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# Complementarity, completeness and quality of long-term faunal archives in an Asian biodiversity hotspot

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**Abstract.** Long-term baselines on biodiversity change through time are crucial to inform conservation decision-making in biodiversity hotspots, but environmental archives remain unavailable for many regions. Extensive palaeontological, zooarchaeological and historical records and indigenous knowledge about past environmental conditions exist for China, a megadiverse country experiencing large-scale biodiversity loss, but their potential to understand past human-caused faunal turnover is not fully assessed. We investigate a series of complementary environmental archives to evaluate the quality of the Holocene-historical faunal record of Hainan Island, China's southernmost province, for establishing new baselines on postglacial mammalian diversity and extinction dynamics. Synthesis of multiple archives provides an integrated model of long-term biodiversity change, revealing that Hainan has experienced protracted and ongoing human-caused depletion of its mammal fauna from prehistory to the present, and that past baselines can inform practical conservation management. However, China's Holocene-historical archives exhibit substantial incompleteness and bias at regional and country-wide scales, with limited taxonomic representation especially for small-bodied species, and poor sampling of high-elevation landscapes facing current-day climate change risks. Establishing a clearer understanding of the quality of environmental archives in threatened ecoregions, and their ability to provide a meaningful understanding of the past, is needed to identify future conservation-relevant historical research priorities.

**Key words:** extinction, China, Hainan, historical baseline, Holocene, zooarchaeology

**1. INTRODUCTION**

Effective conservation of threatened global biodiversity hotspots urgently requires scientific evidence to inform and guide management [*1*]. However, whereas biodiversity richness is greatest in the tropics, biodiversity data richness is skewed towards the poles, especially for long-term datasets needed to understand population dynamics, responses to potential threats, and biodiversity change through time [*2-3*]. Gaps in conservation-relevant data availability are of particular concern in decision-making and prioritisation for eastern and southeast Asian terrestrial ecosystems, which are experiencing extreme anthropogenic pressure and contain the world's highest numbers of threatened vertebrates and plants [*4,5*]. Identifying the different types of environmental data that exist for these biodiversity hotspots, and determining their information-content and conservation usefulness, is therefore a vital conservation research priority [*6*].

Conservation planning typically uses modern-day ecological data, with very limited use of longer-term records [*6,7*]. However, there is increasing recognition that long-term environmental archives, including fossil, zooarchaeological and historical records, can contribute to conservation research, policy and practice by providing unique insights about diversity and composition of past ecosystems, biotic responses to environmental change, species and ecosystem vulnerability to past stressors, and extinction rates and dynamics [*8,9*]. Many ecosystems, particularly those with long histories of human presence, are likely to have experienced an "extinction filter" whereby biodiversity that was vulnerable to past human pressures has already been lost, making assumptions about ecology, biogeography and extinction risk based only on modern-day data potentially incomplete or misleading [*10*]. Approaches for integrating past and present environmental data are now explored by the emerging disciplines of conservation palaeobiology and historical ecology, which aim to model future biodiversity scenarios and identify management tools and restoration targets based on historical baselines [*6-9*].

Unfortunately, assessing the information-content of environmental archives and incorporating historical baselines into conservation planning remains challenging for biodiversity hotspots due to limited availability of relevant archives for many regions, especially in the tropics [*6,11*]. China represents an important exception. This huge (9.6 million $km^2$), 'megadiverse' country contains >10% of global mammal species and covers a diverse range of habitats [*12*], but has experienced human overpopulation, resource overexploitation and habitat modification throughout the climatically stable postglacial Holocene Epoch and historical period [*13,14*], leading to catastrophic ongoing biodiversity loss including ecosystem functional and compositional collapse, population extirpations and species extinctions [*15-17*]. Multiple environmental archives, spanning different temporal depths and spatio-temporal resolutions across the Holocene-historical period, are available to investigate postglacial human-ecosystem interactions and impacts in China, including palaeontological and zooarchaeological records [*11,17,18*], a written record going back over two millennia with abundant information on past environmental conditions [*16*], and a rich body of indigenous knowledge about past and present biodiversity held by China's large rural population [*19*].

China's long-term archives have been used to reconstruct regional ecological histories and investigate historical and prehistoric human-environmental interactions [*13*]. They also have the potential to provide important insights into the changing status of China's biodiversity and make predictive hypotheses to guide conservation management. However, although 253 mainland Chinese Holocene archaeological and palaeontological sites contain identified wild mammal species (figure 1a) [*17*], the ability of these archives to define past biodiversity baselines and faunal responses to human activities has not been fully assessed. Previous Chinese Holocene-historical faunal studies have focused on using specific archives to identify extinct species [*20*] and reconstruct the past ecology and distribution of threatened species [*16,21*]. However, important wider questions remain unexplored about the quality of China's environmental archives, the relative contribution of different historical baselines for understanding patterns and processes of biodiversity change, and the ability of long-term datasets to provide a meaningful understanding of the past of use for conservation.

