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

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Article

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Turvey, ST, Walsh, C, Hansford, JP, Crees, JJ, Bielby, J, Duncan, C, Hu, K and Hudson, MA (2019) Complementarity, completeness and quality of long-term faunal archives in an Asian biodiversity hotspot. Philosophical Transactions of the Royal Society B: Biological Sciences. 374 (1788). ISSN

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

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18 *Channel Islands*

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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

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71 potentially incomplete or misleading [10]. Approaches for integrating past and
72 present environmental data are now explored by the emerging disciplines of
73 conservation palaeobiology and historical ecology, which aim to model future
74 biodiversity scenarios and identify management tools and restoration targets
75 based on historical baselines [6-9].

76 Unfortunately, assessing the information-content of environmental archives
77 and incorporating historical baselines into conservation planning remains
78 challenging for biodiversity hotspots due to limited availability of relevant
79 archives for many regions, especially in the tropics [6,11]. China represents an
80 important exception. This huge (9.6 million km²), ‘megadiverse’ country contains
81 >10% of global mammal species and covers a diverse range of habitats [12], but
82 has experienced human overpopulation, resource overexploitation and habitat
83 modification throughout the climatically stable postglacial Holocene Epoch and
84 historical period [13,14], leading to catastrophic ongoing biodiversity loss
85 including ecosystem functional and compositional collapse, population
86 extirpations and species extinctions [15-17]. Multiple environmental archives,
87 spanning different temporal depths and spatio-temporal resolutions across the
88 Holocene-historical period, are available to investigate postglacial human-
89 ecosystem interactions and impacts in China, including palaeontological and
90 zooarchaeological records [11,17,18], a written record going back over two
91 millennia with abundant information on past environmental conditions [16], and
92 a rich body of indigenous knowledge about past and present biodiversity held by
93 China’s large rural population [19].

94 China’s long-term archives have been used to reconstruct regional ecological
95 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

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3 120 inherent limitations in using environmental archives to inform conservation
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10 123 **2. MATERIAL AND METHODS**
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15 125 **(a) Regional study system**
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17 126 Hainan Island, China’s southernmost province, is a 33,920km² subtropical-
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19 127 tropical continental-shelf island in the South China Sea (figure 1b). Hainan
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21 128 probably became isolated from mainland China through marine transgression
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23 129 during the early Holocene between 7,100-10,500 yr BP [22]. Its current-day land
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25 130 mammal fauna contains 83 recorded species and is relatively depauperate,
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27 131 lacking numerous species known from mainland China and southeast Asia [12]
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29 132 (electronic supplementary material, table S1). This fauna includes the Hainan
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31 133 gibbon (*Nomascus hainanus*), one of the world’s rarest mammals, with a global
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33 134 population of only 27 surviving individuals [23]. Ancient DNA analysis of
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35 135 historical museum collections has recently shown that the last population of Père
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37 136 David’s deer or milu (*Elaphurus davidianus*), which has been extinct in the wild
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39 137 for over a century, occurred on Hainan during the mid-1800s [24]. The current
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41 138 depauperate state of Hainan’s mammal fauna may therefore represent depletion
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43 139 following additional past extinctions. Because faunal turnover on an island is not
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45 140 influenced by population migration, Hainan constitutes a “closed system” for
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47 141 investigating extinction dynamics. However, the magnitude, timing, and drivers
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49 142 of any such events have not been investigated.
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52 143 In addition to occasional historical accounts by visiting naturalists [e.g. 25],
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54 144 three main temporally non-overlapping Holocene-historical faunal archives are
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145 available for Hainan: **(1)** A rich fossil deposit from Luobidong Cave, dated to
 146 10,642±207 yr BP [26], containing abundant mammal material [27] and
 147 therefore providing a faunal baseline approximately at the point when Hainan
 148 became an island (figure 1b); **(2)** Hainan's gazetteer record, covering the late
 149 Ming Dynasty, Qing Dynasty and Republican Period, and containing considerable
 150 local environmental data including animal records [28]; **(3)** Indigenous
 151 knowledge about past and present biodiversity, possessed by Li and Miao ethnic
 152 communities in Hainan's forested interior [19].

