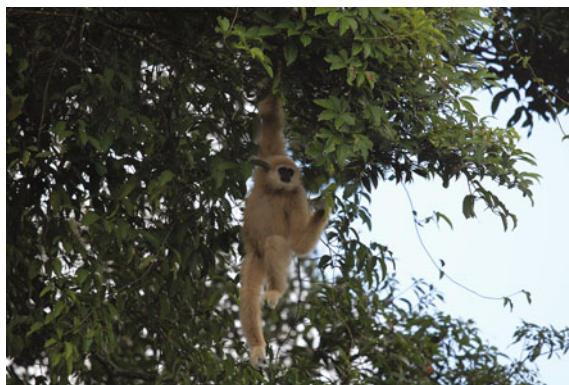


Chapter 2

The Role of Historical and Fossil Records in Predicting Changes in the Spatial Distribution of Hylobatids

Helen J. Chatterjee



Subadult female white-handed gibbon monitoring the surrounding, Khao Yai National Park, Thailand. Photo credit: Ulrich H. Reichard

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Introduction

Southeast Asia has experienced considerable palaeo-environmental and more recent environmental changes which have affected the spatial distribution of the region's fauna and flora. Interpreting and predicting changes in the spatial distribution of rare or endangered taxa is useful for both macro-evolutionary studies and for conservation action planning. Furthermore, quantifying these changes, spatially and temporally, provides valuable biogeographic information that can be used to understand the tolerance of species to environmental fluctuations (Stigall and Lieberman 2006). This is especially important for taxa such as hylobatids, where all but one of the species is listed as endangered or critically endangered by the IUCN (2015).

Environmental change in Southeast Asia continues to be a source of biogeographic interest. It is argued that the region is experiencing the highest relative rates of deforestation and forest degradation in the humid tropics (Koh and Sodhi 2010). Southeast Asia is widely acknowledged as one of the world's most significant biodiversity hotspots (e.g., Myers et al. 2000; Sodhi et al. 2004; Edwards et al. 2011). It is home to 5 of the 25 regionally defined biodiversity hotspots (comprising Sundaland, Wallacea, Philippines, Indo-Burma and South-Central China: Myers et al. 2000) and as such contains exceptional concentrations of endemic species which are undergoing extensive habitat loss. In light of the rapid rate of deforestation, and the high concentration of endemic species in the region, it is predicted that Southeast Asia could lose 13–42 % of local populations by the end of this century, at least 50 % of which could represent global species extinction (Brook et al. 2003). Given the relatively high diversity of hylobatids, with 19 recognized species (Anandam et al. 2013), the hominoids could be more severely affected compared to non-hominoid groups.

Habitat loss and fragmentation are likely to be exacerbated by other anthropogenic pressures including human-induced climate change and associated rapid industrialization, economic growth and human population migration in the future. South Asia and Southeast Asia have been identified as regions likely to experience more pronounced climate change and it has been argued that such ecoregions require more detailed impact assessments to inform effective conservation (Li et al. 2013). Southeast Asia has a long history of environmental change dating back many millions of years and these changes are responsible for the region's biogeographic uniqueness. It has been suggested that in order to achieve long-term success in protecting and conserving Southeast Asia's biodiversity it is vital to understand its historical biogeography (Koh and Sodhi 2010; Woodruff 2010).

Historical Biogeography and Species Ranges Changes in Southeast Asia

Dramatic plate tectonic and orogenic activity in Southeast Asia during the Cenozoic, gave rise to various land mass changes, which in tandem with glacial activity, affected the areas geomorphology, climate, flora and fauna (Chatterjee

2009). Palaeo-environmental changes dating back 15–20 million years impacted the extent of emergent land which provided both pathways and barriers to faunal and floral dispersal and vicariance events. In turn, climatic variations associated with glacial periodicity during the Pleistocene also affected sea levels and hence the extent of exposed land. Similarly, climatic changes associated with these fluctuations affected the type of ecosystems that could be sustained on exposed land (see Chatterjee 2009 and references therein).

Whilst climatic deterioration from the late Miocene onwards negatively affected some primate fauna, this does not appear to be the case regarding hylobatids (Jablonski 1993). Indeed, from both paleontological and palaeo-environmental records of China, in spite of increased seasonality and habitat fragmentation, hylobatids were among the most successful primates (Jablonski 1993; Jablonski et al. 2000). This scenario is in contrast to the hypothesis that in hominoids certain life history traits such as relatively long gestation times, long weaning periods, long inter-birth intervals, lower intrinsic rates of population increase and preferences for higher-quality fruits, imply higher vulnerability to environmental changes (Jablonski et al. 2000).