In this study, we assess the extent to which long-term faunal archives can contribute unique conservation-relevant information on Chinese biodiversity in two ways. We use a series of environmental archives available for a regional Chinese study system to define successive Holocene faunal baselines, identify differences in species composition between past and present, reconstruct the timing and drivers of past biodiversity loss, and determine the extent that different archives can complement each other to reconstruct faunal dynamics through time. We also identify and quantify patterns of incompleteness and bias in Chinese faunal archives at both regional and country-wide scales. These analyses establish a new framework for assessing the unique opportunities and inherent limitations in using environmental archives to inform conservation planning.

## 2. MATERIAL AND METHODS

### (a) Regional study system

Hainan Island, China's southernmost province, is a 33,920km$^2$ subtropical-tropical continental-shelf island in the South China Sea (figure 1b). Hainan probably became isolated from mainland China through marine transgression during the early Holocene between 7,100-10,500 yr BP [*22*]. Its current-day land mammal fauna contains 83 recorded species and is relatively depauperate, lacking numerous species known from mainland China and southeast Asia [*12*] (electronic supplementary material, table S1). This fauna includes the Hainan gibbon (*Nomascus hainanus*), one of the world's rarest mammals, with a global population of only 27 surviving individuals [*23*]. Ancient DNA analysis of historical museum collections has recently shown that the last population of Père David's deer or milu (*Elaphurus davidianus*), which has been extinct in the wild for over a century, occurred on Hainan during the mid-1800s [*24*]. The current depauperate state of Hainan's mammal fauna may therefore represent depletion following additional past extinctions. Because faunal turnover on an island is not influenced by population migration, Hainan constitutes a "closed system" for investigating extinction dynamics. However, the magnitude, timing, and drivers of any such events have not been investigated.

In addition to occasional historical accounts by visiting naturalists [e.g. *25*], three main temporally non-overlapping Holocene-historical faunal archives are available for Hainan: **(1)** A rich fossil deposit from Luobidong Cave, dated to 10,642±207 yr BP [*26*], containing abundant mammal material [*27*] and therefore providing a faunal baseline approximately at the point when Hainan became an island (figure 1b); **(2)** Hainan's gazetteer record, covering the late Ming Dynasty, Qing Dynasty and Republican Period, and containing considerable local environmental data including animal records [*28*]; **(3)** Indigenous knowledge about past and present biodiversity, possessed by Li and Miao ethnic communities in Hainan's forested interior [*19*].

**(b) Hainan fossil data**

The Luobidong cave fauna contains 38 identifiable mammal species (corrected to taxonomy in [*12*]), including 12 unknown on Hainan today in Proboscidea, Perissodactyla, Artiodactyla, Carnivora, Rodentia and Chiroptera: Asian elephant (*Elephas maximus*), tapir (*Tapirus* sp.), buffalo (*Bubalus* sp.), serow (*Capricornis* sp.), tufted deer (*Elaphodus cephalophus*), Reeves' muntjac (*Muntiacus reevesi*), tiger (*Panthera tigris*), dhole (*Cuon alpinus*), hog badger (*Arctonyx collaris*), greater bandicoot rat (*Bandicota indica*), vole (*Microtus* sp.), hairy-winged bat (*Harpiocephalus* sp.). Regional mammal extinctions are unlikely to be associated with Holocene climate change, which was very limited compared to Late Pleistocene change [*29,30*]. We identify two competing hypotheses: (1) human-caused extinction; (2) stochastic extinction on a closed island system [*31,32*]. We tested between these hypotheses by assessing likelihood of stochastic extinction across the Holocene for regionally extirpated megafaunal mammals. We conducted population viability analysis (PVA) for the three largest regionally extinct herbivores (Asian elephant, buffalo, tapir) and largest regionally extinct carnivore (tiger) in the Luobidong fauna, as these species are most vulnerable to stochastic extinction due to low population densities and large spatial requirements [*33*]. We ran PVA base models in Vortex v.10 [*34*] over an 8,000-year period, in 50 evenly-spaced survival-level increments between 5% and 95% inclusive, including catastrophes as a stochastic extinction driver and with Latin hypercube sensitivity analysis of different variables (electronic supplementary material, text S1, table S2).

**(c) Hainan historical data**

We surveyed 44 gazetteer volumes dating between 1521-1935 AD from Hainan [*28*]. We recorded animals listed in the 'beasts' (*shou*) sections and/or that accompanied separate reports of gibbons, excluding obviously mythical or fantastical reports (electronic supplementary material, table S3). Hainan was periodically administered with nearby mainland provinces, so we confirmed that records referred to Hainan from supporting information. For selected animal records (see Results), we conducted optimal linear estimation (OLE), a probabilistic approach that uses temporal distributions of independent sighting events to estimate an extinction date [*35*], implemented using the "sExtinct" package [*36*] in R [*37*].

**(d) Hainan local ecological knowledge**

We conducted interviews in January-April 2015 in villages close to seven Hainanese protected areas (Bawangling, Diaoluoshan, Jianfengling, Wuzhishan and Yinggeling National Nature Reserves; Jiaxi and Limushan Provincial Nature Reserves; figure 1b). Local people use animal and plant resources collected from inside these protected areas [*23*]. We randomly selected 10 villages around each reserve and aimed to conduct 10 interviews per village. We used a standard anonymous questionnaire for all interviews, which took up to 1 hour to complete, with interviews mainly conducted in Mandarin or Hainanese and recorded in Chinese (electronic supplementary material, text S2). Respondent selection criteria/methods and interview protocols are given in ref. *19*. Project design was approved by the Zoological Society of London's Ethics Committee.

