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### Article

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1 **Long-term archives reveal shifting extinction selectivity**

2 **in China's postglacial mammal fauna**

3

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12 **Keywords:** China, extinction filter, historical archives, Holocene, range loss

13 Ecosystems have been modified by human activities for millennia, and insights about  
14 ecology and extinction risk based only on recent data are likely to be both incomplete and  
15 biased. We synthesize multiple long-term archives (>250 archaeological and  
16 palaeontological sites dating from the early Holocene to the Ming Dynasty, and >4400  
17 historical records) to reconstruct the spatiotemporal dynamics of Holocene-modern range  
18 change across China, a megadiverse country experiencing extensive current-day  
19 biodiversity loss, for 34 mammal species over three successive postglacial time intervals.  
20 Our combined zooarchaeological, palaeontological, historical and current-day datasets  
21 reveal that both phylogenetic and spatial patterns of extinction selectivity have varied  
22 through time in China, probably in response both to cumulative anthropogenic impacts (an  
23 “extinction filter” associated with vulnerable species and accessible landscapes being  
24 affected earlier by human activities) and also to quantitative and qualitative changes in  
25 regional pressures. China has experienced few postglacial global species-level mammal  
26 extinctions, and most species retain over 50% of their maximum estimated Holocene range  
27 despite millennia of increasing regional human pressures, suggesting that the potential still  
28 exists for successful species conservation and ecosystem restoration. Data from long-term  
29 archives also demonstrate that herbivores have experienced more historical extinctions in  
30 China, and carnivores have until recently displayed greater resilience. Accurate assessment  
31 of patterns of biodiversity loss, and the likely predictive power of current-day correlates of  
32 faunal vulnerability and resilience, is dependent upon novel perspectives provided by long-  
33 term archives.

34 **1. Introduction**

35 Humans have been a dominant driver of patterns in species diversity, distribution and extinction  
36 throughout recent millennia [1,2]. Integrating historical archives into macroecological research  
37 and environmental management might therefore provide novel insights on past ecosystem  
38 structure and human-mediated faunal turnover that are unavailable from short-term studies [3].  
39 In particular, identifying biological and environmental factors that can predispose species to be  
40 vulnerable or resilient to extinction has been a major area of research during the development of  
41 predictive conservation science [4-6]. In recent years, palaeoecological research has generated  
42 substantial insights into the dynamics and ecosystem effects of biodiversity loss through  
43 geological “deep time” and into the Late Quaternary [7-8]. However, correlates of extinction risk  
44 are typically studied in modern-day systems, which have experienced an “extinction filter” and  
45 have already lost biodiversity that was more vulnerable to past human pressures, so that insights  
46 from such studies are therefore potentially both incomplete and biased [9]. Without a  
47 comparative assessment of long-term correlates of extinction risk, it is also impossible to  
48 determine whether risk factors remain constant through time, and therefore whether assessment  
49 of current-day species threat status is informative for predicting future extinction risk [10].  
50 Despite their importance, however, multi-decadal or longer datasets are used in relatively few  
51 studies of extinction ecology [3], and most assessments of past species extinction risk have had  
52 to be conducted at coarse species-level or country-level resolutions rather than at population-  
53 level or higher spatial resolutions, due to limited data availability and resolution [11,12].

54         Understanding past environmental baselines and the extent to which human activities  
55 have already disrupted biodiversity, and whether extinction selectivity is constant or changing  
56 through time, is of particular importance for eastern and southeast Asia. Asian terrestrial

57 ecosystems are now experiencing extreme anthropogenic pressure and contain the world's  
58 highest numbers of threatened vertebrate and plant species [13,14], and assessing the predictive  
59 power of correlates of vulnerability or resilience to regional human activities is an urgent  
60 conservation concern. This region also has a long history of human occupation [15], and has  
61 experienced increasing human overpopulation, resource overexploitation and habitat  
62 modification, with these pressures having escalated in intensity throughout much of the  
63 postglacial Holocene Epoch [16-18]. The Holocene was a climatically stable interval relative to  
64 the rest of the Late Quaternary, and few if any Holocene vertebrate extinctions, global or  
65 regional, can be interpreted as non-anthropogenically mediated [2]. Asian ecosystems therefore  
66 have the potential to represent important study systems for investigating long-term human  
67 impacts on biodiversity, and employing restricted time windows for ecological analysis of Asian  
68 faunas could have particularly significant implications for understanding regional extinction  
69 dynamics and vulnerability.

70         Reconstructing past human-caused faunal turnover across much of southeast Asia  
71 remains hindered by limited availability of long-term archives [19]. However, China—a huge  
72 (~9.6 million km<sup>2</sup>), “megadiverse” country that contains over 10% of the world's extant mammal  
73 species and covers a diverse range of habitat types including boreal and tropical forest,  
74 grasslands and deserts [20]—possesses a rich Late Quaternary palaeontological and  
75 zooarchaeological record containing abundant mammal material [17,19], with the potential to  
76 provide important insights into the changing historical status of regional biodiversity. These data  
77 have rarely been synthesized or investigated within a quantitative analytical framework [21].  
78 However, they provide a unique resource for understanding extinction selectivity and faunal  
79 responses to human activities in a global conservation hotspot, and historical patterns across

80 China's huge geographic area and megadiverse fauna have wider implications for understanding  
81 human-caused extinction dynamics through time. Here, we use a new georeferenced database of  
82 Holocene archaeological and palaeontological sites on mainland China from which wild  
83 mammals identifiable to species level have been recorded, and a further new database of  
84 historical Chinese mammal locality records, to investigate species responses to human impacts  
85 through time across a regional mammal fauna. We demonstrate how past environmental  
86 baselines provided by long-term faunal archives can provide novel and essential insights into the  
87 patterns, magnitude and drivers of biodiversity change, and can inform the use of current-day  
88 data for assessing future risk.