Hylobatids are predicted to have expanded their range from a putative gibbon ancestor in Eastern Indochina from approximately 10.5 million years ago, after which time hylobatids differentiated and radiated southwards (Chatterjee 2006). These radiation events occurred in tandem with considerable environmental changes, which raises interesting questions about hylobatid species tolerance. Regardless of the limitations of the sparse fossil record for hylobatids (Jablonski 1993; Jablonski et al. 2000; Jablonski and Chaplin 2009), gibbons and the siamangs were able to alter their spatial distribution in order to adapt to changing environmental conditions. This concept is supported when historical and fossil data are considered in the context of present and future predicted habitat ranges.

To predict the tolerance of Chinese hylobatids to changing environmental conditions, Chatterjee et al. (2012) used Ecological Niche Modelling (ENM) based on fossil, historical and present-day distribution data. The study developed a database of locality data for Chinese hylobatids from the published literature spanning three time intervals: fossil (Pliocene to earliest Holocene), historical (265 AD–1945) and modern (1945 AD to the present). The ENM software DIVA-GIS (Hijmans et al. 2005) was used to generate maps showing the distributional ranges for hylobatids in China in each of the three time intervals. Present and future habitat suitability was predicted using global climatic variables including precipitation, temperature and carbon dioxide emissions. According to recent models, mean temperature and precipitation in China are predicted to increase by c.0.71 °C and c.8.4 mm, respectively, over the next 30 years (Liu et al. 2010). These variables were manipulated in line with future climate change predictions to model the effects of these changes on future gibbon habitat suitability.

The results of this study show that Pliocene-Holocene gibbon fossils are distributed from southernmost China to the Yangtze River delta in eastern China (Fig. 2.1) Further, there are more gibbon fossils recorded from the south-western provinces of Yunnan, Guangxi and Hainan compared to more northern and eastern provinces (Guizhou, Guangdong, Hunan, Hubei, Chongqing,

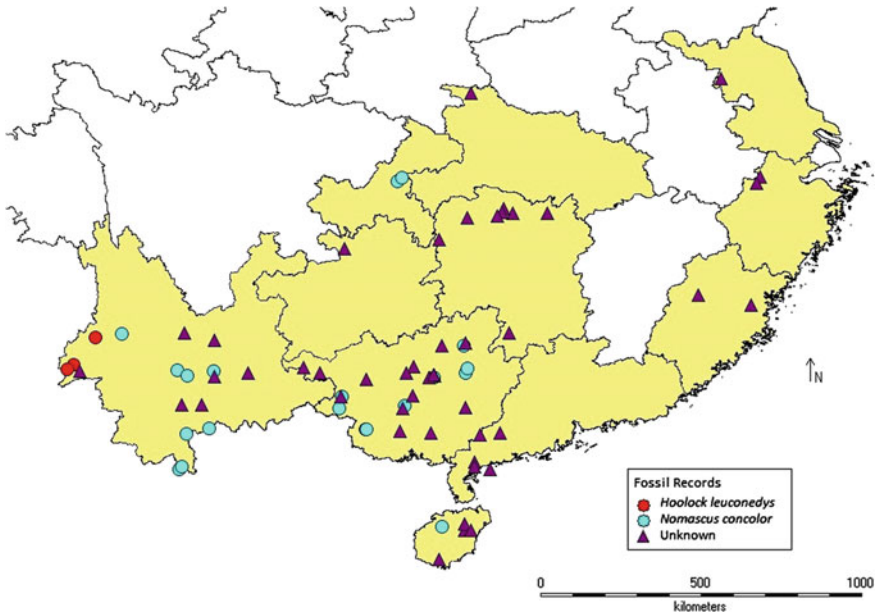


Fig. 2.1 Map of China showing the geographical distribution of fossil gibbons during the Pliocene-Holocene. Reproduced with permission from Chatterjee et al. (2012, Fig. 1). Copyright © 2012, Karger Publishers

Fujian, Zhejiang and Jiangsu), notwithstanding collection biases (Fig. 2.1). Similarly, records regarding the distribution of hylobatids during the Chinese historical period (265 AD–1945) indicate that hylobatids ranged across southern China to the north as far as the Yangtze region (Fig. 2.2). Given that such data are broadly congruent with the distribution of older Pliocene and Quaternary fossil gibbon records (Jablonski 1993; Jablonski et al. 2000; Jablonski and Chaplin 2009), hylobatids either remained widely distributed over southern China throughout Pleistocene-Holocene climatic cycles or were able to re-colonize this region relatively rapidly following periods of adverse climate (Chatterjee et al. 2012).

