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3 1 **Bias, incompleteness, and the “known unknowns” in the Holocene faunal record**
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3 **11 Abstract**
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6 **12** Long-term faunal data are needed to track biodiversity change and extinction over wide
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8 **13** spatiotemporal scales. The Holocene record is a particularly rich and well-resolved
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10 **14** resource for this purpose but nonetheless represents a biased subset of the original
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12 **15** faunal composition, both at the site-level assemblage and when data are pooled for
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14 **16** wider-scale analysis. We investigated patterns and potential sources of taxonomic,
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16 **17** spatial and temporal bias in two Holocene datasets of mammalian occurrence and
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18 **18** abundance, one at the global species-level and one at the continental population-level.
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20 **19** Larger-bodied species are disproportionately abundant in the Holocene fossil record,
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22 **20** but this varies according to trophic level, probably due to past patterns of human
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24 **21** subsistence and exploitation. Despite uneven spatial distribution of mammalian
25
26 **22** occurrence records, we found no specific source of sampling bias, suggesting that this
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28 **23** error-type can be avoided by intensive data collection protocols. Faunal assemblages
29
30 **24** are more abundant and precisely dated nearer to the present as a consequence of
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32 **25** taphonomy, past human demography, and dating methods. Our study represents one of
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34 **26** the first attempts to quantify incompleteness and bias in the Holocene mammal record,
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36 **27** and failing to critically assess quality of long-term faunal datasets has major
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38 **28** implications for understanding species decline and extinction risk.
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48 **30 Keywords: bias; Holocene; mammals; extinction; zooarchaeology; fossil record**
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1. Introduction

In order to respond to the ongoing biodiversity extinction crisis [1,2], it is imperative to understand patterns and drivers of species and population losses across taxonomy, time and space. For example, the disappearance of large-bodied mammals across the late Quaternary is known to have reshaped current-day patterns of mammalian diversity [3] and extinction risk [4,5]. Additional vertebrate species extinctions, range contractions and population losses have been documented in the fossil and historical record across continental and insular regions throughout the late Quaternary up to the present day as a result of climatic changes and anthropogenic impacts [6,7]. Long-term archival data are therefore needed to provide context for measuring changes in biodiversity over wide temporal and spatial scales.

The faunal record of the Holocene Epoch, from ~11,700 yr BP to present, is particularly well-suited for this purpose. As the most recent geological epoch, it has a rich and well-resolved record documenting vertebrate occurrences over wide spatiotemporal scales [8] and includes extinct and extant species, permitting analysis of factors that influence both extinction and survival. Furthermore, the relative stability of Holocene climate in comparison with the preceding Late Pleistocene means that anthropogenic drivers of biodiversity loss are generally more straightforward to identify and interpret [7], in comparison to the ongoing debate around human versus climatic drivers of late Quaternary megafaunal extinctions [9,10]. As the time period during which major human demographic, subsistence and technological transitions occurred [11], the Holocene is well suited to track faunal responses to a wide variety of human pressures, from low-density hunter-gatherers to settled farming communities and more recent industrial and urbanised societies.