89

## 90 **2. Methods**

91

### 92 **(a) Data collection**

93 We collected mammal locality data from mainland China (i.e., excluding Hainan and Taiwan)  
94 for three time periods: “modern” (post-AD 2000), “historical” (AD 1900–AD 2000), and  
95 “Holocene” (11,700 BP–AD 1900). We only used two pre-modern time bins (rather than further  
96 subdivision) for three reasons: there was a lack of data across all species at a consistently more  
97 detailed temporal resolution; many Holocene archaeological sites span multiple temporal  
98 horizons, with mammal material not consistently reported from specific levels; and we used pre-  
99 twentieth century temporal boundaries to help identify wild versus domestic *Equus* and *Bubalus*  
100 species (e.g., all *Equus* records before the Late Shang can be interpreted as wild, whereas later  
101 records were conservatively interpreted as either domestic or impossible to distinguish from  
102 domestic on available data; electronic supplementary material, text S1), meaning that we could

103 not reconstruct ranges for these species across more subdivided pre-modern time bins. Mammals  
104 were selected as the focal group for this study as they are the only group of wild animals that are  
105 well-represented in Chinese Holocene sites, and they have received considerable attention in  
106 previous studies of extinction risk, as their current global threat status is well-understood [13,22]  
107 and large-scale macroecological and ecogeographic datasets are available for these taxa [4-  
108 6,11,12,23].

109 We obtained zooarchaeological and palaeontological records of skeletal remains of non-  
110 domesticated and non-commensal mammals identified to species level from published and grey  
111 literature, and from unpublished accession data associated with Holocene collections in the  
112 Institute of Archaeology, Chinese Academy of Social Sciences (Beijing), the Institute of  
113 Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences (Beijing), the  
114 Shanghai Museum of Science and Technology, the Three Gorges Museum (Chongqing), and the  
115 Shaanxi Institute of Archaeology (Xi'an) (supplementary electronic information, table S1). We  
116 also included a further dataset of Holocene records of *Elaphurus davidianus* available in ref. 24.

117 Most Holocene collections reported from China are now unavailable for study, very few  
118 dates/ages associated with these collections represent direct radiometric dates on wild mammal  
119 specimens, and most site reports lack additional information with which to otherwise assess data  
120 quality [25-26]. We therefore had to follow original reported species identifications and site  
121 dates/cultures, and were unable to audit the quality of taxonomic or temporal data in a systematic  
122 manner, in contrast to some other studies of Quaternary biodiversity turnover [27-28]. However,  
123 we excluded alleged Holocene palaeontological sites that have recently been reinterpreted as  
124 probably Late Pleistocene in age [25], and we updated and standardized species taxonomy  
125 following ref. 20 and recent revisions (electronic supplementary material, text S1). We also

126 combined the ranges of (1) all Chinese *Naemorhedus* species, and (2) both Holocene Chinese  
127 rhinoceros species (*Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*), and treated each  
128 grouping as a single species range for each time period, to account for uncertainties in species-  
129 level identification in many records of these widely recorded taxa (electronic supplementary  
130 material, text S1). We interpret all Holocene non-domesticated mammal records as representing  
131 individuals from wild populations that occurred in the vicinity of archaeological/fossil sites  
132 where they were reported (electronic supplementary material, text S1).

133 A minimum of six locality points is required to construct two range polygons, and therefore  
134 to assess whether species data represent single continuous polygons or fragmented geographic  
135 distributions (see below). We analyzed the subset of wild mammal species that are recorded from  
136  $\geq 10$  sites in the Holocene dataset, to allow for further robustness in sample size of locality data  
137 used to build species maps. The number of different reported Holocene localities on mainland  
138 China for these species varied between 10 and 111 (electronic supplementary material, table S2).  
139 Only seven species were recorded from 6-9 Holocene sites (i.e., above minimum map-building  
140 threshold, but excluded from analysis). These species include representatives of several mammal  
141 orders (Artiodactyla, Carnivora, Primates) and span a range of body sizes and ecologies,  
142 indicating that their exclusion from further analysis is unlikely to bias our results. Their  
143 exclusion is supported by uncertainty over taxonomic validity of some species (*Muntiacus*  
144 *gigas*), and/or increased likelihood that skeletal remains could be misidentified due to  
145 morphological similarity with related species (*Gazella subgutturosa*, *Procapra gutturosa*) [29].