In addition to other data presented in ref. *19,38,39*, we collected data on respondent awareness and experience of nine mammal species: wild pig (*Sus scrofa*), rhesus macaque (*Macaca mulatta*), Hainan gibbon, clouded leopard (*Neofelis nebulosa*), Asian black bear (*Ursus thibetanus*), Chinese pangolin (*Manis pentadactyla*), binturong (*Arctictis binturong*), sambar deer (*Rusa unicolor*), giant anteater (*Myrmecophaga tridactyla*). Most of these species are known or suspected to occur in Hainan [*12,40*]; giant anteaters are native to the Neotropics and were a negative control to check response accuracy. We showed colour photographs of these mammals (sourced from www.arkive.org and the Zoological Society of London), shown in the same order given above in all interviews, and asked respondents to name species and provide further ecological/morphological details to confirm recognition. If respondents did not recognize photographs, we used standard Chinese names to prompt recall. We asked if respondents had encountered animals in the photographs (including sightings, hearing gibbon song, and diagnostic footprints/sign), and if so where and how recently. We also asked if respondents knew about any animals that had existed in the past but no longer occurred locally, and whether they knew any old stories that described animals that had only existed in the past.

Encounter records were converted to direct calendar years for analysis, following ref. *39*; encounter data reported below represent converted data. Differences in species last-encounter histories for 1990-2015 were analysed using generalised linear models (GLM) in R. Frequency of last-encounter dates per species per year was expressed as a proportion of total number of observations for each species encounter-history dataset, and regressed on year (predictor) [*41*]. We used a binomial error structure unless data showed overdispersion, when a quasibinomial error structure was used. Last-encounter history trajectories between species over time were considered significantly different if confidence intervals of regression slopes did not overlap; 83% confidence intervals were used for comparison because these give an approximate $\alpha$=0.05 test, whereas comparisons using 95% confidence intervals are too conservative [*42*]. Lower encounter-history slopes indicate fewer encounters have occurred close to the present. The oldest 5% of records for each species all date from before 1990, so there was no need to further exclude these data from analysis to reduce the effect of long encounter data “tails” (which produce flatter overall encounter-history slopes that are harder to differentiate statistically) [*41*].

**(e) Bias in China’s Holocene record**

We investigated whether representation of past mammalian diversity in China’s Holocene faunal record is biased by exploring whether biological/ecological traits other than abundance can predict the number of Holocene site records for mainland Chinese species. We considered body mass and geographic range, which are both predictors of fossil species occurrence in other systems [*43,44*].

We used phylogenetic comparative methods to account for biases associated with shared evolutionary history, and ran all models using the pgls function in the R package "caper" [*45*], using the dated mammal supertree of ref. *46* and with taxonomy standardized between datasets (electronic supplementary material, text S1). We first investigated the relationship between body mass and site records for 493 species, using log-transformed body mass estimates (electronic supplementary material, text S1, table S4). This dataset contained a high proportion of species with 0 site records (n=377); because zero-inflated datasets can create problems for quantifying relationships between variables, we conducted bootstrapping to understand how removal of different proportions of species with 0 site records affected parameter estimates and robustness of model inferences (electronic supplementary material, text S1). We then investigated the predictive power of both body mass and geographic range. Many Chinese mammal ranges have decreased over the Holocene, making modern-day distributions inappropriate proxies for past distributions [*16,17*]. Standardised Holocene range estimates are available for 34 species [*17*], so we analysed this reduced species subset using both body mass and Holocene range as predictors of site records (electronic supplementary material, table S4).

We also investigated whether China's Holocene faunal record is spatially biased and representative of past ecological diversity, using two approaches. We used nearest-neighbour analysis in ArcGIS Pro v.2.3.0 [*47*] to test whether Holocene sites are spatially clustered, by measuring mean nearest-neighbour distance between sites and comparing this with expected mean nearest-neighbour distances for a point set with a random distribution. We also carried out chi-squared tests in R on number of sites present in each mainland Chinese ecoregion as defined in the Terrestrial Ecosystems of the World dataset [*48*], to test whether spatial distribution of sites shows biogeographic bias. We calculated expected values manually by multiplying mean site density across China by total area of each ecoregion, excluding all ecoregions under 15,000km$^2$ (size of smallest ecoregion containing at least one site) to reduce the number of low expected counts.

## 3. RESULTS

### (a) Hainan's long-term archives

PVA base models for elephant, buffalo, tapir and tiger populations on Hainan quickly grew to their carrying capacities and remained stable with no incidences of extinction in the absence of catastrophes. Modelled stochastic catastrophes had to be severe to drive populations to extinction (*Elephas maximus*: all extinct at ≤82% survival, all survive at ≥88% survival; *Bubalus* sp.: all extinct at ≤44% survival, all survive at ≥64% survival; *Tapirus* sp.: all extinct at ≤64% survival, all survive at ≥84% survival; *Panthera tigris*: all extinct at ≤31% survival, all survive at ≥58% survival).