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3 55 However, faunal records in long-term environmental archives only ever represent a
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5 56 biased subsample of an ecosystem or community [12], due to multiple processes that
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7 57 influence patterns of taxonomic composition and abundance during the deposition and
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9 58 excavation of faunal assemblages. First-order (pre-excavation) taphonomic
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11 59 modifications of fossil assemblages can include biotic disturbances from other
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13 60 organisms (e.g. trampling, scavenging and burrowing animals, or plant root growth),
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15 61 and abiotic disturbances such as wind, rain, floods and heat [13]. Intrinsic qualities of
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17 62 the faunal deposition can also affect its survival; for example, the largest, hardest,
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19 63 densest bones and teeth generally survive best in response to weathering, burial and
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21 64 decomposition [14,15], potentially biasing the relative representation of different-sized
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23 65 species or individuals (e.g. ontogenetic stages) in the faunal record. Other ecological
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25 66 traits are less well understood in terms of their role in controlling relative patterns of
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27 67 preservation in bone deposits, but factors such as trophic guild [16] and habitat [17] can
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29 68 also affect the frequency with which different species are represented in faunal
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31 69 archives.
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38 70 It is also important to distinguish between faunal assemblages from natural fossil
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40 71 (palaeontological) sites and those from archaeological sites. In general, fossil sites have
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42 72 been deposited by 'natural' (non-anthropogenic) means, for example from animals
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44 73 dying, decomposing, and being buried and preserved by natural sedimentological
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46 74 processes, or through accumulation of prey species by non-human predators such as
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48 75 raptors. By contrast, faunal remains from archaeological sites (hereafter
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50 76 'zooarchaeological' assemblages) are by definition found in human contexts such as
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52 77 killing sites, refuse pits or deliberate burials, which reflect prehistoric or historical
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54 78 processes of animal exploitation such as hunting, herding or domestication. A human
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56 79 selection filter reflecting subsistence, social and cultural preferences (both positive and
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3 80 negative) towards certain species has therefore further influenced the composition of
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5 81 zooarchaeological assemblages in addition to non-anthropogenic first-order
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8 82 taphonomic modifications, and it may not be easy to disentangle these biases from an
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10 83 understanding of which species were formerly present and/or abundant in the local
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12 84 environment [15]. As human populations rapidly expanded during the Holocene from
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15 85 the Neolithic agricultural revolution onwards, zooarchaeological assemblages are by far
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17 86 the most abundant source of faunal records for this time period [8,18].

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19 87 Most second-order (post-excavation) changes arise from sampling strategy and can
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21 88 therefore be partly controlled for by standardised excavation methods on a site-by-site
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23 89 basis, although the extent to which standardised methods are used is not necessarily
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25 90 reported [19]. Indeed, there has been a notable recorded bias in historical excavations,
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27 91 which often focused primarily on the discovery and description of larger fossil
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29 92 specimens and associated skeletal elements, meaning that large-bodied species have
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31 93 been relatively well-documented whereas many smaller-bodied species remain poorly
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33 94 known from environmental archives [20]. Furthermore, when records are pooled into
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35 95 larger datasets, uneven patterns of site distribution across landscapes can be
36
37 96 problematic for spatial analysis. Whilst the discovery and location of palaeontological
38
39 97 and archaeological sites is always partly opportunistic and random, spatial bias in the
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41 98 spread of sites can further distort our understanding of underlying natural faunal
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43 99 distributions. For example, sites can be actively searched for in areas of cultural
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45 100 interest, or where archaeological or fossil material is known to survive well. Countries
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47 101 also differ greatly both physically (e.g. topography, underlying geology, extent of urban
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49 102 versus rural areas) and in their political and economic histories, all of which can affect
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51 103 the amount of excavation, i.e. sampling, that has been undertaken.
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3 104 The variety of dating methods used for zooarchaeological analysis also means that
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5 105 the precision and accuracy of dating may vary across time. Direct dating methods such
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8 106 as radiocarbon dating have been widely used in an effort to establish reliable
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10 107 megafaunal extinction chronologies and modern human arrival dates during important
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12 108 periods of late Quaternary environmental change, in order to disentangle potential
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15 109 extinction drivers [21,22]. However, for the more climatically stable and human-
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17 110 dominated Holocene, research has instead tended to focus on how faunal assemblages
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19 111 reflect past human society and culture [23] rather than on composition and dynamics of
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21 112 the faunal communities themselves. As a consequence there is often little incentive to
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24 113 date individual bones, and zooarchaeological assemblages are often simply associated
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26 114 with the age of their associated archaeological site. Reported dating of faunal material
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29 115 can thus vary from broad temporal categories such as 'Late Mesolithic', a period
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31 116 potentially spanning a couple of thousand years, to a specific cultural period defined to
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34 117 a couple of hundred years. The extent of this disparity in dating methods, and any
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36 118 associated bias that it may place on the precision and resolution of available faunal
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38 119 records over time, should therefore also be carefully considered where records have
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41 120 been combined into large datasets.