153

154 **(b) Hainan fossil data**

155 The Luobidong cave fauna contains 38 identifiable mammal species (corrected to
 156 taxonomy in [12]), including 12 unknown on Hainan today in Proboscidea,
 157 Perissodactyla, Artiodactyla, Carnivora, Rodentia and Chiroptera: Asian elephant
 158 (*Elephas maximus*), tapir (*Tapirus* sp.), buffalo (*Bubalus* sp.), serow (*Capricornis*
 159 sp.), tufted deer (*Elaphodus cephalophus*), Reeves' muntjac (*Muntiacus reevesi*),
 160 tiger (*Panthera tigris*), dhole (*Cuon alpinus*), hog badger (*Arctonyx collaris*),
 161 greater bandicoot rat (*Bandicota indica*), vole (*Microtus* sp.), hairy-winged bat
 162 (*Harpiocephalus* sp.). Regional mammal extinctions are unlikely to be associated
 163 with Holocene climate change, which was very limited compared to Late
 164 Pleistocene change [29,30]. We identify two competing hypotheses: (1) human-
 165 caused extinction; (2) stochastic extinction on a closed island system [31,32]. We
 166 tested between these hypotheses by assessing likelihood of stochastic extinction
 167 across the Holocene for regionally extirpated megafaunal mammals. We
 168 conducted population viability analysis (PVA) for the three largest regionally
 169 extinct herbivores (Asian elephant, buffalo, tapir) and largest regionally extinct

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3 170 carnivore (tiger) in the Luobidong fauna, as these species are most vulnerable to
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5 171 stochastic extinction due to low population densities and large spatial
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8 172 requirements [33]. We ran PVA base models in Vortex v.10 [34] over an 8,000-
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10 173 year period, in 50 evenly-spaced survival-level increments between 5% and 95%
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12 174 inclusive, including catastrophes as a stochastic extinction driver and with Latin
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14 175 hypercube sensitivity analysis of different variables (electronic supplementary
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16 176 material, text S1, table S2).
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22 178 **(c) Hainan historical data**

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24 179 We surveyed 44 gazetteer volumes dating between 1521-1935 AD from Hainan
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26 180 [28]. We recorded animals listed in the ‘beasts’ (*shou*) sections and/or that
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28 181 accompanied separate reports of gibbons, excluding obviously mythical or
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30 182 fantastical reports (electronic supplementary material, table S3). Hainan was
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32 183 periodically administered with nearby mainland provinces, so we confirmed that
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34 184 records referred to Hainan from supporting information. For selected animal
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36 185 records (see Results), we conducted optimal linear estimation (OLE), a
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38 186 probabilistic approach that uses temporal distributions of independent sighting
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40 187 events to estimate an extinction date [35], implemented using the “sExtinct”
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42 188 package [36] in R [37].
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50 190 **(d) Hainan local ecological knowledge**

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52 191 We conducted interviews in January-April 2015 in villages close to seven
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54 192 Hainanese protected areas (Bawangling, Diaoluoshan, Jianfengling, Wuzhishan
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56 193 and Yinggeling National Nature Reserves; Jiayi and Limushan Provincial Nature
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58 194 Reserves; figure 1b). Local people use animal and plant resources collected from
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195 inside these protected areas [23]. We randomly selected 10 villages around each
 196 reserve and aimed to conduct 10 interviews per village. We used a standard
 197 anonymous questionnaire for all interviews, which took up to 1 hour to
 198 complete, with interviews mainly conducted in Mandarin or Hainanese and
 199 recorded in Chinese (electronic supplementary material, text S2). Respondent
 200 selection criteria/methods and interview protocols are given in ref. 19. Project
 201 design was approved by the Zoological Society of London's Ethics Committee.

202 In addition to other data presented in ref. 19,38,39, we collected data on
 203 respondent awareness and experience of nine mammal species: wild pig (*Sus*
 204 *scrofa*), rhesus macaque (*Macaca mulatta*), Hainan gibbon, clouded leopard
 205 (*Neofelis nebulosa*), Asian black bear (*Ursus thibetanus*), Chinese pangolin (*Manis*
 206 *pentadactyla*), binturong (*Arctictis binturong*), sambar deer (*Rusa unicolor*), giant
 207 anteater (*Myrmecophaga tridactyla*). Most of these species are known or
 208 suspected to occur in Hainan [12,40]; giant anteaters are native to the Neotropics
 209 and were a negative control to check response accuracy. We showed colour
 210 photographs of these mammals (sourced from www.arkive.org and the
 211 Zoological Society of London), shown in the same order given above in all
 212 interviews, and asked respondents to name species and provide further
 213 ecological/morphological details to confirm recognition. If respondents did not
 214 recognize photographs, we used standard Chinese names to prompt recall. We
 215 asked if respondents had encountered animals in the photographs (including
 216 sightings, hearing gibbon song, and diagnostic footprints/sign), and if so where
 217 and how recently. We also asked if respondents knew about any animals that had
 218 existed in the past but no longer occurred locally, and whether they knew any
 219 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].