Present-day distribution of hylobatids in China, as elsewhere, has been dramatically affected by widespread habitat loss, along with other population stressors such as poaching. Although gibbon species diversity in China is relatively high with at least eight species and subspecies, their density is low with fewer than 300 individuals recorded by the IUCN and two species may already be extirpated from China (IUCN 2015). Current gibbon populations are restricted to the southernmost provinces of Yunnan, Guangxi and Hainan, suggesting that the greatest range shift in Chinese hylobatids took place between the late Holocene historical period and the modern era (from 1945 onwards). During these time periods northern populations had disappeared from China and remaining southern populations were considerably reduced and pushed to the far southwest of China (Chatterjee et al. 2012).

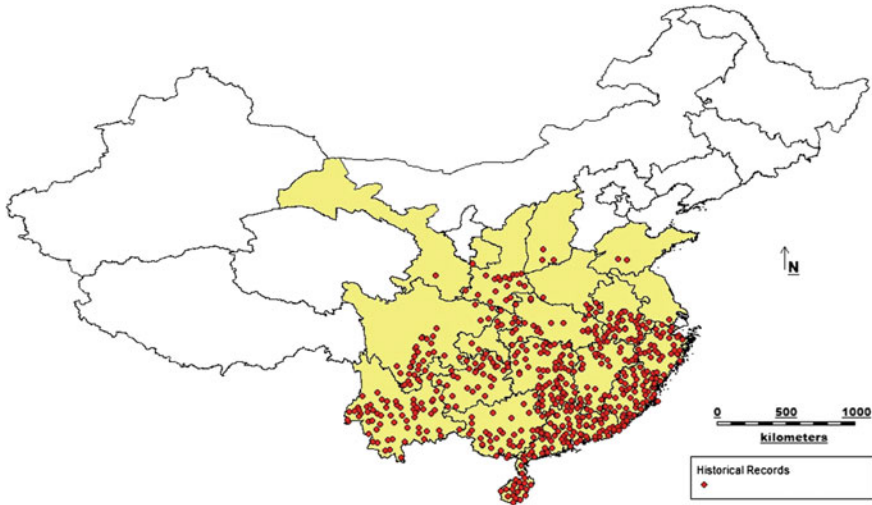


Fig. 2.2 Map of China showing the geographical distribution of gibbons during the historical period (AD 265–1945). Reproduced with permission from Chatterjee et al. (2012, Fig. 2). Copyright © 2012, Karger Publishers

The results of the ENM indicate that the areas suitable for hylobatids in Yunnan, Guangxi and Hainan are geographically restricted, with large parts of these provinces characterized by low-to-medium habitat suitability. Interestingly, the analysis shows that there are areas beyond modern gibbon ranges which are characterized by high-to-excellent habitat suitability, including parts of central China. This suggests that hylobatids in China are currently occupying sub-optimal locations. Moreover, it shows that not only recent historical events (e.g., habitat destruction) have affected population numbers, but that they are also responsible for causing adverse range shifts which may affect the success of remaining populations. When future climatic changes are considered, the study predicts that in the next 30 years, the suitability of habitats for hylobatids will be downgraded across south-western China, and Yunnan will be the only area to contain suitable habitats for hylobatids (Chatterjee et al. 2012, Fig. 7). Given the ongoing issues of habitat loss, poaching and other direct anthropogenic factors which are impacting gibbon population numbers and ranges, the added potential impact of anthropogenic climate change is likely to cause further population deterioration (Chatterjee et al. 2012).

Whilst the results of this study are only a proxy for the likely future spatial distribution of hylobatids in China, based on modelling predictions, they demonstrate the importance of considering past, fossil and historical distributions when studying range changes in endangered and critically endangered species. It also shows the value of incorporating historical biogeographic and environmental data in spatial distribution analyses.