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43 121 In summary, it cannot be assumed that even the recent faunal record faithfully
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45 122 reflects source communities either at the site- or landscape-level, and the potential
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47 123 extent to which pre- and post-excavation biases may actively distort interpretation of
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49 124 underlying patterns of species distributions, range shifts and extinctions should be
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51 125 critically assessed. To address this substantial but often overlooked concern, we
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53 126 therefore quantified taxonomic, spatial and temporal incompleteness/unevenness in
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55 127 two Holocene mammal datasets, and investigated how potential sources of bias
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57 128 influence our understanding of: (i) species-level extinction at the global scale; (ii)
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3 129 population-level change for individual species at the regional scale. These
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5 130 complementary analyses into the quality of the recent faunal record provide important
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7 131 implications for the use of Holocene and older datasets in informing ecological
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9 132 baselines, reconstructing extinction processes, and assessing extinction risk.
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14 134 **2. Materials and methods**

15 135 16 17 136 **(a) Global faunal record**

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20 137 We compiled a global dataset of 255 mammal species that are known to have become
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22 138 globally extinct during the postglacial period (from the Holocene to the recent historical
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24 139 period), together with their recorded country-level geographic occurrences, description
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26 140 dates (or date of first publication if the taxon has remained formally undescribed
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28 141 beyond initial identification as a new species), and estimated body mass [7] (see
29
30 142 electronic supplementary material, table S1). This comprehensive dataset includes both
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32 143 species that were originally described from extant populations that have subsequently
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34 144 become extinct ('modern', e.g. thylacine *Thylacinus cynocephalus*), and species that have
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36 145 only been recorded from the Holocene fossil and/or zooarchaeological records and
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38 146 never observed alive in recent times by scientists ('fossil', e.g. woolly mammoth
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40 147 *Mammuthus primigenius*). Body mass data for a small number of extinct mammals were
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42 148 taken from the PanTHERIA database [24], whilst data for remaining species were taken
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44 149 from previously published body mass estimates for Holocene extinct mammals derived
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46 150 from regression equations based on extant congeners or skeletal measurement
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48 151 parameters [5].
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57 152 In order to investigate whether pre- and post-excavation modifications to fossil
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59 153 assemblages are potentially biasing the taxonomic composition of the Holocene faunal
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3 154 record, we first investigated whether there was a relationship between species body
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5 155 mass and description date in the overall dataset. We then investigated this relationship
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8 156 in a more nuanced way, by assessing whether the relationship between body mass and
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10 157 description date was modified by whether extinct species were modern or fossil, and
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12 158 whether species inhabited continental or insular regions or both. We conducted
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15 159 analyses using phylogenetic generalised least squares (PGLS), which fits a linear model
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17 160 controlling for the non-independence between species resulting from phylogenetic
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20 161 structure in the data. Although species description date is not itself a heritable trait, it
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22 162 may correlate with traits such as body mass. Following refs [25, 26], we arbitrarily
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24 163 selected the first phylogenetic tree from 1000 available trees in ref. [27]. We used the
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26 164 pgl function in the R package 'caper' [28], with taxonomy standardised between
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29 165 datasets where possible. In total, 89 extinct mammal species in our dataset were absent
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31 166 from the phylogeny (electronic supplementary material, table S2), so this analysis was
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34 167 undertaken with a reduced dataset of 166 species.
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38 169 **(b) Continental zooarchaeological record**

40 170 We used an extensive dataset of 18,588 zooarchaeological records for 23 large mammal
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43 171 species (>2kg) in Europe spanning the Holocene, which has previously been used to
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45 172 reconstruct long-term processes of mammalian range decline and extinction [29]
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48 173 (electronic supplementary material, table S3). These data also represent a subset of a
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50 174 larger Holocene vertebrate database that has been widely used to investigate regional
51
52 175 faunal turnover, refugia and extinction across various vertebrate taxa [8].
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57 177 *(i) Taxonomic bias*