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

263 We also investigated whether China’s Holocene faunal record is spatially
264 biased and representative of past ecological diversity, using two approaches. We
265 used nearest-neighbour analysis in ArcGIS Pro v.2.3.0 [47] to test whether
266 Holocene sites are spatially clustered, by measuring mean nearest-neighbour
267 distance between sites and comparing this with expected mean nearest-
268 neighbour distances for a point set with a random distribution. We also carried
269 out chi-squared tests in R on number of sites present in each mainland Chinese

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3 270 ecoregion as defined in the Terrestrial Ecosystems of the World dataset [48], to
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5 271 test whether spatial distribution of sites shows biogeographic bias. We
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8 272 calculated expected values manually by multiplying mean site density across
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10 273 China by total area of each ecoregion, excluding all ecoregions under 15,000km²
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12 274 (size of smallest ecoregion containing at least one site) to reduce the number of
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15 275 low expected counts.
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20 277 **3. RESULTS**

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24 279 **(a) Hainan’s long-term archives**

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26 280 PVA base models for elephant, buffalo, tapir and tiger populations on Hainan
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28 281 quickly grew to their carrying capacities and remained stable with no incidences
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30 282 of extinction in the absence of catastrophes. Modelled stochastic catastrophes
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32 283 had to be severe to drive populations to extinction (*Elephas maximus*: all extinct
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34 284 at ≤82% survival, all survive at ≥88% survival; *Bubalus* sp.: all extinct at ≤44%
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36 285 survival, all survive at ≥64% survival; *Tapirus* sp.: all extinct at ≤64% survival, all
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38 286 survive at ≥84% survival; *Panthera tigris*: all extinct at ≤31% survival, all survive
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40 287 at ≥58% survival).

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42 288 Hainan’s gazetteer record contains 104 land mammal “types” (excluding
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44 289 bats, which are usually classified separately as “flying creatures” or “insects” and
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46 290 were not catalogued here). Of these, 84 do not obviously correspond with
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48 291 domestic taxa (electronic supplementary material, table S3). Interpretation and
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50 292 identification of records, although often aided by accompanying brief
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52 293 descriptions, is inevitably subjective (e.g. “cat” may refer to domestic or wild
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54 294 taxa). We are able to identify 15 recognisable species of Artiodactyla, Carnivora,

295 Erinaceomorpha, Lagomorpha, Pholidota and Primates: wild pig, sambar, red
 296 muntjac (*Muntiacus muntjak*), Eld's deer (*Rucervus eldii*), Asian black bear,
 297 clouded leopard, leopard cat (*Prionailurus bengalensis*), wolf (*Canis lupus*), dhole,
 298 yellow-throated marten (*Martes flavigula*), Hainan gymnure (*Neohylomys*
 299 *hainanensis*), Hainan hare (*Lepus hainanus*), Chinese pangolin, rhesus macaque,
 300 Hainan gibbon. Some species are referenced with multiple historical names (to a
 301 maximum of five for black bear). Other types refer to wider species groups (e.g.
 302 "porcupines", "squirrels") or cannot be identified beyond a broad taxonomic
 303 category (e.g. 16 small carnivore types cannot be identified beyond Viverridae,
 304 Herpestidae or Mustelidae). Records of "wild cattle" may refer to gaur (*Bos*
 305 *gaurus*), which are not otherwise recorded from Hainan, but also possibly to
 306 other wild/domestic ungulates. Deer referred to as "milu" are reported until
 307 1917, but these cannot definitely be identified as Père David's deer because
 308 reported deer nomenclature is confused; 14 deer types are recorded, some with
 309 similar names (e.g. "mi" [elk]), and including other species otherwise unknown
 310 from Hainan (e.g. water deer, musk deer) that probably represent
 311 misidentifications. Occasional mentions of other regionally extinct or otherwise
 312 unknown species are clearly allegorical or poetic (e.g. 1908: "The wind brings
 313 the stink of a crouching tiger"), so are ignored here.

