Long-term archives reveal shifting extinction selectivity in China's postglacial mammal fauna

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

1. Introduction

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

Understanding past environmental baselines and the extent to which human activities have already disrupted biodiversity, and whether extinction selectivity is constant or changing through time, is of particular importance for eastern and southeast Asia. Asian terrestrial ecosystems are now experiencing extreme anthropogenic pressure and contain the world's highest numbers of threatened vertebrate and plant species [13,14], and assessing the predictive power of correlates of vulnerability or resilience to regional human activities is an urgent conservation concern. This region also has a long history of human occupation [15], and has experienced increasing human overpopulation, resource overexploitation and habitat modification, with these pressures having escalated in intensity throughout much of the postglacial Holocene Epoch [16-18]. The Holocene was a climatically stable interval relative to the rest of the Late Quaternary, and few if any Holocene vertebrate extinctions, global or regional, can be interpreted as non-anthropogenically mediated [2]. Asian ecosystems therefore have the potential to represent important study systems for investigating long-term human impacts on biodiversity, and employing restricted time windows for ecological analysis of Asian faunas could have particularly significant implications for understanding regional extinction dynamics and vulnerability.

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

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

2. Methods

(a) Data collection

We collected mammal locality data from mainland China (i.e., excluding Hainan and Taiwan) for three time periods: "modern" (post-AD 2000), "historical" (AD 1900–AD 2000), and "Holocene" (11,700 BP–AD 1900). We only used two pre-modern time bins (rather than further subdivision) for three reasons: there was a lack of data across all species at a consistently more detailed temporal resolution; many Holocene archaeological sites span multiple temporal horizons, with mammal material not consistently reported from specific levels; and we used pre-twentieth century temporal boundaries to help identify wild versus domestic *Equus* and *Bubalus* species (e.g., all *Equus* records before the Late Shang can be interpreted as wild, whereas later records were conservatively interpreted as either domestic or impossible to distinguish from domestic on available data; electronic supplementary material, text S1), meaning that we could not reconstruct ranges for these species across more subdivided pre-modern time bins. Mammals were selected as the focal group for this study as they are the only group of wild animals that are well-represented in Chinese Holocene sites, and they have received considerable attention in previous studies of extinction risk, as their current global threat status is well-understood [13,22] and large-scale macroecological and ecogeographic datasets are available for these taxa [4-6,11,12,23].

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

Most Holocene collections reported from China are now unavailable for study, very few dates/ages associated with these collections represent direct radiometric dates on wild mammal specimens, and most site reports lack additional information with which to otherwise assess data quality [25-26]. We therefore had to follow original reported species identifications and site dates/cultures, and were unable to audit the quality of taxonomic or temporal data in a systematic manner, in contrast to some other studies of Quaternary biodiversity turnover [27-28]. However, we excluded alleged Holocene palaeontological sites that have recently been reinterpreted as probably Late Pleistocene in age [25], and we updated and standardized species taxonomy following ref. 20 and recent revisions (electronic supplementary material, text S1). We also combined the ranges of (*1*) all Chinese *Naemorhedus* species, and (*2*) both Holocene Chinese rhinoceros species (*Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*), and treated each grouping as a single species range for each time period, to account for uncertainties in species-level identification in many records of these widely recorded taxa (electronic supplementary material, text S1). We interpret all Holocene non-domesticated mammal records as representing individuals from wild populations that occurred in the vicinity of archaeological/fossil sites where they were reported (electronic supplementary material, text S1).

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

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

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

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

(b) Species maps

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

We used IUCN guidelines for species mapping [44] to build up historical and Holocene locality points onto modern range polygons. We connected each locality point by a straight line to its two nearest features: either two other points outside the base polygon, or one point and one polygon, whichever was nearest. In the absence of two features, we used the Chinese border, on the assumption (in the almost complete absence of available Holocene species locality data from elsewhere in Asia) that before range declines caused by human activity, most species' ranges extended into adjacent regions of neighbouring countries and were not limited by political boundaries. If IUCN ranges were fragmented into more than one polygon, we connected locality points to the nearest polygon. We otherwise assumed that ranges were continuous unless they included known topographical barriers/unsuitable habitat (e.g., Tibetan Plateau, Gobi Desert). If polygons were contained within larger ones, they were dissolved. Once we had connected all points and features, we merged polygons within each temporal layer. We then converted each layer to Cylindrical Equal Area projection and calculated the area in km^2. We then calculated proportion of range lost for each species between Holocene-historical, historical-modern, and Holocene-modern intervals.