146 We obtained most of our historical records from the compendium of localities for Chinese  
147 mammals in ref. 30, which contains data from published and unpublished Chinese sources dating  
148 from 1930 onwards, and further data on Chinese mammals from Russian literature dating back to



149 1888. We supplemented this list with additional locality records from refs 31-40, and from the  
150 entire run of the China Journal of Science and Arts (35 volumes, 1923-1941). Historical records  
151 were typically reported at the county level; we excluded data if they referred to larger and/or  
152 more vaguely described geographic regions (e.g., “central and southern areas of Jiangsu”), or if  
153 they were reported by a Western author using an idiosyncratic early transliteration system (i.e.,  
154 not Wade-Giles or pinyin transliteration) and could not be matched to known modern localities.  
155 Historical data generally refer to wild mammal observations that were approximately  
156 contemporaneous with publication date of each reference, or date from a few years beforehand  
157 (although we note that some records for *Equus ferus* [35-39] refer to nineteenth century locality  
158 records, but with the assumption that the species was likely to have persisted in these regions  
159 into the twentieth century); we therefore interpret historical locality records as representing an  
160 approximate baseline for geographic distributions of wild mammal populations at the beginning  
161 of the twentieth century. For the 34 wild mammal species recorded from  $\geq 10$  sites in our  
162 Holocene dataset, two species (*Bubalus mephistopheles* and *Elaphurus davidianus*) had no  
163 twentieth century Chinese records, and the number of historical localities for other species varied  
164 between 5 and 249 (electronic supplementary material, table S2).

165 We used IUCN range maps as modern mammal ranges. These were downloaded from the  
166 IUCN website as vector polygon shapefiles [41] and converted to Cylindrical Equal Area  
167 projection in the mapping software ArcMAP [42]. We removed parts of IUCN ranges  
168 specifically noted as regions where species were now extinct (e.g., for *Ursus arctos* and *U.*  
169 *thibetanus*), and included them within historical ranges. We then clipped all range maps to a map  
170 of China.

171

172 **(b) Species maps**

173 We assigned all historical and Holocene locality points a geographic coordinate (latitude-  
174 longitude) by searching for the records in a georeferencing facility (primarily using iTouch [43]),  
175 and then checked coordinate locations to ensure they corresponded with original Holocene or  
176 historical mapped localities [e.g., in ref. 30], and/or found a third reference to verify locations.  
177 We built up comparative historical and Holocene ranges for each species using current-day  
178 ranges as baselines onto which locality records from older time periods were also incorporated  
179 (i.e., historical ranges combined modern and historical data; Holocene ranges also included older  
180 zooarchaeological and palaeontological data), based on the assumption that species ranges are  
181 unlikely to have experienced marked natural expansions or shifts beyond the early Holocene  
182 after modern postglacial climatic and environmental conditions became established. This enabled  
183 us to reconstruct past species' extent of occurrence (EOO), a measure of range extent calculated  
184 as the area within a convex hull polygon that encloses all points with no internal angle measuring  
185  $>180^\circ$  [44]. This method allows for reasonable comparison of relative changes in distribution  
186 between species and time periods for the same geographic area despite underlying unevenness in  
187 distribution of data [44,45], and has previously been used to reconstruct species distributions  
188 using presence-only Quaternary and older fossil data [46,47].

189 We used IUCN guidelines for species mapping [44] to build up historical and Holocene  
190 locality points onto modern range polygons. We connected each locality point by a straight line  
191 to its two nearest features: either two other points outside the base polygon, or one point and one  
192 polygon, whichever was nearest. In the absence of two features, we used the Chinese border, on  
193 the assumption (in the almost complete absence of available Holocene species locality data from  
194 elsewhere in Asia) that before range declines caused by human activity, most species' ranges

195 extended into adjacent regions of neighbouring countries and were not limited by political  
196 boundaries. If IUCN ranges were fragmented into more than one polygon, we connected locality  
197 points to the nearest polygon. We otherwise assumed that ranges were continuous unless they  
198 included known topographical barriers/unsuitable habitat (e.g., Tibetan Plateau, Gobi Desert). If  
199 polygons were contained within larger ones, they were dissolved. Once we had connected all  
200 points and features, we merged polygons within each temporal layer. We then converted each  
201 layer to Cylindrical Equal Area projection and calculated the area in km<sup>2</sup>. We then calculated  
202 proportion of range lost for each species between Holocene-historical, historical-modern, and  
203 Holocene-modern intervals.

204       Whilst some other studies [e.g., 48] have investigated range change with historical point  
205 locality data using an alternative area of occupancy (AOO) approach [44,45], this method is not  
206 feasible to use in this study, as our baseline current-day ranges are EOO polygons which cannot  
207 be compared directly with past point locality data in a straightforward manner. We also sought to  
208 avoid methods such as AOO that rely heavily on the actual number and distribution of individual  
209 data, as differences in the spatial patterning and quantity of past locality records available for  
210 different species reflect pre- and post-excavation biases as well as underlying ecological  
211 variation in species distributions (e.g., variation in zooarchaeological species distribution records  
212 can reflect complex variation in factors such as past settlement patterns and faunal exploitation  
213 by prehistoric communities, and also more recent archaeological search effort [49]).

214       We also reconstructed separate modern, historical, and Holocene spatial patterns of mammal  
215 species richness across China. For each interval, we layered and merged all species maps. We  
216 overlaid a 100×100km grid cell, and calculated number of species in each grid cell. We then

217 calculated proportion of species lost for each grid cell between Holocene-modern, Holocene-  
218 historical, and historical-modern intervals.