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3 178 We converted the number of zooarchaeological records for each species into the
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5 179 proportion of sites occupied across its extent of occurrence (defined as a minimum
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8 180 convex polygon enclosing all sites). This was to account for: (i) species' differing range
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10 181 sizes (which might skew the overall abundance of each species), and (ii) areas of Europe
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12 182 with low densities of zooarchaeological sites, which might artificially lower estimated
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14 183 abundance for species' ranges that fell within these areas (electronic supplementary
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16 184 material, table S3). As a proxy measure for zooarchaeological abundance, 'proportion of
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18 185 occupied sites' will hereafter be referred to as 'abundance'. We excluded two species
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20 186 from analyses: (i) wild horse (*Equus ferus*), because accurate records for this species
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22 187 only cover the first half of the Holocene due to identification problems with domestic
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24 188 horses in the later Holocene [30]; (ii) fallow deer (*Dama dama*), because its abundance
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26 189 and distribution were heavily affected by human-mediated introduction beyond its
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28 190 natural European range [31].
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33 191 We compared observed zooarchaeological abundance with ecological variables that
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35 192 could potentially influence whether a species might be recorded in the
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37 193 zooarchaeological record. Due to the small size of the response variable ($n=21$) we
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39 194 selected only two predictor variables, body mass and trophic level
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41 195 (herbivore/carnivore), on the basis that body mass represents a useful proxy for a
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43 196 range of other life-history variables (e.g. reproductive output) [32], and that humans are
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45 197 likely to interact differently with herbivores and carnivores, e.g. as subsistence versus
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47 198 competitors for prey. We predominantly used life-history data from the PanTHERIA
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49 199 database [24]; data on the extinct aurochs (*Bos primigenius*) were taken from a global
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51 200 database of late Quaternary mammals [33]. Body mass was logarithmically transformed
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53 201 for analysis. We analysed determinants of abundance using generalised linear models
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55 202 (GLMs) with quasibinomial errors to account for the response variable being a
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3 203 proportion and displaying overdispersion. We calculated “quasi-AICs” (QAICs) using the
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5 204 R package AICcmodavg [34] for model comparison, with the model with the lowest
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8 205 QAIC value interpreted as having the best explanatory power for explaining the
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10 206 influence of body mass and trophic level on zooarchaeological abundance. We also re-
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12 207 ran the analysis including species as a random effect.