314 Two well-described species from Hainan's gazetteer record (wolf, 7 records,
 315 1618-1931; dhole, 15 records, 1521-1935) are not present today on Hainan,
 316 although they still occur in nearby mainland China and southeast Asia [12,40].
 317 We conducted OLE on dated records for each species, giving estimated extinction
 318 dates of 1941 for wolf (95% CI=1931-2079), and 1942 for dhole (95% CI=1935-
 319 1993).

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3 320 We interviewed 709 respondents in villages across Hainan (mean age=50.1,
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5 321 range=20-94, male:female=83:17%), who reported past encounter data for
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7 322 seven of our eight target Chinese mammals. We excluded reports that were
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9 323 obviously not of wild animals (e.g. “on television”, “in a market”), and data from
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11 324 two respondents who claimed to have seen giant anteaters. Six respondents
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13 325 reported possible old sightings (20-60 years ago) of binturong, a species not
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15 326 confirmed from Hainan [40], but only provided basic descriptions and did not
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17 327 differentiate it from other regionally occurring civets, so we do not consider
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19 328 these uncertain reports further. Our interview dataset shows substantial
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21 329 between-species variation in numbers of respondents reporting encounters and
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23 330 last-encounter dates, interpreted as reflecting variation in species’ regional
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25 331 abundance and recent survivorship (table 1). Pig and macaque have the highest
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27 332 encounter-history slopes, followed by gibbon, bear, clouded leopard, sambar and
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29 333 pangolin; pig, macaque and gibbon all have significantly higher encounter-
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31 334 history slopes compared to bear, clouded leopard, sambar and pangolin (figure 2,
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33 335 table 1). Only 20 respondents named specific animals they thought had existed in
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35 336 the past but were now locally extinct; these included pangolin (n=6), bear (n=3),
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37 337 parrot (n=3), snake/python (n=3), turtle (n=3), gibbon (n=2), tiger (n=1), wild
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39 338 pig (n=1), and muntjac (n=1).
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50 340 **(b) Quality of China’s Holocene record**

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52 341 In full analysis of 493 species, body mass was a significant predictor of site
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54 342 records for Chinese mammals (est=1.829, S.E.=0.488, t-value=3.746, p<0.001;
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56 343 df=369, R²=0.03, lambda=0.596), with larger-bodied species present in more
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58 344 sites (figure 3). Bootstrapping treatments yielded a positive significant
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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*: $\text{est}=-0.0007$, $\text{S.E.}=0.011$, $t\text{-value}=-0.071$, $p=0.944$; *geographic range*: $\text{est}=-0.000002$, $\text{S.E.}<0.001$, $t\text{-value}=-0.627$, $p=0.535$; $\text{df}=31$, $R^2<0.001$, $\lambda=0.099$), probably representing a Type II error associated with small sample size.

Holocene sites are significantly more clumped than expected under a random distribution ($z\text{-score}=-14.61$, $p<0.0001$), 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 ($\chi^2=494.35$, $\text{df}=47$, $p<0.0001$; 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 ($O=2$, $E=12.39$).

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366 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

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3 370 historical datasets that can potentially inform evidence-based management in a
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5 371 biodiversity hotspot. Through the use of diverse analyses, we highlight the types
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8 372 of novel insights provided by long-term faunal records on historical
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10 373 environmental baselines and patterns and dynamics of biodiversity change, but
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12 374 also key issues regarding quality and completeness of faunal records, and the
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15 375 extent to which data incompleteness and bias might limit integration of
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17 376 environmental archives into conservation decision-making in global-priority
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22 378 Our analyses of Holocene-historical faunal records from Hainan demonstrate
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24 379 how regional archives can contribute unique new perspectives that improve our
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26 380 understanding of biogeography, ecosystem composition and extinction
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29 381 vulnerability, with direct relevance for conservation research and practical
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31 382 management. Firstly, the long-term archives available for Hainan provide a new
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33 383 baseline on the island’s past postglacial species diversity that is unattainable
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36 384 from modern-day data. The Holocene fossil and historical records, and additional
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38 385 insights from ancient DNA analysis of museum archives [24], together reveal that
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40 386 the current depauperate state of Hainan’s mammal fauna is a historically recent
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43 387 rather than a long-term “natural” ecological condition, with 14 species in six
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45 388 orders (17% of Hainan’s present-day mammalian species richness) recorded in
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47 389 postglacial faunal archives but unknown from Hainan today. It is possible that
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50 390 some bats and rodents recorded at Luobidong might be undetected rather than
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52 391 extinct today, as Hainan’s small mammal fauna remains relatively understudied
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55 392 [49]. However, Holocene-historical archives also demonstrate that Hainan
56
57 393 formerly contained a typical southeast Asian large mammal fauna comprising a
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394 diverse assemblage of megaherbivores, megacarnivores, mesoherbivores and
395 mesocarnivores, which have now largely disappeared from the island.