219

### 220 **(c) Statistical analysis**

221 We used the proportion of each Holocene species range lost by the start of the twentieth century,  
222 and then further lost between the start of the twentieth century and the present, to investigate  
223 whether any biological traits affected species' susceptibility to range loss and whether  
224 susceptibility varied over time. We chose body mass and trophic level as predictors, as these are  
225 known to act as proxies for many other life history traits [50] and have been identified as key  
226 intrinsic biological parameters associated with increased extinction vulnerability that could have  
227 driven extinction filters [11]; there were insufficient species in our sample (n=34) to investigate a  
228 wider range of potential variables within a statistical framework. We also tested for an  
229 interaction between body mass and trophic level, to investigate specifically whether any signal  
230 from either predictor is driven by elevated past vulnerability of large-bodied herbivores, a pattern  
231 seen in studies of modern-day mammal extinction risk [5]. We obtained life history data from the  
232 PanTHERIA database [23], with trophic level defined as three categories: 1=herbivore,  
233 2=omnivore, 3=carnivore, following ref. 23. Where direct species data were unavailable in this  
234 reference, we obtained alternate data from ref. 20 or from closely related species (*Bubalus*  
235 *bubalis* data for *B. mephistopheles*; *Capricornis sumatraensis* for *C. milneedwardsi*; *Equus*  
236 *caballus* for *E. ferus*) (electronic supplementary material, text S1). We modelled proportion of  
237 range lost against body mass, trophic level, and the interaction of these terms. For this species-  
238 level analysis, we used a phylogenetic generalized least-squares (PGLS) model approach to  
239 account for non-independence of species due to shared ancestry, implemented using the R

240 package ‘caper’ [51]. We used Akaike’s information criterion corrected for small sample size  
241 ( $AIC_C$ ) to compare models, and used  $\Delta AIC_C$  to rank them relative to the top-ranked model (i.e.,  
242 model with lowest  $AIC_C$ ). We considered all models with  $\Delta AIC_C$  values below 2 as well-  
243 supported [52]. We did not investigate variable importance via model averaging because of the  
244 small number of variables under consideration. We assessed structural goodness-of-fit using  
245 adjusted  $r^2$  values from the outputs of the PGLS function.

246       Next, we investigated environmental characteristics associated with variation in regional  
247 species losses between successive time periods. The response variable was proportion of species  
248 lost per grid cell before and after AD 1900, to control for geographic variation in former  
249 Holocene regional species richness; this variable was logit transformed [53]. We tested for the  
250 potential effect of Human Footprint Index (HFI), a composite index of relative human influence  
251 (associated with likelihood of anthropogenic exploitation, conflict, habitat loss and resource  
252 competition) derived from current human population density, land use and infrastructure [54].  
253 We recognize that HFI data represent current-day conditions, and so might be less relevant for  
254 investigating pre-modern patterns of biodiversity turnover; however, comparable data are  
255 unavailable for pre-modern periods (especially as a single composite measure spanning multiple  
256 Holocene time points, to be comparable with our Holocene mammal dataset). We also tested for  
257 potential effects of other environmental variables that have all been associated widely with  
258 mammal population decline. The most commonly supported variables, which we included here,  
259 are: elevation (extinction vulnerability might be associated with habitat breadth and ecological  
260 adaptability, and/or elevational variation in anthropogenic activity), annual precipitation and  
261 annual temperature (extinction vulnerability might be associated with variation in productivity  
262 and resource availability regulated by these predictors), and actual evapotranspiration and

263 potential evapotranspiration (extinction vulnerability might be associated with variation in joint  
264 or potential availability of energy and water, as measured respectively by these indices) [50,55].  
265 We did not model all of the large number of combinations of these variables or their interactions,  
266 as it is important to maintain clear biological hypotheses about which combinations might be  
267 important. We therefore only modelled ten combinations to investigate different hypotheses  
268 associated with specific effects of climatic, anthropogenic, and physical factors:

- 269 (1) All six variables previously identified as important predictors of extinction risk might be  
270 important in predicting Chinese mammal loss (model a);
- 271 (2) Changing climatic factors are important extinction drivers, so physical factors  
272 (elevation, HFI) were successively excluded from analysis (models b-c);
- 273 (3) Actual and potential evapotranspiration are closely correlated, with similar expected  
274 relationships to extinction risk, so we excluded the former from analysis (model d);
- 275 (4) Annual precipitation and mean annual temperature are closely correlated and again have  
276 similar expected effects on extinction risk, so we included all variables except mean  
277 temperature and the previously excluded actual evapotranspiration to have a dataset  
278 with reduced multicollinearity (model e);
- 279 (5) To test additive effects of human activities and climatic changes, two of the largest  
280 extinction drivers, we included only HFI and the reduced climate dataset (model f);
- 281 (6) Effects of climate change and extreme weather can be most extreme at high elevations,  
282 so we included only elevation and the reduced climate dataset (model g);
- 283 (7) High-altitude species can be sensitive to extinction processes [56], so we modelled  
284 effects of elevation only (model h);

- 285 (8) Human activities are among the most important extinction drivers, so we modelled  
286 effects of HFI only (model i);
- 287 (9) To investigate effects of non-collinear climatic variables while excluding physical  
288 factors, we modelled effects of annual precipitation and potential evapotranspiration  
289 (model j).

290 We overlaid maps of predictor variables on a map of China, with data aggregated to  
291 100×100km grid cell level. To control for known spatial variation in Holocene and historical  
292 sampling, we only analyzed cells containing Holocene records when investigating pre-twentieth  
293 century regional species loss, and only analyzed cells containing historical records when  
294 investigating twentieth century to current-day loss; including cells lacking pre-modern records  
295 would likely underestimate regional declines, as absence of species records for these cells might  
296 reflect incomplete sampling rather than true absence. We modelled how proportion of species  
297 lost changed as a function of different predictors using generalized linear models, specifying a  
298 binomial error structure. As for the previous analysis, we compared and ranked model  
299 performance using AIC and determined support for each model using  $\Delta AIC$ , considering models  
300 with  $\Delta AIC_c$  below 2 as well-supported.