Hainan's gazetteer record contains 104 land mammal "types" (excluding bats, which are usually classified separately as "flying creatures" or "insects" and were not catalogued here). Of these, 84 do not obviously correspond with domestic taxa (electronic supplementary material, table S3). Interpretation and identification of records, although often aided by accompanying brief descriptions, is inevitably subjective (e.g. "cat" may refer to domestic or wild taxa). We are able to identify 15 recognisable species of Artiodactyla, Carnivora, Erinaceomorpha, Lagomorpha, Pholidota and Primates: wild pig, sambar, red muntjac (*Muntiacus muntjak*), Eld's deer (*Rucervus eldii*), Asian black bear, clouded leopard, leopard cat (*Prionailurus bengalensis*), wolf (*Canis lupus*), dhole, yellow-throated marten (*Martes flavigula*), Hainan gymnure (*Neohylomys hainanensis*), Hainan hare (*Lepus hainanus*), Chinese pangolin, rhesus macaque, Hainan gibbon. Some species are referenced with multiple historical names (to a maximum of five for black bear). Other types refer to wider species groups (e.g. "porcupines", "squirrels") or cannot be identified beyond a broad taxonomic category (e.g. 16 small carnivore types cannot be identified beyond Viverridae, Herpestidae or Mustelidae). Records of "wild cattle" may refer to gaur (*Bos gaurus*), which are not otherwise recorded from Hainan, but also possibly to other wild/domestic ungulates. Deer referred to as "milu" are reported until 1917, but these cannot definitely be identified as Père David's deer because reported deer nomenclature is confused; 14 deer types are recorded, some with similar names (e.g. "mi" [elk]), and including other species otherwise unknown from Hainan (e.g. water deer, musk deer) that probably represent misidentifications. Occasional mentions of other regionally extinct or otherwise unknown species are clearly allegorical or poetic (e.g. 1908: "The wind brings the stink of a crouching tiger"), so are ignored here.

Two well-described species from Hainan's gazetteer record (wolf, 7 records, 1618-1931; dhole, 15 records, 1521-1935) are not present today on Hainan, although they still occur in nearby mainland China and southeast Asia [*12,40*]. We conducted OLE on dated records for each species, giving estimated extinction dates of 1941 for wolf (95% CI=1931-2079), and 1942 for dhole (95% CI=1935-1993).

We interviewed 709 respondents in villages across Hainan (mean age=50.1, range=20-94, male:female=83:17%), who reported past encounter data for seven of our eight target Chinese mammals. We excluded reports that were obviously not of wild animals (e.g. “on television”, “in a market”), and data from two respondents who claimed to have seen giant anteaters. Six respondents reported possible old sightings (20-60 years ago) of binturong, a species not confirmed from Hainan [*40*], but only provided basic descriptions and did not differentiate it from other regionally occurring civets, so we do not consider these uncertain reports further. Our interview dataset shows substantial between-species variation in numbers of respondents reporting encounters and last-encounter dates, interpreted as reflecting variation in species' regional abundance and recent survivorship (table 1). Pig and macaque have the highest encounter-history slopes, followed by gibbon, bear, clouded leopard, sambar and pangolin; pig, macaque and gibbon all have significantly higher encounter-history slopes compared to bear, clouded leopard, sambar and pangolin (figure 2, table 1). Only 20 respondents named specific animals they thought had existed in the past but were now locally extinct; these included pangolin (n=6), bear (n=3), parrot (n=3), snake/python (n=3), turtle (n=3), gibbon (n=2), tiger (n=1), wild pig (n=1), and muntjac (n=1).

**(b) Quality of China's Holocene record**

In full analysis of 493 species, body mass was a significant predictor of site records for Chinese mammals (est=1.829, S.E.=0.488, t-value=3.746, $p<0.001$; df=369, $R^2=0.03$, lambda=0.596), with larger-bodied species present in more sites (figure 3). Bootstrapping treatments yielded a positive significant relationship between log-transformed body mass and site number, showing that our results are robust to the proportion of zeroes present in the dataset (electronic supplementary material, text S1, figure S1). In reduced analysis of 34 species, neither body mass nor geographic range were significant predictors of site number (*body mass*: est=-0.0007, S.E.=0.011, t-value=-0.071, p=0.944; *geographic range*: est=-0.000002, S.E.<0.001, t-value=-0.627, p=0.535; df=31, $R^2$<0.001, lambda=0.099), probably representing a Type II error associated with small sample size.

Holocene sites are significantly more clumped than expected under a random distribution (z-score=-14.61, p<0.0001), with mean expected and observed nearest-neighbour distances showing a ratio of 0.52 (50.65km:97.38km). Site density differs significantly across mainland Chinese ecoregions (chi-sq=494.35, df=47, p<0.0001; electronic supplementary material, figure S2, table S5). The three ecoregions with the greatest number of sites compared with expected values are the Yellow River Plain mixed forest (O=69, E=11.77), Dabashan evergreen forest (O=22, E=4.56) and Yangtze Plain evergreen forest (O=25, E=11.87), and the three ecoregions with the lowest number of sites compared with expected values are the Taklimakan desert (O=2, E=20.16), Central Tibetan Plateau alpine steppe (O=2, E=17.04) and Alashan Plateau semi-desert (O=2, E=12.39).

