.		x					
Lorisidae	1	0	0	0	0	0	0
Cercopithecidae	10	1	4	1	1	2	0
Macaca sp.		x	x	x	x		
Macaca nemestrina	x		x			x	
Macaca assamensis	x						
Macaca arctoides	x						
Macaca mulatta	x		x				
Macaca fascicularis	x						
Trachypithecus sp.	0		x			x	
Presbytis sp.	5						
Hylobatidae	3	0	0	0	0	0	0
Pongidae	0	0	1	1	0	1	0
Pongo sp.							
Pongo pygmaeus			x	x		x	
Hominidae	1	0	0	0	0	1	0
Homo sp.						x	
Homo sapiens	x						
Manidae	2	0	0	0	0	0	0
Leporidae	1	0	0	0	0	0	0
Rodentia							
Rodentia indet		x	x				
Sciuridae	26	0	0	0	0	5	3
Ratufa sp.	2						
Callosciurus notatus	x						
Callosciurus nigrovittatus	x						
Callosciurus flavimanus	x						
Callosciurus finlaysoni	x					x	
Callosciurus prevostii	x						
Sundasciurus sp.	3						

Table 1. continue.

	Thailand 1979	Ban Fa Suai I mixed	Ban Fa Suai II mixed	Tham Phrakai Phet	Khok Sung	TWN mixed	Khao Panam
Tamiops sp.	2						
Menetes berdmorei	x					x	
Rhinosciurus laticaudatus	x						
Lariscus insignis	x						
Dremomys rufigenis	x						
Petaurista elegans	x						
Petaurista petaurista	x					x	
Petaurista alborufus	x						
Aeromys tephromelas	x						
Hylopetes phayrei	x					x	x
Hylopetes alboniger	x						
Hylopetes lepidus	x						
Hylopetes platyurus	x						
Hylopetes spadiceus							x
Petinomys setosus	x						
Belomys pearsoni	x					x	x
Rhizomyidae	3	0	0	0	0	0	0
Muridae	36	1	0	0	0	14	7
Muridae indet.		x					
Eothenomys melanogaster	x						
Vandeleuria oleracea	x					x	x
Chiromyscus chiropus	x						
Hapalomys longicaudatus	x					x	
Chiropodomys gliroides	x					x	x
Bandicota savilei	x						
Bandicota indica	x					x	
Mus shortridgei	x					x	x
Mus pahari	x					x	
Mus caroli	x						
Mus cervicolor	x					x	x
Mus cookii	x					x	x
Mus musculus	x						
Niviventer fulvescens						x	
Rattus berdmorei	x					x	
Rattus mackensiei	x						
Rattus bowersi	x						
Rattus whiteheadi	x						
Rattus rajah	x						
Rattus surifer	x					x	
Rattus cremoriventer	x						
Rattus confucianus	x						
Rattus rapit	x						
Rattus bukit	x						
Rattus hinpoon	x						
Rattus norvegicus	x						

Table 1. continue.

	Thailand 1979	Ban Fa Suai I mixed	Ban Fa Suai II mixed	Tham Phrakai Phet	Khok Sung	TWN mixed	Khao Panam
Rattus nitidus	x						
Rattus losea	x						
Rattus argentiventer	x						
Rattus remotus	x						
Rattus koratensis	x						
Rattus exulans	x						
Rattus rattus	x					x	
Rattus muelleri	x						
Rattus edwardsi	x						
Rattus sabanus	x					x	x
Rattus sikkimensis	x					x	x
Hystricidae	3	2	1	1	0	0	2
Hystrix sp.		x					x
Hystrix brachyura	x	x	x				
Hystrix hodsoni	x						x
Hystrix indica				x			
Atherurus macrourus	x	x					
Stenidae	4	0	0	0	0	0	0
Delphinidae	7	0	0	0	0	0	0
Balaenopteridae	2	0	0	0	0	0	0
Carnivora							
Carnivora indet.		x					
Haenydae	0	1	0	1	1	0	0
Hyaenidae indet.		x					
Crocuta crocuta				x	x		
Canidae	2	2	1	0	1	0	0
Canis aureus	x						
Cuon sp.		x			x		
Cuon alpinus	x	x	x				
Ursidae	2	3	3	2	0	0	0
Ursus indet.			x				
Ursus thibetanus	x	x	x	x			
Ursus malayanus	x	x					
Ailuropoda melanolueca		x	x	x			
Mustelidae	8	0	0	0	0	0	0
Mustela sp	3						
Martes flavigula	x						
Arctonyx collaris	x						
Melogale personata	x						
Lutra lutra	x	x					
Lutra perspicillata	x						
Aonyx cinerea	x						
Viverridae	12	0	0	0	0	0	0

Table 1. continue.