396 Hainan's long-term archives also provide a baseline for reconstructing
397 relative extinction timings for different components of the island's large mammal
398 fauna over time. The largest-bodied herbivores and carnivores present at
399 Luobidong (elephants, tapirs, buffalos, tigers) had already disappeared by the
400 time historical accounts of Hainan's biodiversity and natural resources were first
401 recorded. Although the exact timing of extinctions remains unclear, these species
402 are not referenced in Hainan's gazetteer archive dating from the 1500s onwards,
403 and Hainan was described as "without horses or tigers" as early as 80 CE [13].
404 Smaller-bodied mesoherbivores and mesocarnivores survived until much more
405 recently. Père David's deer persisted on Hainan until at least the nineteenth
406 century [24] and possibly until 1917 based on gazetteer records; and OLE
407 analysis of gazetteer records for wolf and dhole together with indigenous
408 knowledge from local respondents demonstrates these species persisted into the
409 mid-twentieth century but apparently disappeared before living memory.

410 Comparison of different probabilistic methods for inferring extinction using
411 sighting records suggests OLE is more robust than other approaches, and
412 generally gives accurate predictions when applied to >5 records [50], although
413 use of >10 records is recommended by ref. 51, a condition fulfilled by dhole but
414 not wolf. We also note that estimated extinction dates for wolf and dhole
415 represent last-occurrence dates only, because OLE relies on the implicit
416 assumption that recording effort never falls to zero [35], but Hainan's gazetteer
417 record stops at the end of the Nationalist Era.

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

431 Further analysis of baseline data from long-term archives also identifies the
432 likely driver of extinctions in Hainan’s postglacial mammal fauna. Our PVA
433 results show that, unlike some other Late Quaternary island systems with
434 isolated large-bodied mammal populations [32,53], Hainan is large enough to
435 support long-term viable populations of megaherbivores and megacarnivores
436 that were present when the island became isolated in the early Holocene, with
437 natural catastrophes required to cause stochastic extinction in model
438 simulations considered too severe to be ecologically plausible (i.e. requiring
439 destruction of $\geq 12\%$ of the island’s carrying capacity). We can therefore exclude
440 the hypothesis of stochastic extinction, and identify human activity as the only
441 plausible driver of Holocene mammalian losses on Hainan. Prehistoric human-
442 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

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3 468 is similar to the staggered extinction dynamics seen in several continental
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5 469 mammal faunas across the Holocene-historical period [56,57]. These findings
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8 470 reveal that Hainan is now experiencing “empty forest syndrome” [58], and with
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10 471 the Hainan gibbon “merely” the latest of Hainan’s mammals to be sliding towards
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12 472 extinction. They also raise key questions for future investigation: why has
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14 473 Hainan’s mammal fauna been so vulnerable to extinction, given that its forest
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16 474 cover remained fairly extensive until the twentieth century [13,59]; how did
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18 475 gibbons manage to survive; and what does this long-term perspective suggest
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21 476 about the future of Hainan’s biodiversity?