301

### 302 **3. Results**

303 Our Holocene database contains 253 Chinese archaeological and palaeontological sites with  
304 identified wild mammal species, dating from the early Holocene (~11,000 BP) to the Ming  
305 Dynasty (14th-17th century AD), and distributed across 20 of China's 21 mainland provinces, all  
306 five provincial-level autonomous regions, and three of China's four provincial-level  
307 municipalities (electronic supplementary material, figure S1, table S1). Thirty-four wild mammal

308 species are recorded from  $\geq 10$  sites, including representatives of Artiodactyla, Carnivora,  
309 Perissodactyla, Primates, Proboscidea and Rodentia and comprising a broad range of biological  
310 and ecological attributes, including a body mass range of  $\sim 0.25$ -3,300kg (table 1). For these 34  
311 species, we compiled over 4400 historical locality records from the early twentieth century  
312 onwards (electronic supplementary material, figure S1, tables S2-S3), derived current-day  
313 geographic ranges and built up comparative twentieth century and Holocene ranges (figure 1;  
314 electronic supplementary material, figure S2), and used this series of range maps across three  
315 successive postglacial time intervals as the basis for high-resolution analysis of species responses  
316 to human impacts through time.

317 Mammal species vary from having lost less than 1% of their original Holocene range in  
318 China (e.g., *Arctonyx collaris*, *Hystrix brachyura*, *Viverricula indica*, *Vulpes vulpes*) to having  
319 become regionally or globally extinct (e.g., *Bubalus mephistopheles*, *Elaphurus davidianus*,  
320 *Equus ferus*) (table 1). Most species (73.5%) have lost less than 50% of their Chinese range  
321 across the Holocene, although the remaining subset have all lost over 90% of their range during  
322 this interval. In total, 22.8% of combined species' original Holocene ranges have now been lost  
323 in China, with 15.0% lost before AD 1900, and 7.8% lost after AD 1900.

324 For explaining the proportion of initial Holocene species' range that was lost before AD  
325 1900, the model with the best support (lowest AICc) contains body mass alone, although the  
326 model containing both body mass and trophic level (with no interaction) is almost equally well-  
327 supported, suggesting that trophic level is also an influential predictor (table 2; electronic  
328 supplementary material, text S2). Based on these models, larger-bodied species and herbivores  
329 are both more likely to have lost relatively more geographic range before AD 1900. Both models  
330 explain almost half of total variation in past range loss ( $r^2=0.430$ - $0.469$ ). Conversely, the strong



331 signal of body mass for explaining range loss is lost after AD 1900. The most well-supported  
332 model now contains only trophic level (table 2), and all well-supported models explain much less  
333 of total variation in recent range loss ( $r^2=0.159-0.247$ ). It is also worth noting that if we used a  
334  $\Delta AICc$  threshold of 6 rather than 2, as suggested by ref. 57, all four models would be considered  
335 well-supported for explaining recent range loss.

336         Analysis of changing spatial patterns of mammal species richness and variation in  
337 regional losses over time across China for different intervals at a  $100\times 100$ km grid cell resolution  
338 (figure 2; electronic supplementary material, figure S3) shows that the proportion of species lost  
339 before AD 1900 is explained by a single parsimonious model (model a) containing all six of our  
340 predictors (table 3). In this model, fewer species have been lost in grid cells with higher  
341 elevation, lower HFI, higher annual precipitation, lower annual temperature, lower actual  
342 evapotranspiration, and higher potential evapotranspiration. This model explains almost half of  
343 total variation in species lost per grid cell ( $r^2=0.468$ ) (electronic supplementary material, text S2).  
344 Conversely, five different models, containing different combinations of climatic, anthropogenic,  
345 and physical variables (models b-f), are all well-supported to explain proportion of species lost  
346 after AD 1900, with AIC values within 2 units of each other, but these models all explain only  
347 very low levels of variation ( $r^2=0.064-0.069$ ) (table 3).

348

#### 349 **4. Discussion**

350 Our findings provide new evidence for previously identified relationships between extinction  
351 risk and biological or environmental factors. Analysis of variation in species extinction risk  
352 supports the known positive relationship between extinction risk and body size, which is  
353 associated with lower population densities and intrinsic rates of increase in larger-bodied species,

354 making them more vulnerable to anthropogenic and non-anthropogenic environmental pressures,  
355 and such species are also preferentially exploited by humans [4-6,13]. Analysis of variation in  
356 regional extinction risk supports known relationships between extinction risk and several  
357 climatic, anthropogenic, and physical variables [50]; for example, populations occurring at lower  
358 elevations are known to be more vulnerable to extinction due to greater human population  
359 growth and habitat conversion in these accessible regions, and many threatened species now  
360 restricted to high-elevation refugia formerly had broader elevational distributions [21,55]. More  
361 importantly, our combined zooarchaeological, palaeontological, historical and current-day  
362 datasets reveal that both phylogenetic and spatial patterns of extinction selectivity have varied  
363 through time in China, with body mass decreasing in significance as a predictor of species  
364 extinction risk, and a marked reduction in ability of our models to explain variation in species  
365 extinction risk or regional extinction risk using any of our chosen biological or environmental  
366 variables. These novel findings demonstrate the presence of important extinction filters affecting  
367 current-day ecological data that can bias our understanding of faunal vulnerability and resilience  
368 in the absence of novel perspectives provided by long-term archives.