## 4. DISCUSSION

Our investigation of multiple Chinese long-term environmental archives, spanning different temporal resolutions and spatial scales, provides a new assessment of the conservation-relevant information-content of different historical datasets that can potentially inform evidence-based management in a biodiversity hotspot. Through the use of diverse analyses, we highlight the types of novel insights provided by long-term faunal records on historical environmental baselines and patterns and dynamics of biodiversity change, but also key issues regarding quality and completeness of faunal records, and the extent to which data incompleteness and bias might limit integration of environmental archives into conservation decision-making in global-priority regions.

Our analyses of Holocene-historical faunal records from Hainan demonstrate how regional archives can contribute unique new perspectives that improve our understanding of biogeography, ecosystem composition and extinction vulnerability, with direct relevance for conservation research and practical management. Firstly, the long-term archives available for Hainan provide a new baseline on the island's past postglacial species diversity that is unattainable from modern-day data. The Holocene fossil and historical records, and additional insights from ancient DNA analysis of museum archives [*24*], together reveal that the current depauperate state of Hainan's mammal fauna is a historically recent rather than a long-term "natural" ecological condition, with 14 species in six orders (17% of Hainan's present-day mammalian species richness) recorded in postglacial faunal archives but unknown from Hainan today. It is possible that some bats and rodents recorded at Luobidong might be undetected rather than extinct today, as Hainan's small mammal fauna remains relatively understudied [*49*]. However, Holocene-historical archives also demonstrate that Hainan formerly contained a typical southeast Asian large mammal fauna comprising a diverse assemblage of megaherbivores, megacarnivores, mesoherbivores and mesocarnivores, which have now largely disappeared from the island.

Hainan's long-term archives also provide a baseline for reconstructing relative extinction timings for different components of the island's large mammal fauna over time. The largest-bodied herbivores and carnivores present at Luobidong (elephants, tapirs, buffalos, tigers) had already disappeared by the time historical accounts of Hainan's biodiversity and natural resources were first recorded. Although the exact timing of extinctions remains unclear, these species are not referenced in Hainan's gazetteer archive dating from the 1500s onwards, and Hainan was described as "without horses or tigers" as early as 80 CE [*13*]. Smaller-bodied mesoherbivores and mesocarnivores survived until much more recently. Père David's deer persisted on Hainan until at least the nineteenth century [*24*] and possibly until 1917 based on gazetteer records; and OLE analysis of gazetteer records for wolf and dhole together with indigenous knowledge from local respondents demonstrates these species persisted into the mid-twentieth century but apparently disappeared before living memory. Comparison of different probabilistic methods for inferring extinction using sighting records suggests OLE is more robust than other approaches, and generally gives accurate predictions when applied to >5 records [*50*], although use of >10 records is recommended by ref. *51*, a condition fulfilled by dhole but not wolf. We also note that estimated extinction dates for wolf and dhole represent last-occurrence dates only, because OLE relies on the implicit assumption that recording effort never falls to zero [*35*], but Hainan's gazetteer record stops at the end of the Nationalist Era.

These archives also demonstrate that the decline of Hainan's mammal fauna is ongoing. Our large-scale dataset of species sightings over recent decades shows that bears, clouded leopards, sambar and pangolins all have lower encounter-history slopes in comparison to encounter data for the Hainan gibbon, one of the world's rarest mammals, with fewer sightings of these species close to the present suggestive of steeply declining populations. Although this pattern might be explained partly by differing species detectabilities, with gibbons potentially easier to detect due to their diurnal activity and singing behaviour, we consider it sadly likely that remnant populations of some or all of these other species are now on the verge of extinction if not already gone, especially because there are currently no species-specific conservation programmes to help safeguard any mammal species on Hainan other than Hainan gibbon or Eld's deer [*23,52*].

Further analysis of baseline data from long-term archives also identifies the likely driver of extinctions in Hainan's postglacial mammal fauna. Our PVA results show that, unlike some other Late Quaternary island systems with isolated large-bodied mammal populations [*32,53*], Hainan is large enough to support long-term viable populations of megaherbivores and megacarnivores that were present when the island became isolated in the early Holocene, with natural catastrophes required to cause stochastic extinction in model simulations considered too severe to be ecologically plausible (i.e. requiring destruction of ≥12% of the island's carrying capacity). We can therefore exclude the hypothesis of stochastic extinction, and identify human activity as the only plausible driver of Holocene mammalian losses on Hainan. Prehistoric human-environment interactions and demographic changes on Hainan are poorly understood, making it difficult to determine specific activities that caused past extinctions. Hainan's ecosystems were being heavily exploited for natural resources by the 18th century for trade with mainland China [*13*], but the island's megafauna was already extinct by this point. Neolithic cultures have been present on Hainan since at least 6,000 yr BP [*54*], and aboriginal peoples are known to have transformed Hainan's environment to some degree through hunting and agricultural conversion during recent millennia, but prehistoric human populations have generally been assumed to be too small to cause much environmental impact [*13*]. However, evidence for heavy metal pollution from around 4,000 yr BP, associated with appearance of abundant archaeological sites on Hainan, indicates intensification of regional human activities (e.g. agricultural development, deforestation, metal utilization) that could have been associated with mammal extinctions [*55*].