The large-scale range contraction seen in Chinese hylobatids in fact seem to have occurred during a time period when environmental conditions were stable,

compared to the fluctuations experienced in the Quaternary (Chatterjee et al. 2012). Although hylobatids' life history traits are expected to make them more vulnerable to environmental changes (Jablonski et al. 2000), historical and fossil records show the opposite (Jablonski 1993; Chatterjee et al. 2012). The ENM study reveals that the range changes observed in Chinese hylobatids can be attributed to past and ongoing anthropogenic activity rather than natural environmental change. The key finding of Chatterjee et al. (2012) is that the current-day distribution of hylobatids in China represents only their realized niche as a result of widespread recent habitat destruction, and not their fundamental niche of actual environmental tolerances. This is critically important for conservation planning since the findings of this study suggest that plans based on these modern distributions alone are likely to be artificially restrictive and pessimistic (Chatterjee et al. 2012).

To understand the history of biodiversity hotspots, refugia and biogeographic transitions, integrating historical biogeography into conservation planning is highly relevant (Willis et al. 2007; Woodruff 2010). Whilst hotspots capture present-day areas of exceptional species richness (Woodruff 2010), Pleistocene refugia are thought to have enabled these species to survive environmental challenges in the past. For example, during cooler Pleistocene glacial conditions rainforests retreated to the hills of peninsular Malaysia, western Sumatra, the Mentawi Islands and the centre of Borneo, and during warmer periods rainforests were replaced by savannah woodland or grassland on the emerged Sunda plains and elsewhere (Heaney 1991; Morley 2000, 2007).

By modelling changes in the distribution of major forest types during the last full 120,000-year glacial cycle, it was found that they expanded their ranges rather than contracted them during warm phases (Cannon et al. 2009). Thus, it is plausible that it is today's rainforests that are refugial and not those of the last glacial maximum (Cannon et al. 2009). In this regard, the changes experienced in Southeast Asian forests are the opposite of those in better-known temperate regions; rather than shrinking during cooler periods, lowland evergreen rainforests doubled in size (Woodruff 2010). Expansion of the forests may also have impacted the spatial distribution of the associated fauna, resulting in highly unusual present-day faunal and floral distribution patterns (Woodruff 2010). The biogeographic history of Southeast Asia could affect responses of species to land-use and climate change in the future, which could have considerable implications for conservation planning (Woodruff 2010).

Predicting Future Biogeographic Changes

Southeast Asia was almost entirely covered by rainforest 8000 years ago but it is predicted that the region could lose three quarters of its original forests by 2100 and up to 42 % of its biodiversity (Koh and Sodhi 2010; Sodhi et al. 2004). These biogeographic changes will occur in the backdrop of changes brought about by anthropogenic climate change, but the effects that climate change will have on

Southeast Asian biodiversity is difficult to predict. Whilst a species may appear to make an individualistic response to climate change, the species' dispersal abilities, niche breadth and ecological plasticity also play a role (Parmesan 2006). Biogeographic interdependence is also likely to be important. There are many examples of plants which are dependent upon specific seed dispersers. Hylobatids, for example, disperse many plant species, including fruit with hard covers and flesh attached to seeds that competitors, such as hornbills, are unable to eat (Kanwatanakid 2000; Kitamura et al. 2004). Further, it appears that some plant species, such as rambutans, may be entirely dependent upon hylobatids for dispersal (Brockelman 2011). Corlett (2009) notes that the survival of plants which respond to climate change through range shifts in their distribution will be tied to seed dispersing frugivorous birds and mammals. It is important therefore to understand the individualistic and ecosystem responses to climate change given the complex inter-relationships exhibited in such biotas.

Predicting the effects of climate change in a region such as Southeast Asia is challenging. The combination of a variety of different ecosystems, the region's varied and dramatic geomorphological history in association with rapid economic and human population growth, creates a complex and dynamic biogeographic landscape. Predictions based on a variety of studies, and discussed by Woodruff (2010), suggest a 2.4–2.7 °C rise in mean annual temperature (4 °C in subtropical China), a 7 % increase in wet season rainfall, a drier dry season, sea level rise of 1–2 m by 2150 and 2.5–5 m by 2300, higher frequency of El Nino Southern Oscillation (ENSO) events and higher frequency of fires. As Woodruff (2010) points out, such projections are not definitive end points but are based on the conditions expected when atmospheric CO₂ is double its pre-industrial concentration. If greenhouse gas emissions are not reduced and other climate change conditions not mitigated, temperatures and sea levels will continue to rise after this point, so most projections are likely to underestimate the effects on biota.