369         The changing pattern of extinction selectivity observed through time in China might  
370 reflect the cumulative impact of ongoing regional human pressures, with vulnerable species  
371 disappearing and accessible landscapes becoming modified earlier on during the Holocene,  
372 leaving a subset of ecologically resilient species and geographically remote landscapes that show  
373 reduced extinction risk. Under this extinction model, the decreasing significance of body mass as  
374 a predictor of species extinction risk might reflect the greater level of geographic range loss  
375 shown by larger-bodied species in China before the twentieth century, with little range left to be  
376 lost for these species over the past century. Similarly, the decreasing significance of all modelled

377 environmental factors for explaining variation in regional extinction risk might reflect the loss of  
378 many Chinese mammal populations that had become restricted by the start of the twentieth  
379 century to remnant refugia associated with specific ecological conditions (e.g., high elevations),  
380 with ‘extinction debt’ in many such landscapes that had already become too degraded to support  
381 viable populations in the long-term [21].

382         Alternatively, shifting extinction selectivity in China’s mammal fauna through time  
383 might be associated with changing regional anthropogenic pressures. Indeed, the decreasing  
384 predictive power over time shown by body mass might not be explained by a simplistic  
385 extinction filter model of near-complete pre-twentieth century range loss in larger-bodied  
386 species, as several large-bodied mammals (e.g., *Capricornis milneedwardsii*, *Cervus elaphus*,  
387 *Rusa unicolor*, *Ursus arctos*, *U. thibetanus*) maintained wide geographic distributions across  
388 China into the twentieth century and even up to the present (table 1). Instead, whereas  
389 mammalian extinction risk in China before AD 1900 was influenced by a series of different  
390 environmental factors, during the twentieth century spatial extinction patterns became more  
391 homogeneous (figure 2b), and our predictive models lose most of their ability to explain  
392 variation in extinction risk. China therefore appears to have become a system in which the “field  
393 of bullets” model of extinction selectivity is likely to apply [58], with extinction becoming  
394 effectively unpredictable in relation to life-history traits or environmental conditions, and small-  
395 bodied and large-bodied species across different landscapes all experiencing population losses. A  
396 comparable global shift in mammalian extinction selectivity across the Holocene has been  
397 interpreted as possibly indicating a change in primary driver of biodiversity loss, from  
398 overexploitation of a taxonomically restricted subset of large-bodied species to wider-scale  
399 habitat destruction [11]. Over the past century, Chinese environments have experienced a

400 massive increase in habitat loss and natural resource exploitation, associated with the country's  
401 human population explosion and well-documented destructive environmental policies, as well as  
402 an increase in the focus and scope of harmful activities (e.g., the mid-twentieth century  
403 ideological “war on nature”, when systematic politically-driven campaigns led to rapid  
404 extirpation of tigers and other large carnivores that had not previously been the focus of heavy  
405 persecution) [59,60]. Geographic expansion of human pressures across China's diverse range of  
406 ecological landscapes during the twentieth century (e.g., onto the high-elevation Qinghai-Tibetan  
407 Plateau [61]) might also explain the decreasing significance of any environmental variables as  
408 good predictors of extinction risk in our analyses (figure 2b).

409         We acknowledge that it is difficult to assess the quality of the data that comprise China's  
410 Holocene faunal record in a systematic manner, in terms of concerns such as robustness of  
411 species identification and dating of sites; such problems are by no means unique to this study,  
412 and remain widespread when dealing more generally with past data [62]. However, following  
413 efforts to minimize the potential effect of sampling bias in archival datasets (e.g., through use of  
414 mapping methods that are not sensitive to the total number and distribution of individual data),  
415 China's long-term, spatiotemporally high-resolution faunal record can still provide an extremely  
416 important new baseline for understanding the magnitude and dynamics of human-caused  
417 biodiversity loss in this conservation hotspot, and this record presents a unique perspective  
418 unavailable from modern-day datasets. Previous studies have investigated range change in a  
419 small number of mammal taxa during recent centuries or millennia using past occurrence records  
420 in China's historical gazetteer (difangzhi) archive, in which some mammals are identifiable to  
421 species or “species group” level [21,63], and our integrated use of multiple archives to achieve a  
422 much longer-term view of changing extinction dynamics across China's mammal fauna through

423 the Holocene represents a further key step in the use of regional environmental records.

424         China's mammal fauna is recognized as being highly threatened today [20,22], but long-  
425 term Holocene archives reveal that postglacial mammalian losses to date have not yet been as  
426 severe as in some other geographic regions (e.g., the Caribbean, Australia [2,11,13]), with few  
427 global species-level extinctions and almost three-quarters of species retaining over 50% of their  
428 maximum estimated Holocene range despite millennia of increasing regional human pressures.  
429 The potential may therefore still exist for successful species conservation and ecosystem  
430 restoration. However, we recognize that this result is scale-dependent, with further local  
431 population extirpation and fragmentation likely to have occurred in many species at finer  
432 landscape levels [64] but undetected by resolution of available historical or IUCN data.  
433 Considerable attention is also paid today to conservation of large carnivores, which are  
434 interpreted as a particularly vulnerable ecological guild [65,66], but long-term data demonstrate  
435 that herbivores have experienced more historical extinctions in China and carnivores have until  
436 recently displayed greater resilience, challenging conservation prioritization based on recent data  
437 alone.