15 208 In order to assess whether any observed relationship between zooarchaeological
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17 209 abundance and body mass or trophic level could either be attributed to taphonomic bias
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19 210 or instead reflected natural patterns, we compared our analysis of zooarchaeological
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21 211 abundance with regressions of population density and body mass from an ecological
22
23 212 dataset of global mammal populations [35]. We selected species with a mean body mass
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25 213 between 0.5kg and 700kg and within the orders Artiodactyla, Carnivora and
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27 214 Perissodactyla, representing the body size distribution and orders that were also
28
29 215 present in the Holocene dataset in order to ensure the two datasets were comparable.
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31 216 This mass range also covered an order of magnitude, considered sufficient to overcome
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33 217 any potential biasing effects on body size-abundance relationships [36]. We compared
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35 218 our Holocene dataset with two different ecological datasets: (i) one from North America
36
37 219 only (as the most faunally intact and environmentally analogous present-day ecosystem
38
39 220 to compare with the Holocene of northern Eurasia); and (ii) all continents pooled
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41 221 together. We also conducted separate regressions for all three datasets by trophic level
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43 222 (herbivore/carnivore). As an additional method of comparison, we calculated
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45 223 confidence intervals for all model slopes (all data, herbivore only and carnivore only)
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47 224 for the three datasets, with significant differences in abundance-body mass
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49 225 distributions interpreted if 95% confidence intervals did not overlap. All analyses were
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51 226 conducted using the glm and glmer packages ‘MASS’ [37] and ‘lme4’ [38] in R3.5.0 [39].
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3 228 *(ii) Spatiotemporal bias*
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5 229 The spatial spread of Holocene faunal data across Europe (electronic supplementary
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7 230 material, figure S1) indicated that numbers of zooarchaeological records differed
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9 231 substantially between countries, with higher representation of records in central and
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11 232 western Europe. We investigated alternative possible explanations for this pattern by
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13 233 calculating the total number of zooarchaeological records (interpreted as a proxy for
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15 234 research output) for each country. To determine whether number of zooarchaeological
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17 235 records per country reflected high output from a few sites rather than wider research
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19 236 effort across multiple sites, we tested the relationship between numbers of
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21 237 zooarchaeological records and zooarchaeological sites per country using Pearson's
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23 238 correlation coefficient. Numbers of records and sites were extremely highly positively
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25 239 correlated ($r = 0.91$, $p < 0.05$, d.f. = 38), so we retained number of zooarchaeological
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27 240 records as the chosen metric for further analysis.
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33 241 One possible explanation for variation in the number of zooarchaeological records
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35 242 across Europe is variation in country wealth and resources available for
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37 243 zooarchaeological research. Gross domestic product (GDP), a country's total economic
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39 244 activity based on market value of all goods and services, is a widely-used appropriate
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41 245 proxy measurement of a country's wealth [40]. However, it has been demonstrated that
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43 246 a country's land area, GDP and population size are all positively correlated [40],
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45 247 meaning that raw data on numbers of zooarchaeological records and GDP might not be
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47 248 appropriate for analysis as both values might show collinearity with land area.
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49 249 Regression analysis confirmed that country land area and GDP across Europe were
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51 250 positively correlated ($r = 0.35$, $p < 0.05$, d.f. = 38). Therefore, (i) we corrected total
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53 251 number of zooarchaeological records by land area into a measure of density of records
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55 252 for each country; and (ii) we used GDP per capita rather than GDP, with data obtained
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3 253 from the World Bank website [41]. We analysed the relationship between the density of
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5 254 zooarchaeological records and GDP per capita for each country using a GLM with
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8 255 quasipoisson errors to account for overdispersion. GDP per capita was logarithmically
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10 256 transformed for analysis.

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12 257 We also investigated whether the spatially uneven spread of zooarchaeological data
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14 258 could instead be related to variable topography across Europe, which might for example
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17 259 affect landscape accessibility for research. We calculated the average elevation for each
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19 260 country using a high-resolution 30-arc seconds (c.1km) elevation map from the
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22 261 WorldClim database [42]. We analysed the relationship between the number of
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24 262 zooarchaeological records and average elevation for each country using a negative
25
26 263 binomial GLM to account for count data with considerable overdispersion. Average
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28 264 elevation was logarithmically transformed for analysis. We also compared the elevation
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30 265 profile for the zooarchaeological dataset to that of Europe to assess whether there were
31
32 266 differences in the overall range of values, and to check that the average elevation was
33
34 267 not being biased by widely outlying values. We calculated the elevation of each
35
36 268 zooarchaeological data point at a 30-arc raster square resolution and then randomly
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38 269 sampled the same number of points from an ArcMap layer of European elevation and
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40
41 270 plotted both datasets as histograms.

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44 271 In order to examine any changes or patterns in dating precision over time, we
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46 272 plotted the lower and upper date range by midpoint for each zooarchaeological record.
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48 273 We also plotted all dated Holocene records against a theoretical linear increase in the
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50 274 number of zooarchaeological records, in order to identify changes in the rate of
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52 275 accumulation of records through time.
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58 59 277 **3. Results**