A considerable challenge with regard to future conservation planning is predicting how climate change will impact the distribution of species. The problem is further compounded in regions such as Southeast Asia where other direct anthropogenic factors, such as deforestation, continue at alarming rates. Woodruff (2010) argues that as land-use and climate change drive more people to become environmental refugees, displaced due to negative environmental impacts such as flooding, human biogeography and migration will also need to play a greater role in conservation planning. This is particularly significant for hylobatids living in areas which are predicted to undergo significant transformations as a result of climate change. For example, 14 million of the 28 million people living in the Mekong Delta in southern Vietnam are predicted to be displaced by a 2 m rise in sea level due to future climate change (Warner et al. 2009). Whilst some people will relocate to urbanized areas others will likely be forced into protected areas which provide habitats for numerous threatened species, including *Nomascus gabriellae* and *Nomascus annamensis*.

Understanding how and where species will shift their ranges in response to climate change can be implied by studying past biogeographic patterns, as outlined

above. In keeping with the notion that it is important to incorporate historical biogeography into present-day and future biogeographic studies, it has been found that species which occur on small islands tend to be smaller subsets of more diverse communities inhabiting larger islands (Okie and Brown 2009). Several authors have proposed that the mid-Pliocene (c.3 million years ago) is a useful model for predicting faunal and floral range changes because global temperatures were on average 3 °C higher than today (Bonham et al. 2009; Haywood et al. 2009; Salzmann et al. 2009). Salzmann et al. (2009) for example, compared past data and models of Middle-Pliocene vegetation with simulations of vegetation distributions for the mid- and late twenty-first century to examine the extent to which the Middle Pliocene can be used as a ‘test bed’ for future climatic warming. Based on the premise that during the Middle Pliocene global temperatures were higher than today, as were higher atmospheric CO₂ concentrations, the study showed it was able to pinpoint specific future temperature and CO₂ levels which were concordant with those experienced in the Middle Pliocene. Their model simulations indicate a generally warmer and wetter climate, and afforded an opportunity to generate shifts in global vegetation patterns as a result of future climate change (Salzmann et al. 2009).

Many extant species living in Southeast Asia during the Pliocene have since survived multiple glacial/interglacial cycles. This ability to adapt may mean that species, such as hylobatids, will be less challenged by future environmental change such as temperature compared to seasonality and the length of the dry season (Woodruff 2010). It is possible that such species may have sufficient genetic variability and ecological plasticity to adapt to future climatic changes (Parmesan 2006). Although this confirms the possibility for hylobatids to adapt to environmental change (Chatterjee et al. 2012), further evidence is needed to fully understand hylobatids’ ecological plasticity to future climate change.

Several studies have also highlighted the importance of considering within- and between-species genetic variability in conservation planning and management, for example Andayani et al. (2001) demonstrated at least two genetically differentiated lineages of *Hylobates moloch* on Java and suggested that the two lineages represent different management units. Given the well-documented challenges in reconstructing hylobatid phylogenetic relationships, revealed by whole genome sequencing (Carbone et al. 2014; Veeramah et al. 2015), understanding inter- and intraspecific genetic variability in gibbons in light of reduced population sizes is an important area of future research. In tandem, the relationships between species range shifts, population size and adaptive capacity are crucial in order to improve conservation planning for the future.

Hylobatid Historical and Fossil Records in Biogeographic Reconstruction

Southeast Asia has a long and complicated biogeographic past, but its history is relatively well studied and there is significant evidence that integrating historical biogeographic information improves our understanding of how species can be

expected to respond to environmental changes (Woodruff 2010). The biggest challenge with regard to hylobatid historical biogeography is the sparseness of the fossil record, which is well documented (Chatterjee 2009; Jablonski and Chaplin 2009; Harrison 2016). This is particularly pertinent for the pre-Pleistocene time periods where the fossil record is very patchy; however, fossil data are especially useful when considered in the light of their associated locality and environmental information. Considerable efforts in documenting the gibbon fossil record have produced extremely valuable resources for investigating the spatial and temporal changes which occurred across hylobatids (Jablonski and Chaplin 2009). These meticulous records comprise species name, locality (including country, province, latitude and longitude) and time period for hylobatids, affording a time slice view of changes in the fossil record over time and space.