438         The ability of HFI to predict the spatial distribution of earlier Holocene species  
439 extinctions in China in our analysis of variation in regional extinction risk provides the important  
440 insight that current-day anthropogenic variables can in some instances be used to hindcast past  
441 conditions. In this case, current-day high-HFI areas [54] include regions such as the North China  
442 Plain and the Yangtze River Valley, which have experienced high human population densities,  
443 cultural intensification and environmental exploitation for millennia [17,18] and also show  
444 elevated pre-twentieth century mammal extinctions (figure 2a). However, our demonstration of  
445 shifting extinction patterns through time might support recognition of a modern "Anthropocene"

446 Epoch, defined by qualitatively more intensive human pressures on global ecosystems during the  
447 past few decades or centuries [67]. The differences that we have detected in extinction dynamics  
448 between past and present therefore have major implications for using long-term archives for  
449 environmental forecasting, in particular for informing current-day conservation and  
450 environmental management, and for using data derived from contemporary systems to predict  
451 future patterns of extinction selectivity. Palaeontological, zooarchaeological and historical  
452 records are an invaluable resource for reconstructing pre-human environments and understanding  
453 the magnitude of human-caused biodiversity loss through time, but interpreting and extrapolating  
454 what they show requires both caution and context.

455

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457 described in this article.

458

459 **Data accessibility statement.** The datasets supporting this article are available as part of the  
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461

462 **Competing interests statement.** We declare we have no competing interests.

463

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465 collected data; J.J.C. and J.B. analyzed data; and S.T.T. and J.J.C. wrote the paper. All authors  
466 gave final approval for publication.

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470

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605 **Table 1.** Holocene, twentieth century and current-day ranges for 34 Chinese mammals, including  
 606 body masses and percentage of Holocene range remaining in later intervals.

607

<b>Species</b>	<b>Body mass (kg)</b>	<b>Holocene range (km<sup>2</sup>)</b>	<b>20th century range (km<sup>2</sup>)</b>	<b>Current-day range (km<sup>2</sup>)</b>
<i>Ailuropoda melanoleuca</i>	118.00	749,840	88,817 (11.8%)	16,285 (2.2%)
<i>Arctonyx collaris</i>	8.17	3,676,360	3,676,360 (100%)	3,657,922 (99.5%)
<i>Bubalus mephistopheles</i>	929.50	1,527,357	0 (0%)	0 (0%)
<i>Canis lupus</i>	31.76	8,721,246	8,721,246 (100%)	7,524,437 (86.3%)
<i>Capreolus pygargus</i>	41.37	4,157,171	3,820,650 (91.9%)	3,817,317 (91.8%)
<i>Capricornis milneedwardsii</i>	110.94	2,104,840	2,103,325 (99.9%)	1,999,527 (95.0%)
<i>Cervus elaphus</i>	240.87	4,816,709	4,449,413 (92.4%)	3,972,736 (82.5%)
<i>Cervus nippon</i>	53.00	2,919,625	274,792 (9.4%)	27,520 (0.9%)
<i>Cuon alpinus</i>	15.80	5,676,234	5,128,031 (90.3%)	4,956,351 (87.3%)
<i>Elaphurus davidianus</i>	165.99	963,240	0 (0%)	0 (0%)
<i>Elephas maximus</i>	3,269.80	2,072,355	5,461 (0.3%)	4,211 (0.2%)
<i>Eospalax fontanierii</i>	0.26	1,231,580	1,213,187 (98.5%)	1,200,262 (97.5%)
<i>Equus ferus</i>	403.60	1,500,557	191,966 (12.8%)	0 (0%)
<i>Hydropotes inermis</i>	12.76	1,744,491	546,152 (31.3%)	145,161 (8.3%)
<i>Hystrix brachyura</i>	8.00	2,433,237	2,417,409 (99.3%)	2,417,409 (99.3%)
<i>Lutra lutra</i>	8.87	3,892,243	3,888,360 (99.9%)	3,785,118 (97.2%)
<i>Macaca mulatta</i>	6.46	2,937,921	2,935,508 (99.9%)	2,844,952 (96.8%)
<i>Meles leucurus</i>	6.25	6,245,111	6,245,111 (100%)	6,175,069 (98.9%)
<i>Muntiacus reevesi</i>	13.50	2,217,096	2,186,594 (98.6%)	2,186,042 (98.6%)
<i>Muntiacus vaginalis</i>	17.61	1,388,769	1,043,690 (75.2%)	1,032,519 (74.3%)
<i>Naemorhedus spp.</i>	28.22	2,213,673	2,212,241 (99.9%)	2,173,200 (98.2%)
<i>Nyctereutes procyonoides</i>	4.22	4,664,834	4,574,286 (98.1%)	4,574,274 (98.1%)
<i>Paguma larvata</i>	4.30	3,084,952	3,084,952 (100%)	3,048,167 (98.8%)