Investigation of multiple complementary faunal archives, stretching from the living memory of local inhabitants back to the early Holocene, thus enables development of an integrated model of long-term mammalian biodiversity change for Hainan (figure 4). This overview of faunal dynamics is only possible through synthesis of different archives, and makes it possible to answer key questions that cannot be addressed using modern-day data: was Hainan's fauna different in the past, and what happened to this fauna between past and present? Long-term archives reveal that rather than having been a naturally depauperate system or having lost biodiversity in a punctuated ancient or recent event, Hainan has experienced protracted and ongoing human-caused depletion of its mammal fauna from prehistory to the present, with its largest-bodied species lost first and followed by progressive loss of smaller-bodied species. This pattern is similar to the staggered extinction dynamics seen in several continental mammal faunas across the Holocene-historical period [*56,57*]. These findings reveal that Hainan is now experiencing "empty forest syndrome" [*58*], and with the Hainan gibbon "merely" the latest of Hainan's mammals to be sliding towards extinction. They also raise key questions for future investigation: why has Hainan's mammal fauna been so vulnerable to extinction, given that its forest cover remained fairly extensive until the twentieth century [*13,59*]; how did gibbons manage to survive; and what does this long-term perspective suggest about the future of Hainan's biodiversity?

This new baseline on past diversity and faunal turnover provides a practical framework for conservation managers to understand the extent of human-caused biodiversity loss on Hainan, and emphasizes the urgent need for active regional conservation programmes for many more species. Our new model of Hainan's long-term extinction dynamics can be compared and contrasted with data for other Asian regions, for example islands that have experienced either survival or extinction of species formerly present on Hainan (e.g. tigers, clouded leopards), to identify intrinsic or extrinsic correlates of species vulnerability and resilience and make predictive hypotheses to inform conservation planning [*31,60,61*]. Integrated faunal archives can also inform direct conservation management, for example to set new restoration or rewilding targets (e.g. reintroduction of extirpated species, such as Père David's deer to Hainan's wetlands; management of disrupted forest regeneration processes requiring mammalian dispersers), or to forecast potential faunal responses to future environmental change scenarios and develop appropriate mitigation strategies against ongoing biodiversity loss.

493 However, despite the invaluable new insights about the status of regional Chinese biodiversity provided by these long-term perspectives, China's environmental archives exhibit extensive problems with incompleteness, representativeness and bias in the information they contain about past faunal baselines, cautioning against their use at face value. Each archive we investigated for Hainan contains only a small percentage of the mammal species occurring on the island today (fossil record=31%, gazetteer record=16%), and only one regionally extinct species (dhole) is definitely included in more than one archive (electronic supplementary material, table S1), suggesting that many more species, potentially including numerous regionally extinct species of unknown identity, remain undocumented. The usefulness of the gazetteer record and potentially also the indigenous knowledge record are limited further due to problems with accurate species identification by untrained observers. We also demonstrate that, in contrast to some other social-ecological systems [*19,62*], Hainan's indigenous knowledge record is an extremely poor source of information on past extinctions, with almost no local awareness of formerly occurring species, and most responses likely "cued" from previous interview questions about named animals (pangolin, bear, gibbon, wild pig).

511 Our analyses of mainland China's faunal record demonstrate similar incompleteness and bias, with only 22% of extant Chinese mammal species represented in Holocene sites, and a strong effect of body mass on likelihood of species representation. Similar biases are observed in many Quaternary and older faunal assemblages, and likely reflect multiple burial and post-burial processes including preferential past human hunting of larger-bodied animals, greater survival of robust skeletal elements, biased excavation procedures,

and/or limited osteological information for species identification of many small-bodied mammals [*44,63*], with few studies available on Chinese Quaternary small mammal assemblages [*64*]. Although it is not possible to quantify how these different processes have biased data for our regional study system, it is therefore likely that Hainan's large-bodied Holocene mammal fauna is better understood than its small-bodied fauna, with potential faunal turnover in Chinese small mammal assemblages more challenging to identify. Distribution of Holocene sites across China is also spatially uneven, and with very different representation of different ecoregions. Far more excavations have been conducted in regions with higher historical human populations (e.g. Yellow River and Yangtze plains) [*18*], constituting an important target for archaeologists but not representative of past human-environmental interactions and impacts across China as a whole, and providing very different power to understand past environments and biodiversity change in different landscapes, notably high-elevation Asian ecosystems facing increased climate change risks today.

Our analyses of the quality of China's Holocene faunal record provide a new baseline for assessing the insights that historical data can provide for conservation, as well as the challenges that necessitate caution and care in interpreting these data, which prevent long-term archives from ultimately being able to answer many questions of importance to conservation biologists. Establishing a clearer understanding of patterns of incompleteness and bias in the faunal record can help identify future research priorities, including increased sampling in understudied ecoregions, or extrapolations to estimate numbers of regionally extinct species that remain unidentified [*65*]. Unfortunately, other biodiversity hotspots do not have the range and resolution of long-term archives available for China, so any region-specific conservation insights from the past will be even more limited for these systems, especially when coupled with problems of specimen preservation exacerbated in tropical environments such as thermal degradation of ancient biomolecules [*24*]. Long-term environmental records provide windows into the past that are essential for understanding environmental baselines and biodiversity change, and enable development of more inclusive decision-making frameworks, but incorporating these records into conservation planning requires careful and nuanced interpretation.