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6 **(a) Global faunal record**7
8 280 The number of extinct species known from Holocene and historical contexts has9
10 281 increased over time since the mid-eighteenth century, with peaks of new species11
12 282 descriptions in the early twentieth century and again close to the present (figure 1).13
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15 283 This pattern has primarily been driven by description of 'fossil' species ($n=199$), with16
17 284 description of 'modern' (historically extant) species ($n=56$) largely concluded by the18
19 285 1950s. Nearly four times as many recently extinct mammal species have been described20
21 286 from islands ($n=196$) compared to continental regions ($n=55$), with four species having22
23 287 past geographic ranges that included both continents and islands. We found a24
25 288 significant negative relationship between description date and body mass across the26
27 289 'fossil' data subset, with larger-bodied species generally described earlier than smaller-28
29 290 bodied species (est=-0.0030, S.E.=0.0013, t-value=-2.000, $p<0.05$; d.f.=109, $R^2=0.048$,30
31 291 lambda=1.00), but not for the 'modern' data subset (est=-0.00025, S.E.=0.00057, t-32
33 292 value=-0.43, $p>0.05$; d.f.=53, $R^2=0.0035$, lambda=1.00) (figure 2). For the combined34
35 293 fossil and modern dataset, we found a significant negative relationship between36
37 294 description date and body mass on continental regions, with larger-bodied species38
39 295 again generally described earlier (est=-0.0031, S.E.=0.0014, t-value=-2.141, $p<0.05$;40
41 296 d.f.=41, $R^2=0.10$, lambda=1.00), and a non-significant relationship on islands (est=-42
43 297 0.00021, S.E.=0.00050, t-value=-0.410, $p>0.05$; d.f.=103, $R^2=0.00163$, lambda=0.973)44
45 298 (figure 2). Reanalysis following removal of major outliers did not change the results46
47 299 (electronic supplementary material, table S5).48
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53 **(b) Continental zooarchaeological record**54
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3 302 The number of zooarchaeological records varied hugely between species in our dataset,
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5 303 from nearly 4000 records for red deer (*Cervus elaphus*) to fewer than 20 records for
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7 304 wolverine (*Gulo gulo*) (electronic supplementary material, table S3). We found a
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9 305 positive but non-significant relationship between zooarchaeological abundance and
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11 306 body mass (0.21 ± 0.11 , $p = 0.07$), and a significant relationship between abundance and
12
13 307 trophic level (1.45 ± 0.39 , $p < 0.01$), with herbivores having a higher number of records
14
15 308 than carnivores. Models with trophic level as the single explanatory variable had the
16
17 309 highest explanatory power, both in our original models and in models that included
18
19 310 species as a random factor (figure 3a, electronic supplementary material, table S4).

20
21
22 311 Modern mammalian population density was significantly negatively associated with
23
24 312 body mass in the global dataset (-0.27 ± 0.09 , $p < 0.01$) (figure 3c), and was negatively
25
26 313 but not quite significantly associated with body mass in the North American data subset
27
28 314 (-0.32 ± 0.16 , $p = 0.054$) (figure 3b). Confidence intervals of slopes for the Holocene
29
30 315 zooarchaeological and North American datasets overlapped, but did not overlap
31
32 316 between the Holocene zooarchaeological and global datasets (electronic supplementary
33
34 317 material, table S4), indicating that these two datasets were significantly different. When
35
36 318 the data were subdivided by trophic guild, we found a significant negative body mass-
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38 319 abundance relationship across all modern mammal population density datasets (figure
39
40 320 3b-c, electronic supplementary material, table S4).

41
42 321 We found no significant body-mass abundance relationships across either trophic
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44 322 level subset of Holocene data. However, for herbivores the slope was negative and 95%
45
46 323 confidence intervals overlapped with modern herbivore datasets, indicating that it was
47
48 324 not significantly different. In contrast, for carnivores the slope was positive and did not
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50 325 overlap with modern carnivore datasets, indicating that it had a significantly different
51
52 326 relationship (figure 3a-c, electronic supplementary material, table S4).