Panthera pardus	52.40	2,981,579	2,772,337 ( <b>93.0%</b> )	2,659,147 ( <b>89.2%</b> )
Panthera tigris	161.92	3,091,975	2,631,057 ( <b>85.1%</b> )	29,423 ( <b>1.0%</b> )
Prionailurus bengalensis	2.78	4,708,612	4,707,595 ( <b>99.9%</b> )	4,072,294 ( <b>86.5%</b> )
Rhinoceros spp.	1,398.08	1,903,944	23,992 ( <b>1.3%</b> )	0 ( <b>0%</b> )
Rhizomys sinensis	1.91	2,013,597	1,964,514 ( <b>97.6%</b> )	1,963,625 ( <b>97.5%</b> )
Rusa unicolor	177.52	2,617,933	1,576,197 ( <b>60.2%</b> )	1,561,201 ( <b>59.6%</b> )
Sus scrofa	84.47	6,554,098	6,539,983 ( <b>99.8%</b> )	6,119,878 ( <b>93.4%</b> )
Ursus arctos	196.29	5,317,488	3,882,979 ( <b>73.0%</b> )	3,364,089 ( <b>63.3%</b> )
Ursus thibetanus	99.71	3,152,699	3,084,106 ( <b>97.8%</b> )	1,696,226 ( <b>53.8%</b> )
Viverricula indica	2.92	2,596,039	2,596,039 ( <b>100%</b> )	2,591,799 ( <b>99.8%</b> )
Vulpes vulpes	4.82	9,327,084	9,327,084 ( <b>100%</b> )	9,327,084 ( <b>100%</b> )

608

609

610

611 **Table 2.** PGLS models investigating variation in proportion of mammal range loss in China,  
 612 before AD 1900 (**A**) and after AD 1900 (**B**), and reporting maximum log-likelihood (LL),  
 613 parameter count (k), change in Akaike’s information criterion (corrected for finite sample size)  
 614 relative to top-ranked model ( $\Delta AIC_c$ ), and  $r^2$ .

615

<b>Model</b>	<b>LL</b>	<b>k</b>	<b><math>\Delta AIC_c</math></b>	<b><math>r^2</math></b>
<b>(A) Proportion of range loss before AD 1900</b>				
Body mass	-58.960	4	0	0.469
Body mass + trophic level	-61.250	2	0.499	0.430
Body mass + trophic level + interaction	-58.824	6	5.979	0.435
Trophic level	-65.890	2	11.714	0.219
<b>(B) Proportion of range loss after AD 1900</b>				
Trophic level	-50.870	2	0	0.159
Body mass + trophic level + interaction	-47.301	6	1.265	0.247
Body mass + trophic level	-50.680	4	2.212	0.140
Body mass	-54.703	2	5.239	0.005

616



617 **Table 3.** Generalized least-squares models to explain variation in proportion of species lost per  
618 100×100km grid cell across China, before AD 1900 (**A**) and after AD 1900 (**B**), and reporting  
619 maximum log-likelihood (LL), parameter count (k), change in Akaike’s information criterion  
620 (corrected for finite sample size) relative to top-ranked model ( $\Delta AIC_c$ ), and  $r^2$ . Abbreviations:  
621 AET, actual evapotranspiration; Elev, elevation; HFI, Human Footprint Index; PET, potential  
622 evapotranspiration; Rain, annual precipitation; Temp, annual temperature.

623

Model	LL	k	$\Delta AIC_c$	$r^2$
<b>(A) Proportion of species lost before AD 1900</b>				
AET+Elev+HFI+PET+Rain+Temp	-1430.126	7	0	0.468
AET+HFI+PET+Rain+Temp	-1439.070	6	15.890	0.462
Elev+HFI+PET+Rain+Temp	-1469.992	6	77.734	0.439
Elev+HFI+PET+Rain	-1498.354	5	132.458	0.418
AET+PET+Rain+Temp	-1549.076	5	233.900	0.381
HFI+PET+Rain	-1498.354	4	251.875	0.373
HFI only	-1601.421	2	332.591	0.342
Elev+PET+Rain	-1619.442	4	372.634	0.329
Elev only	-1719.010	2	567.768	0.256
PET+Rain	-1997.714	3	1127.178	0.051
<b>(B) Proportion of species lost after AD 1900</b>				
AET+PET+Rain+Temp	-1533.476	5	0	0.067
HFI+PET+Rain	-1534.570	4	0.188	0.064
AET+HFI+PET+Rain+Temp	-1533.028	6	1.103	0.069
Elev+HFI+PET+Rain+Temp	-1533.101	6	1.250	0.068
Elev+HFI+PET+Rain	-1534.397	5	1.842	0.065
Elev+PET+Rain	-1535.522	4	2.091	0.062
AET+ Elev+HFI+PET+Rain+Temp	-1532.787	7	2.621	0.069
PET+Rain	-1537.111	3	3.270	0.058
Elev only	-1545.201	2	17.449	0.036
HFI only	-1546.968	2	20.983	0.031

624

625 **Figure Legends**

626

627 **Figure 1.** Composite range maps for six Chinese mammals, showing current-day (dark grey),  
628 20th century (medium grey) and Holocene (light grey) ranges, reconstructed using historical  
629 records (filled circles) and zooarchaeological and palaeontological records (open circles). **A**,  
630 giant panda *Ailuropoda melanoleuca*; **B**, red deer *Cervus elaphus*; **C**, sika deer *Cervus nippon*;  
631 **D**, dhole *Cuon alpinus*; **E**, Asian elephant *Elephas maximus*; **F**, tiger *Panthera tigris*.

632

633 **Figure 2.** Proportion of mammal species lost per 100×100km grid cell across China before AD  
634 1900 (**A**) and after AD 1900 (**B**). Proportion of species lost increases from paler to darker squares  
635 (bins: 0, 0.1-4.0, 4.1-8.0, 8.1-12.0, 12.1-16.0, 16<).