**Data accessibility.** The datasets supporting this paper are available in the supplementary materials.

**Authors' contributions.** S.T.T. designed research; C.W., J.J.C., K.H. and S.T.T. coordinated data collection; C.W., J.H., J.B., C.D., M.A.H., K.H. and S.T.T. interpreted and analysed data; and S.T.T. wrote the paper with support from other authors.

**Competing interests.** We have no competing interests.

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## FIGURE LEGENDS

**Figure 1.** (a) Distribution of 253 Holocene zooarchaeological and palaeontological sites across mainland China with wild mammal records. (b) Map of Hainan, showing location of Luobidong Cave (star) and villages where interviews were conducted (circles). B, Bawangling; D, Diaoluoshan; JN, Jianfengling; JX, Jiaxi; L, Limushan; W, Wuzhishan; Y, Yinggeling.

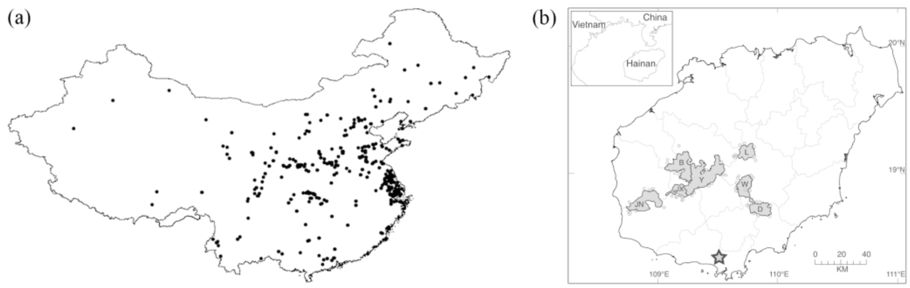
**Figure 2.** Slopes and 83% CIs of local respondent encounter-history data for seven Hainanese mammal species. Left to right: wild pig, rhesus macaque, Hainan gibbon, Asian black bear, clouded leopard, sambar deer, Chinese pangolin.

**Figure 3.** Box plot of body masses for mainland Chinese mammal species that are present or absent in the Holocene zooarchaeological and palaeontological record.

**Figure 4.** Integrated model of long-term mammalian biodiversity change on Hainan based on synthesis of multiple environmental archives, showing progressive depletion of regional mammal fauna across the Holocene to the present as evidenced by different species-specific data sources on temporal patterns of population persistence.

**Table 1.** Summary of respondent encounter history data for seven Hainanese mammals, and species last-encounter history regression slopes with 83% confidence interval upper and lower bounds (df for all regressions=24).

| species | no. of encounter records | mean last-encounter date | % encounters in past 10 yrs (2006-2015) | slope | SD | lower bound (8.5%) | upper bound (91.5%) |
|---|---|---|---|---|---|---|---|
| wild pig | 549 | 2012 | 59.6 | 0.158 | 0.035 | 0.113 | 0.209 |
| rhesus macaque | 432 | 2010 | 54.9 | 0.125 | 0.030 | 0.086 | 0.168 |
| Hainan gibbon | 187 | 1983 | 21.9 | 0.065 | 0.027 | 0.028 | 0.103 |
| Asian black bear | 193 | 1987 | 13.0 | -0.015 | 0.026 | -0.051 | 0.020 |
| clouded leopard | 125 | 1980 | 6.4 | -0.023 | 0.027 | -0.061 | 0.014 |
| sambar deer | 359 | 1993 | 15.3 | -0.025 | 0.017 | -0.049 | -0.001 |
| Chinese pangolin | 495 | 1993 | 11.9 | -0.031 | 0.021 | -0.061 | -0.002 |