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

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

(c) Statistical analysis

We used the proportion of each Holocene species range lost by the start of the twentieth century, and then further lost between the start of the twentieth century and the present, to investigate whether any biological traits affected species' susceptibility to range loss and whether susceptibility varied over time. We chose body mass and trophic level as predictors, as these are known to act as proxies for many other life history traits [50] and have been identified as key intrinsic biological parameters associated with increased extinction vulnerability that could have driven extinction filters [11]; there were insufficient species in our sample (n=34) to investigate a wider range of potential variables within a statistical framework. We also tested for an interaction between body mass and trophic level, to investigate specifically whether any signal from either predictor is driven by elevated past vulnerability of large-bodied herbivores, a pattern seen in studies of modern-day mammal extinction risk [5]. We obtained life history data from the PanTHERIA database [23], with trophic level defined as three categories: 1=herbivore, 2=omnivore, 3=carnivore, following ref. 23. Where direct species data were unavailable in this reference, we obtained alternate data from ref. 20 or from closely related species (*Bubalus bubalis* data for *B. mephistopheles*; *Capricornis sumatraensis* for *C. milneedwardsi*; *Equus caballus* for *E. ferus*) (electronic supplementary material, text S1). We modelled proportion of range lost against body mass, trophic level, and the interaction of these terms. For this species-level analysis, we used a phylogenetic generalized least-squares (PGLS) model approach to account for non-independence of species due to shared ancestry, implemented using the R package ‘caper’ [51]. We used Akaike’s information criterion corrected for small sample size (AIC_C) to compare models, and used ΔAIC_C to rank them relative to the top-ranked model (i.e., model with lowest AIC_C). We considered all models with ΔAIC_C values below 2 as well-supported [52]. We did not investigate variable importance via model averaging because of the small number of variables under consideration. We assessed structural goodness-of-fit using adjusted r^2 values from the outputs of the PGLS function.

Next, we investigated environmental characteristics associated with variation in regional species losses between successive time periods. The response variable was proportion of species lost per grid cell before and after AD 1900, to control for geographic variation in former Holocene regional species richness; this variable was logit transformed [53]. We tested for the potential effect of Human Footprint Index (HFI), a composite index of relative human influence (associated with likelihood of anthropogenic exploitation, conflict, habitat loss and resource competition) derived from current human population density, land use and infrastructure [54]. We recognize that HFI data represent current-day conditions, and so might be less relevant for investigating pre-modern patterns of biodiversity turnover; however, comparable data are unavailable for pre-modern periods (especially as a single composite measure spanning multiple Holocene time points, to be comparable with our Holocene mammal dataset). We also tested for potential effects of other environmental variables that have all been associated widely with mammal population decline. The most commonly supported variables, which we included here, are: elevation (extinction vulnerability might be associated with habitat breadth and ecological adaptability, and/or elevational variation in anthropogenic activity), annual precipitation and annual temperature (extinction vulnerability might be associated with variation in productivity and resource availability regulated by these predictors), and actual evapotranspiration and potential evapotranspiration (extinction vulnerability might be associated with variation in joint or potential availability of energy and water, as measured respectively by these indices) [50,55]. We did not model all of the large number of combinations of these variables or their interactions, as it is important to maintain clear biological hypotheses about which combinations might be important. We therefore only modelled ten combinations to investigate different hypotheses associated with specific effects of climatic, anthropogenic, and physical factors:

(1) All six variables previously identified as important predictors of extinction risk might be important in predicting Chinese mammal loss (model a);

(2) Changing climatic factors are important extinction drivers, so physical factors (elevation, HFI) were successively excluded from analysis (models b-c);

(3) Actual and potential evapotranspiration are closely correlated, with similar expected relationships to extinction risk, so we excluded the former from analysis (model d);

(4) Annual precipitation and mean annual temperature are closely correlated and again have similar expected effects on extinction risk, so we included all variables except mean temperature and the previously excluded actual evapotranspiration to have a dataset with reduced multicollinearity (model e);

(5) To test additive effects of human activities and climatic changes, two of the largest extinction drivers, we included only HFI and the reduced climate dataset (model f);

(6) Effects of climate change and extreme weather can be most extreme at high elevations, so we included only elevation and the reduced climate dataset (model g);

(7) High-altitude species can be sensitive to extinction processes [56], so we modelled effects of elevation only (model h);

(8) Human activities are among the most important extinction drivers, so we modelled effects of HFI only (model i);

(9) To investigate effects of non-collinear climatic variables while excluding physical factors, we modelled effects of annual precipitation and potential evapotranspiration (model j).