	Thailand 1979	Ban Fa Suai I mixed	Ban Fa Suai II mixed	Tham Phrakai Phet	Khok Sung	TWN mixed	Khao Panam
Felidae	9	1	1	1	0	0	1
Felis marmorata	x						
Felis viverrina	x						
Felis bengalensis	x						
Felis planiceps	x						
Felis chaus	x						
Felis temmicki	x						
Neofelis nebilosa	x						
Panthera pardus	x			x			
Panthera tigris	x	x	x				x
Proboscidea							
Proboscidea indet.		x	x				
Stegodontidae	0	1	1	0	1	0	0
Stegodon sp.		x	x				
Stegodon orientalis			x		x		
Elephantidae	1	1	0	0	1	1	0
Elephas sp.		x			x		
Elephas maximus	x					x	
Dugongidae	1	0	0	0	0	0	0
Perissodactyla							
Perissodactyla indet.		x					
Tapiridae	1	1	0	0	0	1	0
Tapirus sp.		x					
Tapirus indicus	x					x	
Rhinocerotidae	4	3	1	1	2	2	0
Rhinoceros unicornis		x			x	x	
Rhinoceros sondaicus	x	x	x	x	x	x	
Rhinoceros sinensis		x					
Dicerorhinus sumatraensis	x						
Artiodactyla							
Artiodactyla indet.		x	x				
Suidae	1	2	1	2	1	2	1
Sus sp.		x					
Sus scrofa	x	x	x	x		x	
Sus barbatus		x		x	x	x	
Tragulidae	2	0	0	0	0	0	0
Cervidae	6	6	4	3	3	4	2
Muntiacus sp.		x		x			
Muntiacus muntjak	x	x	x			x	
Muntiacus vuquangensis		x					
Muntiacus feae	x						
Axis porcinus	x	x	x	x	x	x	
Cervidae indet.		x		x			
Cervus sp.		x	x				x
Cervus unicolor	x	x	x	x	x	x	
Cervus eldii	x	x			x	x	x

Table 1. continue.

	Thailand 1979	Ban Fa Suai I mixed	Ban Fa Suai II mixed	Tham Phrakai Phet	Khok Sung	TWN mixed	Khao Panam
Cervus schomburgki	x						
Cervus nippon		x	x				
Bovidae	4	5	1	3	3	4	1
Bovidae indet.		x	x				
Bubalus sp.				x			
Bubalus bubalis	x	x			x	x	
Bos sp.		x	x				
Bos javanicus	x	x		x		x	
Bos gaurus	x	x			x	x	x
Bos sauveli	x	x		x	x	x	
Pseudoryx sp.		x					
Naemorhedae	2	4	1	1	1	1	0
Naemorhedus sp.		x	x	x			
Naemorhedus caudatus		x					
Naemorhedus goral	x	x					
Capricornis sumatraensis	x	x			x	x	
Hippopotaidae	0	0	0	0	0	0	1
Hippopotamus sp.							x

data. Systematic field collection campaigns should therefore be organized and new local specialized paleontologists and zooarchaeologists trained.

14.3.2 A lack of data regarding the osteology of modern taxa

The second limitation to our knowledge of small vertebrate and ancient reptile faunas is the lack of data regarding the skeletal morphology of modern taxa. Indeed, in order to be identified, the bones found in archaeological/paleontological deposits must be compared with those of modern species. However, the osteological morphologies of modern reptiles and of many other small vertebrates are at best unpublished, if not totally unknown. Indeed, scientists working on the modern record of these groups rely most often on external phenotype and genetic data to identify taxa, and rarely describe skeletal elements. An important work of osteological description of the wide diversity of species found in Southeast Asia should therefore be continued beyond the works carried out on the taxa that are the best represented in archaeological sites, namely monitor lizards (Bochaton et al., 2019a) and turtles (Pritchard et al., 2009). This anatomical work, which is of interest for the study of both modern and very ancient fauna, will have to be carried out in parallel with the application of advanced molecular methods, such as the exploration of the use of paleoproteomics, in order to be able to identify reliably and precisely the species present in the archaeological and paleontological deposits of Southeast Asia.

14.3.3 A lack of exchanges between scientific communities from different backgrounds

The lack of data concerning reptiles of the past could also partly be related to the lack of dialogue between paleontologists, archaeologists, and biologists working on modern fauna. This difficulty is not specific to Southeast Asia but is reinforced in this geographical area due to language barriers and the diversity of origins of researchers involved in the area, whether local or not. Real awareness-raising work must be carried out so that the interest of data regarding ancient wild fauna is known to archaeologists, especially those working on historical periods that are sometimes unaware of the relevance of making an extra effort to collect tiny bone remains of small vertebrates in the framework of their excavations. A dialogue must also be established in a more direct way between specialists of the past and the biologists able to help with the set up of reference work regarding the osteology of modern taxa, as well as with researchers and stakeholders who could be interested and involved in the potential use of fossil data for the implementation of biodiversity conservation and restoration policies.