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24 477 This new baseline on past diversity and faunal turnover provides a practical
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26 478 framework for conservation managers to understand the extent of human-
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28 479 caused biodiversity loss on Hainan, and emphasizes the urgent need for active
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30 480 regional conservation programmes for many more species. Our new model of
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32 481 Hainan’s long-term extinction dynamics can be compared and contrasted with
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34 482 data for other Asian regions, for example islands that have experienced either
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36 483 survival or extinction of species formerly present on Hainan (e.g. tigers, clouded
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38 484 leopards), to identify intrinsic or extrinsic correlates of species vulnerability and
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41 485 resilience and make predictive hypotheses to inform conservation planning
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43 486 [31,60,61]. Integrated faunal archives can also inform direct conservation
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45 487 management, for example to set new restoration or rewilding targets (e.g.
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47 488 reintroduction of extirpated species, such as Père David’s deer to Hainan’s
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49 489 wetlands; management of disrupted forest regeneration processes requiring
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51 490 mammalian dispersers), or to forecast potential faunal responses to future
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53 491 environmental change scenarios and develop appropriate mitigation strategies
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55 492 against ongoing biodiversity loss.
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3 493 However, despite the invaluable new insights about the status of regional
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5 494 Chinese biodiversity provided by these long-term perspectives, China's
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8 495 environmental archives exhibit extensive problems with incompleteness,
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10 496 representativeness and bias in the information they contain about past faunal
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12 497 baselines, cautioning against their use at face value. Each archive we investigated
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14 498 for Hainan contains only a small percentage of the mammal species occurring on
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16 499 the island today (fossil record=31%, gazetteer record=16%), and only one
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18 500 regionally extinct species (dhole) is definitely included in more than one archive
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20 501 (electronic supplementary material, table S1), suggesting that many more
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22 502 species, potentially including numerous regionally extinct species of unknown
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24 503 identity, remain undocumented. The usefulness of the gazetteer record and
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26 504 potentially also the indigenous knowledge record are limited further due to
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28 505 problems with accurate species identification by untrained observers. We also
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30 506 demonstrate that, in contrast to some other social-ecological systems [19,62],
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32 507 Hainan's indigenous knowledge record is an extremely poor source of
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34 508 information on past extinctions, with almost no local awareness of formerly
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36 509 occurring species, and most responses likely "cued" from previous interview
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38 510 questions about named animals (pangolin, bear, gibbon, wild pig).
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45 511 Our analyses of mainland China's faunal record demonstrate similar
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47 512 incompleteness and bias, with only 22% of extant Chinese mammal species
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49 513 represented in Holocene sites, and a strong effect of body mass on likelihood of
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51 514 species representation. Similar biases are observed in many Quaternary and
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53 515 older faunal assemblages, and likely reflect multiple burial and post-burial
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55 516 processes including preferential past human hunting of larger-bodied animals,
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57 517 greater survival of robust skeletal elements, biased excavation procedures,
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3 518 and/or limited osteological information for species identification of many small-
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5 519 bodied mammals [44,63], with few studies available on Chinese Quaternary small
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8 520 mammal assemblages [64]. Although it is not possible to quantify how these
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10 521 different processes have biased data for our regional study system, it is therefore
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12 522 likely that Hainan’s large-bodied Holocene mammal fauna is better understood
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15 523 than its small-bodied fauna, with potential faunal turnover in Chinese small
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17 524 mammal assemblages more challenging to identify. Distribution of Holocene
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19 525 sites across China is also spatially uneven, and with very different representation
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22 526 of different ecoregions. Far more excavations have been conducted in regions
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24 527 with higher historical human populations (e.g. Yellow River and Yangtze plains)
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26 528 [18], constituting an important target for archaeologists but not representative
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28 529 of past human-environmental interactions and impacts across China as a whole,
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30 530 and providing very different power to understand past environments and
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33 531 biodiversity change in different landscapes, notably high-elevation Asian
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35 532 ecosystems facing increased climate change risks today.

38 533 Our analyses of the quality of China’s Holocene faunal record provide a new
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40 534 baseline for assessing the insights that historical data can provide for
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42 535 conservation, as well as the challenges that necessitate caution and care in
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44 536 interpreting these data, which prevent long-term archives from ultimately being
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46 537 able to answer many questions of importance to conservation biologists.
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48 538 Establishing a clearer understanding of patterns of incompleteness and bias in
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50 539 the faunal record can help identify future research priorities, including increased
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52 540 sampling in understudied ecoregions, or extrapolations to estimate numbers of
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54 541 regionally extinct species that remain unidentified [65]. Unfortunately, other
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56 542 biodiversity hotspots do not have the range and resolution of long-term archives
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543 available for China, so any region-specific conservation insights from the past
544 will be even more limited for these systems, especially when coupled with
545 problems of specimen preservation exacerbated in tropical environments such
546 as thermal degradation of ancient biomolecules [24]. Long-term environmental
547 records provide windows into the past that are essential for understanding
548 environmental baselines and biodiversity change, and enable development of
549 more inclusive decision-making frameworks, but incorporating these records
550 into conservation planning requires careful and nuanced interpretation.