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3 327 The number of zooarchaeological records varied considerably between countries
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5 328 (figure 4). However, when country size was controlled for, we found no association
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7
8 329 between the density of zooarchaeological records and a country's GDP per capita (0.37
9
10 330 ± 0.31 , $p = 0.24$) or average elevation (-0.20 ± 0.16 , $p = 0.21$). Elevation profiles showed
11
12 331 that zooarchaeological records were present up to 2000 metres above sea level (m.a.s.l.)
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14
15 332 but were generally absent at higher elevations (electronic supplementary material,
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17 333 figure S2). Whilst the overall elevation profile for Europe reaches 3000 m.a.s.l., over
18
19 334 95% of the continent is below 2000 m.a.s.l., indicating that the two datasets were not
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21
22 335 significantly different.

23
24 336 The precision of dating for records across the Holocene was also temporally
25
26 337 uneven. Overall, the average date range for each zooarchaeological record became
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28 338 narrower closer to the present, with this shift becoming particularly marked around 0
29
30 339 BC/AD (figure 5). Accumulation of successive records across the Holocene was not
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32
33 340 linear over time, showing a low rate of accumulation during the early Holocene,
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36 341 relatively steady accumulation for much of the mid-Holocene, and accelerating in the
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38 342 later Holocene close to the present.

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42 43 344 **4. Discussion**

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46 47 48 346 **(a) Bias in Holocene mammal baselines and extinction risk**

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50 347 Our analysis of description dates for globally extinct mammals demonstrates that we
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52 348 still have an incomplete and biased understanding of mammalian extinctions and past
53
54 349 levels of biodiversity even for the Holocene, the most recent interval of geological time,
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56 350 with numbers of ongoing new species descriptions continuing to increase over time.
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58 351 Indeed, the discovery curve of recently extinct mammals shows a nearly exponential

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3 352 increase from the 1950s onwards, rather than any signs of levelling off close to the
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5 353 present. This pattern contrasts markedly with the global trajectory of species
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8 354 descriptions for extant mammals over recent decades, which continue to increase but at
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10 355 a relatively reduced rate compared to the total number of extant species already known
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12 356 [43]. Estimating the number of recently extinct mammal species that remain to be
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14
15 357 discovered and described is therefore an important research goal. However,
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17 358 extrapolating the number of undescribed species from a temporal pattern of past
18
19 359 species descriptions is associated with large margins of error unless the inventory of a
20
21 360 group is largely complete and beginning to level off over time, which is demonstrably
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23
24 361 not the case for recently extinct mammals [44,45]. Rapid advancements in ancient DNA
25
26 362 and genomics have also facilitated the identification of new species based on fossil
27
28 363 material and museum specimens in recent years, and these techniques will doubtless
29
30 364 only increase our ability to describe new species into the future [46]. Overall, it
31
32
33 365 therefore remains surprisingly challenging to make even basic assumptions about past
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35 366 patterns of diversity, biogeography, community composition, and severity and dynamics
36
37 367 of past human impacts for one of the most-studied and ecologically significant animal
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39 368 groups.

42
43 369 Our analysis also highlights that we have a poorer understanding of past diversity
44
45 370 of recently extinct small-bodied mammals, notably rodents and bats, compared to
46
47 371 larger-bodied species (e.g. carnivores, artiodactyls, perissodactyls, proboscideans).
48
49 372 Small mammals continue to be described regularly from the Holocene palaeontological
50
51 373 and zooarchaeological records, whilst the largest species were mostly described by AD
52
53 374 1900. The earlier discovery of larger-bodied mammals in the Holocene record is
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55 375 associated in part with taphonomic processes that preferentially select for the
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57 376 deposition and survival of larger skeletal elements [15]. It also probably reflects the
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3 377 common historical preference for taxonomists to describe larger, 'charismatic' species
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5 378 first for scientific kudos [7,20]. Even without explicit size-based biases in fossil
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8 379 preservation or description, specific targeted sampling strategies such as fine-mesh
9
10 380 sieving are needed to recover remains of smaller vertebrates and invertebrates, and
11
12 381 these were not widely employed until the latter half of the twentieth century [47]. Once
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14 382 recovered, smaller bones and teeth can also be more difficult to identify to species level
15
16 383 [48], so that the quality of described data can easily be biased towards larger species in
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18
19 384 Holocene faunal assemblages.