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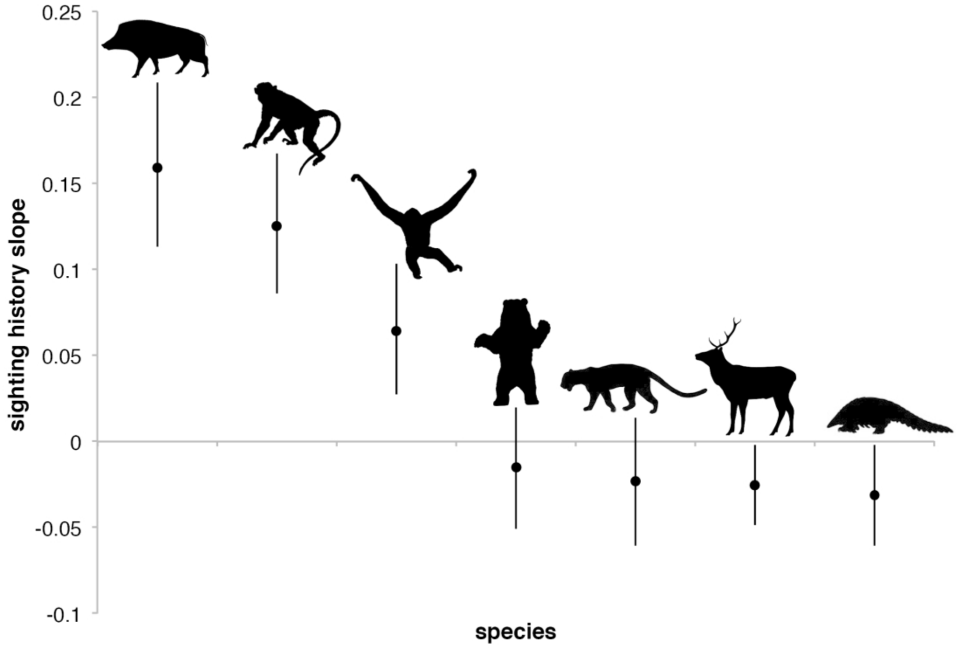


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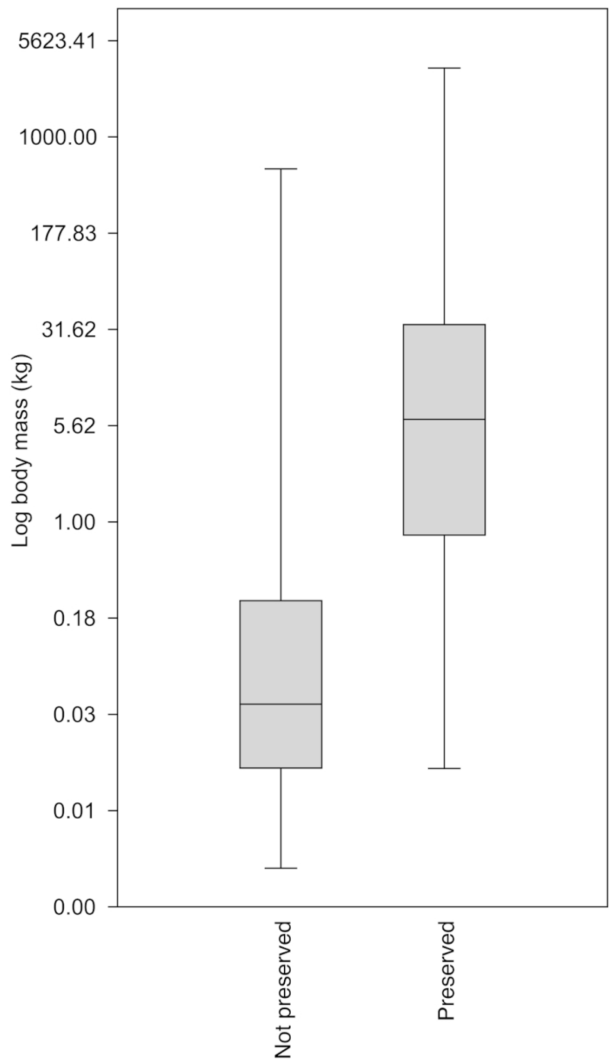


Figure 3. Box plot of body masses for mainland Chinese mammal species that are present or absent in the Holocene zooarchaeological and palaeontological record.

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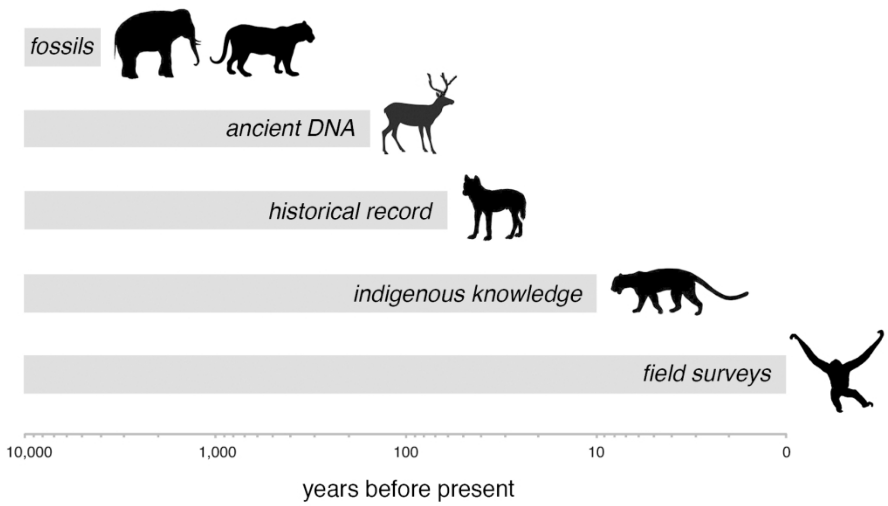


Figure 4. Integrated model of long-term mammalian biodiversity change on Hainan based on synthesis of multiple environmental archives, showing progressive depletion of regional mammal fauna across the Holocene to the present as evidenced by different species-specific data sources on temporal patterns of population persistence.

167x102mm (300 x 300 DPI)