551

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

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

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

558 **Funding.** Funding was provided by a Royal Society University Research Fellowship to
559 S.T.T. (UF130573) and the Arcus Foundation.

560 **Acknowledgements.** We thank the indigenous communities of Hainan for sharing their
561 indigenous knowledge. Data collection was supported by Michelle Wong, Hongyu Fu,
562 Qiaomei Li, Yuegui Lin, Cong Zhou, Hao Zhang, Jinghua Zhang, Helen Nash, Peng Zhang,
563 the management offices and reserve staff of Hainan's protected areas, and the Hainan
564 Provincial Forestry Department. We thank Hannah O'Regan and Claire Risley for advice
565 on analysis.

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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, Jiayi; 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.

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753 **Table 1.** Summary of respondent encounter history data for seven Hainanese
754 mammals, and species last-encounter history regression slopes with 83%
755 confidence interval upper and lower bounds (df for all regressions=24).
756

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

757

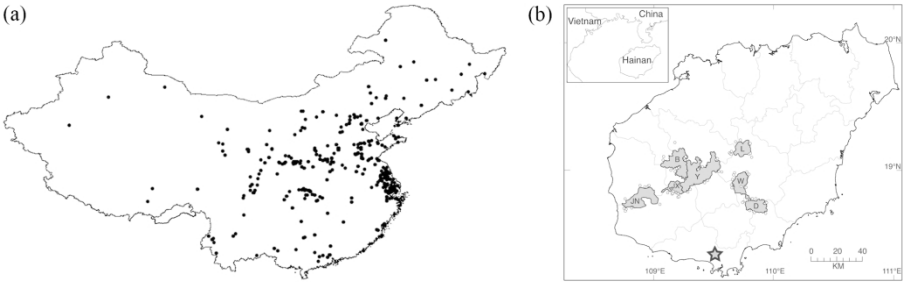


Figure 1. (a) Distribution of 253 Holocene zooarchaeological and palaeontological sites across mainland China with wild mammal records. (b) Map of Hainan, showing location of Luobidong Cave (star) and villages where interviews were conducted (circles). B, Bawangling; D, Diaoluoshan; JN, Jianfengling;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

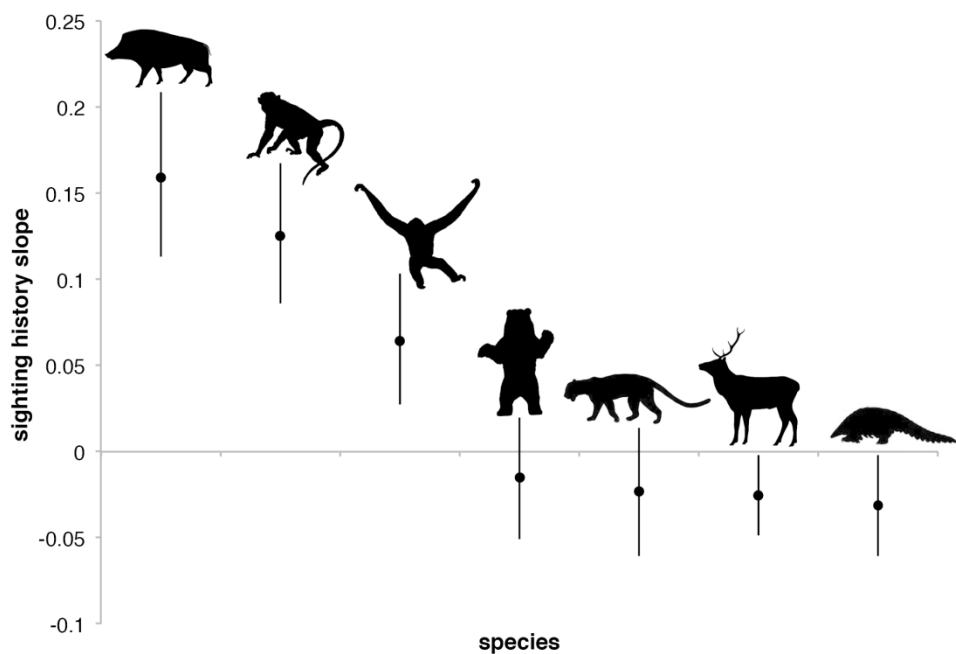


Figure 2. Slopes and 83% CIs of local respondent encounter-history data for seven Hainanese mammal species. Left to right: wild pig, rhesus macaque, Hainan gibbon, Asian black bear, clouded leopard, sambar deer, Chinese pangolin.