Historical records, in contrast to fossil records, have been relatively underexploited in spatial distribution analyses. In China, hylobatids formed a popular subject for paintings and sculptures and allude to the higher status attributed to hylobatids compared to other primates in Chinese culture. Geissmann (2008) was perhaps the first to investigate historical records for hylobatids and reported evidence from Van Gulik (1967) showing that as early as the Zhou dynasty (221–1027 BC) the Chinese singled out the gibbon as “the aristocrat among apes and monkeys” (van Gulik 1967, Preface). It is thought that this cultural interest in hylobatids stems from the belief that hylobatids were able to absorb the largest amount of “qi” (the key to longevity and immortality) and circulate it in the body. Other evidence that demonstrated the important role of *Nomascus* gibbons in Chinese culture includes literature and poems dating back to the Han dynasty (206 BC–220 AD) and Song dynasty (960–1279 AD). The cultural interest in hylobatids in China later spread to other Asian countries such as Japan and Korea. Historical Chinese poems, paintings and literature not only provide evidence of the cultural importance of hylobatids, but the localities of where these paintings and artistic compositions were found provide geographic information about their distribution. For example, based on historical records, Geissmann (2008) showed that in the tenth century, the distribution of the ancient Chinese hylobatids ranged over large parts of China, around 75 % of the country, down from the south all the way up to the Yellow River, which is concordant with Chatterjee et al. (2012). Geissmann¹ also points out that historical Chinese literature and art documents demonstrate that *Nomascus* gibbons lived in regions where winters were severe and notes that poets refer to seeing hylobatids in winter. Van Gulik refers to the below poem by Li Po (701–762 AD) about *Nomascus* gibbons in southern Anhui province:

The splendor of the mountains shivers under the accumulated snow.
Like shadows the gibbons are hanging from the cold branches... (cited in Van Gulik 1967, p. 61)

¹<http://www.hylobatids.de/main/index.html>.

This evidence indicates that the hylobatids referred to in this poem inhabited considerably cooler environments than many extant hylobatid populations, most of which are restricted to tropical and subtropical forests. This exemplifies the intriguing possibility of using historical data to interpret past species ranges and indicates the possibility that hylobatids are able to adapt to different environments outside of their usual or preferred niche. In a similar vein to Jablonski's fossil record data, historical records for mammals in China collated by Wen (2009) provide details of species distributions. Based on the same records in some cases to those described by Geissmann (2008), Wen's data is based on historical books, manuscripts, illustrations and other texts. Aside from translation issues (Wen 2009 is in Chinese) one of the biggest challenges in using these data in spatial distribution analyses is interpreting the exact geographic locality to which the records pertain, and by extension therefore the exact species to which they refer. Most records refer to fairly broad geographic areas (c.10–100 km) within Chinese provinces which cover very large areas (many hundreds of kms) so pinpointing the exact location of a record can be problematic. However, by documenting these records and building up species distribution maps, studies such as Chatterjee et al. (2012) have shown that historical data can provide a useful tool for investigating the change in species distributions over time and can help to shed light on a species' adaptability when considered in the context of fossil and modern data.

Notwithstanding the limitations of gibbon fossil and historical data, including taphonomic and collecting biases, several studies have shown that incorporating these data into spatial distribution analysis affords a unique insight into how species respond to change over time and therefore how these data might be used to make predictions for the future (Woodruff 2010; Chatterjee et al. 2012). There are many inherent problems with historical and fossil data, not least the fact that the further back in time you go the poorer the spatial and temporal resolution of records is likely to be. The aforementioned studies have shown however, that not considering past species' responses to environmental change may provide a false or inaccurate view of its current and future success. Willis et al. (2007) have argued for the value of including historical records older than 50 years in conservation planning, despite the fact that this is not commonplace. They suggest that as well as using past data to interpret spatial range changes over time, these data also provide evidence of natural fluctuations in population size prior to the onset of anthropogenic activity. Furthermore, that data from the fossil record could be used to determine thresholds of natural variability and highlight those populations where the decline is real; in this way such studies could be used to identify conservation priorities (Willis et al. 2007).

In conclusion, given the dramatic population declines seen in many hylobatid species in the past 50–100 years and the continuing anthropogenic pressure these species face, including future climatic changes, the value of incorporating fossil and historical data in future conservation planning and studies of range shifts should not be underestimated.

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