International work and research projects aimed at addressing these various identified difficulties are beginning to emerge with the aim of writing the first lines of the history of reptile biodiversity in Southeast Asia (e.g., Bochaton et al., 2019b; Claude et al., 2019). However, in order to be fully profitable in the long term, we believe that projects concerning ancient fauna should takes into account the recommendations formulated below.

14.4 Recommendations

The improvement of our knowledge of ancient Southeast Asian biodiversity must be based on the competence of local researchers. This principle is of critical importance as such study must contribute to raise local public awareness about the human impact on the environment, and about the protection of tropical biodiversity. The appropriation of this research by foreign researchers seems, indeed, difficult to accommodate with a local assimilation of these societal issues. However, although skills are available internationally to train local specialists, a founding generation of local specialist is struggling to emerge due to the lack of attractiveness of academic careers in the region. Thus, many young researchers who have obtained a PhD abroad tend to move towards administrative careers that are more locally valued. This phenomenon blocks the emergence of a local research of international significance and the transmission of knowledge with students often forced to leave local universities to train abroad. From a more academic point of view, it is necessary to maintain a scientific community interesting in the anatomy and systematic of both modern and fossil taxa as such expertise tends to disappear including in northern countries with strong research infrastructures (Gruwier and de

Vos, 2015). Such competences are however essential for the study of the past biodiversity and the history of environmental human impact.

Another issue concerns the dissemination of the scientific information. Indeed, two parallel scientific literatures coexist without communicating with each other. One is written in the local language (often inaccessible to foreign researchers) and the other is written in a foreign language (sometimes inaccessible to local researchers). Policies could be decided upon to limit these problems, such as the obligation to include an abstract (and if possible a title) in local language in international publications (often in English), and at least a version of the title in English in local language publications so that both productions could be equally found and read on the internet.

The establishment of regional reference work on the osteology of modern taxa must be undertaken ambitiously but in accordance with the specificities of Southeast Asia. It would indeed be counterproductive to establish a collection of skeletons of modern species at a single location given the existing general demand for such resource at the regional scale. It would also be unethical to massively collect specimens from their natural environment to build such a collection at a time when many Southeast Asian species are protected and threatened with extinction. Hopefully, technologies enable to scan 3D skeletons already prepared in museum collections around the world. Several websites also allow the free storage and access of such 3D models, which enable their diffusion to all researchers and institutions regardless of their available financial capacity. Such approaches are expensive at the outset but more cost-effective and sustainable in the long term. Similar work has already been initiated, for instance by the United States natural history museums (Watkins-Colwell et al., 2018).

Regarding more specifically the Pleistocene large mammalian Southeast Asian fauna, the regional reevaluation of the stratigraphic, taphonomic and paleoenvironmental available data (Bekken et al., 2004; Huffman et al., 2006, 2010; Turvey, 2013; Van den Bergh, 1999; Zeitoun et al., 2010, 2015, 2016, 2019) has demonstrated that reference to historical paleontological collections compose of artificial mixing of remains coming from several sites should be abandoned. In the same way, such mixing and similar approximation should be avoided and more attention should be paid on detailed stratigraphic and chronological interpretation of individual deposit. More generally, studies of sites reporting long record sequences should be promoted and the discoveries of more sites stimulated to deliver information regarding biodiversity dynamics and its interrelationship with humans from the Late Pleistocene to the start of the 20th century.

14.5 *Potential application of past biodiversity data in current biodiversity issues*

The current image of the past biodiversity of Thailand is that human did not influence the environment prior to the economic revolution of 1950 that saw the beginning of an exponential growth of human populations. This idea is present in most of tropical areas and is rooted in the idea that pre-modern populations had not the power and the technological capacities to exploit their environment at a broad scale. This is, however, prove wrong by archaeological evidence in many area including in Thailand were palynological data indicate that mass deforestation started more than 4000 years ago (White et al., 2004). However, paleobiodiversity data would be the only way to obtain a reliable image of the evolution of vertebrate diversity through time in relation to climate change and human impact. The acquisition of such data could have several applications to restore and protect the modern rich and threatened biodiversity of this area (Barnosky et al., 2017; Rick and Lockwood, 2013). First, these data would enable to study the undisturbed states of the ecosystems. Indeed, it is currently very challenging to assess whether a seemingly undisturbed ecosystem represent a true pristine environment or was modified in the past by human activities. This is an important issue as so called "pristine" ecosystems are used in a broad range of ecological studies as well as baseline to asses' biodiversity perturbation and faunal restauration goals. The study of past climate change also provide interesting comparison points to predict the responses of faunal communities to ongoing and future climate change as models can be tested on events that happened in the past. Similarly, past extinction events linked to human impact can help to better understand extinction patterns and thus to predict and try to avoid future extinctions (Bochaton et al., 2021). These data are also relevant to assess the conservation status of modern taxa in more detail for instance by providing additional data regarding the evolution of their distribution ranges through time (Claude et al., 2019). Finally, paleobiodiversity and archaeological data have a strong media potential and are a very easy way to raise the awareness of the public about environmental issues.

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