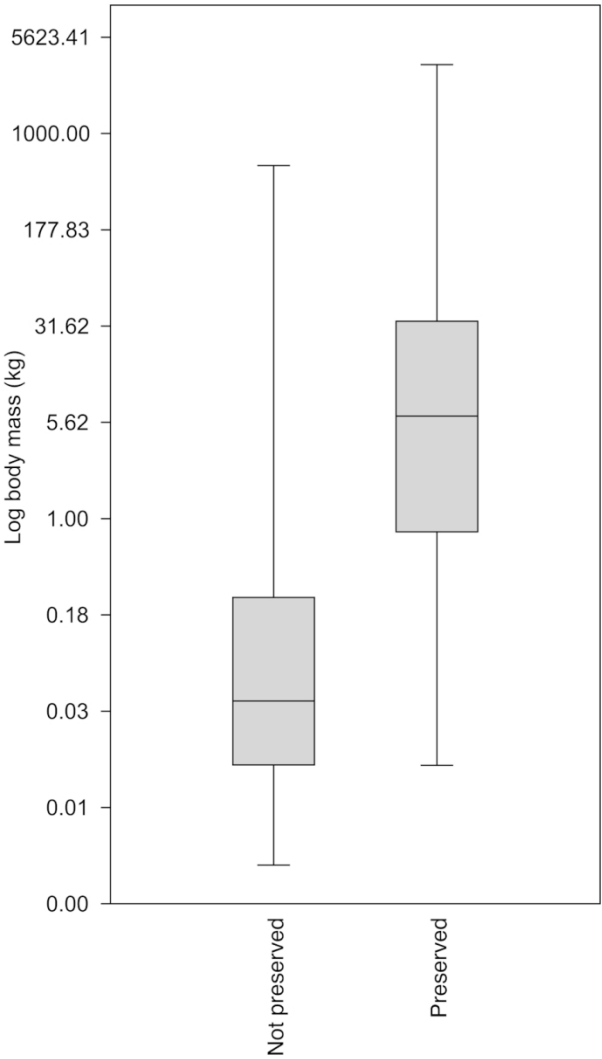


Figure 3. Box plot of body masses for mainland Chinese mammal species that are present or absent in the Holocene zooarchaeological and palaeontological record.

100x161mm (300 x 300 DPI)

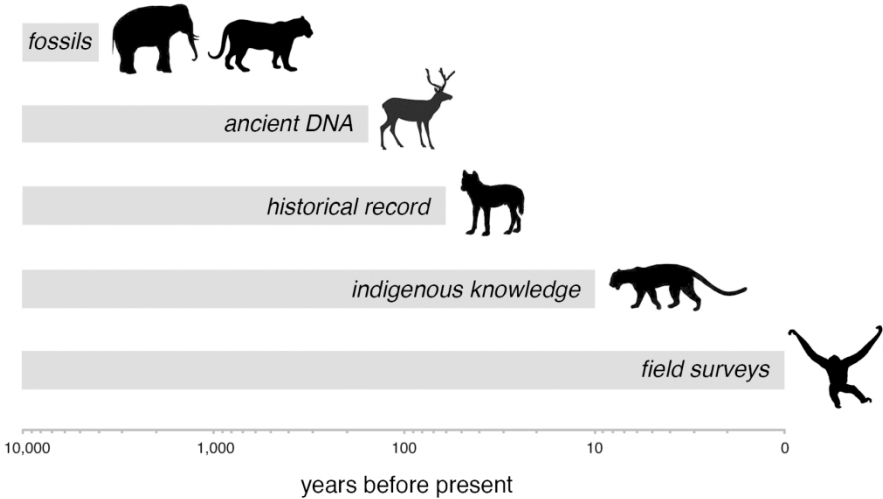


Figure 4. Integrated model of long-term mammalian biodiversity change on Hainan based on synthesis of multiple environmental archives, showing progressive depletion of regional mammal fauna across the Holocene to the present as evidenced by different species-specific data sources on temporal patterns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

167x102mm (300 x 300 DPI)