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

3. Results

Our Holocene database contains 253 Chinese archaeological and palaeontological sites with identified wild mammal species, dating from the early Holocene (~11,000 BP) to the Ming Dynasty (14th-17th century AD), and distributed across 20 of China's 21 mainland provinces, all five provincial-level autonomous regions, and three of China's four provincial-level municipalities (electronic supplementary material, figure S1, table S1). Thirty-four wild mammal species are recorded from ≥10 sites, including representatives of Artiodactyla, Carnivora, Perissodactyla, Primates, Proboscidea and Rodentia and comprising a broad range of biological and ecological attributes, including a body mass range of ~0.25-3,300kg (table 1). For these 34 species, we compiled over 4400 historical locality records from the early twentieth century onwards (electronic supplementary material, figure S1, tables S2-S3), derived current-day geographic ranges and built up comparative twentieth century and Holocene ranges (figure 1; electronic supplementary material, figure S2), and used this series of range maps across three successive postglacial time intervals as the basis for high-resolution analysis of species responses to human impacts through time.

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

For explaining the proportion of initial Holocene species' range that was lost before AD 1900, the model with the best support (lowest AICc) contains body mass alone, although the model containing both body mass and trophic level (with no interaction) is almost equally well-supported, suggesting that trophic level is also an influential predictor (table 2; electronic supplementary material, text S2). Based on these models, larger-bodied species and herbivores are both more likely to have lost relatively more geographic range before AD 1900. Both models explain almost half of total variation in past range loss (r^2=0.430-0.469). Conversely, the strong signal of body mass for explaining range loss is lost after AD 1900. The most well-supported model now contains only trophic level (table 2), and all well-supported models explain much less of total variation in recent range loss (r^2=0.159-0.247). It is also worth noting that if we used a ΔAICc threshold of 6 rather than 2, as suggested by ref. 57, all four models would be considered well-supported for explaining recent range loss.

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

4. Discussion

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

The changing pattern of extinction selectivity observed through time in China might reflect the cumulative impact of ongoing regional human pressures, with vulnerable species disappearing and accessible landscapes becoming modified earlier on during the Holocene, leaving a subset of ecologically resilient species and geographically remote landscapes that show reduced extinction risk. Under this extinction model, the decreasing significance of body mass as a predictor of species extinction risk might reflect the greater level of geographic range loss shown by larger-bodied species in China before the twentieth century, with little range left to be lost for these species over the past century. Similarly, the decreasing significance of all modelled environmental factors for explaining variation in regional extinction risk might reflect the loss of many Chinese mammal populations that had become restricted by the start of the twentieth century to remnant refugia associated with specific ecological conditions (e.g., high elevations), with ‘extinction debt’ in many such landscapes that had already become too degraded to support viable populations in the long-term [21].

Alternatively, shifting extinction selectivity in China’s mammal fauna through time might be associated with changing regional anthropogenic pressures. Indeed, the decreasing predictive power over time shown by body mass might not be explained by a simplistic extinction filter model of near-complete pre-twentieth century range loss in larger-bodied species, as several large-bodied mammals (e.g., *Capricornis milneedwardsii, Cervus elaphus, Rusa unicolor, Ursus arctos, U. thibetanus*) maintained wide geographic distributions across China into the twentieth century and even up to the present (table 1). Instead, whereas mammalian extinction risk in China before AD 1900 was influenced by a series of different environmental factors, during the twentieth century spatial extinction patterns became more homogeneous (figure 2b), and our predictive models lose most of their ability to explain variation in extinction risk. China therefore appears to have become a system in which the “field of bullets” model of extinction selectivity is likely to apply [58], with extinction becoming effectively unpredictable in relation to life-history traits or environmental conditions, and small-bodied and large-bodied species across different landscapes all experiencing population losses. A comparable global shift in mammalian extinction selectivity across the Holocene has been interpreted as possibly indicating a change in primary driver of biodiversity loss, from overexploitation of a taxonomically restricted subset of large-bodied species to wider-scale habitat destruction [11]. Over the past century, Chinese environments have experienced a massive increase in habitat loss and natural resource exploitation, associated with the country's human population explosion and well-documented destructive environmental policies, as well as an increase in the focus and scope of harmful activities (e.g., the mid-twentieth century ideological "war on nature", when systematic politically-driven campaigns led to rapid extirpation of tigers and other large carnivores that had not previously been the focus of heavy persecution) [59,60]. Geographic expansion of human pressures across China's diverse range of ecological landscapes during the twentieth century (e.g., onto the high-elevation Qinghai-Tibetan Plateau [61]) might also explain the decreasing significance of any environmental variables as good predictors of extinction risk in our analyses (figure 2b).

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

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

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

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

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Data accessibility statement. The datasets supporting this article are available as part of the electronic supplementary material (tables S1 and S3).

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

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

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

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

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

Model	**LL**	**k**	**ΔAIC_C**	**r^2**
(A) Proportion of range loss before AD 1900				
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) Proportion of range loss after AD 1900				
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

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

Model	**LL**	**k**	**ΔAIC_C**	**r^2**
(A) Proportion of species lost before AD 1900				
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) Proportion of species lost after AD 1900				
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

Figure Legends

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

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