21
22 385 The extinct Holocene mammal fauna currently consists largely of insular species,
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24 386 with geographic hotspots of known global Holocene species extinctions including the
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26 387 Caribbean, Madagascar and insular Mediterranean, and with the vast majority of insular
27
28 388 species (nearly 82%) only described during the last 100 years. However, we only found
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30 389 a significant relationship between body mass and description date for continental
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32 390 regions, and not for insular regions. On islands, this lack of significance is at least partly
33
34 391 attributable to the general pattern of reduced body masses observed in extinct and
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36 392 extant insular mammals, associated with ecological resource limitation driving dwarfing
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38 393 of large-bodied lineages under the 'island rule' [49]. By contrast, continental regions
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40 394 harboured a wider range of body masses, with the largest generally being found and
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42 395 described first. Many species may also have been described later from insular regions
43
44 396 due to their increased geographic remoteness and inaccessibility, and because many
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46 397 major island systems are located in the tropics where preservation of long-term
47
48 398 environmental archives is generally poorer and more recently developed techniques
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50 399 can be required to identify and date regional faunal remains [50,51]. Tropical species
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52 400 also tend to exhibit smaller geographic range sizes, which has also been shown to be a
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54 401 negative correlate of description date in mammals [52].
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3 402 Small body size has been associated with an overall lower risk of extinction for
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5 403 mammals in both the past [5] and the present [53,54], principally because smaller-
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7 404 bodied species have higher reproductive rates that enable faster population growth and
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9 405 recovery [53]. However, this pattern may be more complicated within specific
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11 406 geographical areas and ecoregions, with higher levels of recent extinction and current
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13 407 risk observed in the smallest-bodied species for some regional faunas (e.g. Australia,
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15 408 Caribbean) [53–55], and it has been recognised that the very smallest species in some
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17 409 vertebrate groups may be at higher risk of extinction due to small geographic range
18
19 410 sizes [58]. Our analyses indicate that our baseline understanding of mammalian
20
21 411 diversity remains incomplete at both global and regional levels, with our knowledge of
22
23 412 the extent of recent small mammal extinctions in particular likely to be underestimated
24
25 413 due to incomplete and biased sampling. This bias in our baseline hinders our ability to
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27 414 compare recent levels of species losses and assess relative patterns of extinction risk
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29 415 across fundamental gradients of mammalian diversity and ecology.
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38 417 **(b) Bias in zooarchaeological data through space and time**

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40 418 Bias in species occurrence data has been studied extensively in ecological [59],
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42 419 historical [60,61] and palaeontological [62,63] datasets; however, our analysis
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44 420 represents, to our knowledge, the first attempt to directly quantify multiple sources of
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46 421 bias in a large zooarchaeological dataset. Due to the fact that patterns of human
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48 422 influence may differ between zooarchaeological deposits, we note that our analysis
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50 423 relates specifically to large mammals for the European Holocene, and may not
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52 424 necessarily reflect patterns of bias in other zooarchaeological datasets.
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57 425 Our results show that body mass scales inversely to population density in natural
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59 426 populations of large mammals, a relationship that has also been demonstrated
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3 427 elsewhere [64,65]. We would therefore expect fewer large-bodied species to be present
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6 428 in the zooarchaeological record if zooarchaeological abundance reflected underlying
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8 429 patterns of ecological abundance and rarity in sampled source communities. By
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10 430 contrast, abundance increases with higher body mass in our zooarchaeological dataset;
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12 431 although this relationship was not significant, its slope did differ significantly from that
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14 432 of the global ecological mammal dataset. The power of body mass-abundance
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16 433 relationships in the North American and zooarchaeological datasets may have been
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18 434 reduced by the small sample sizes and smaller range of body masses available for
19
20 435 analysis, with paucity of data points leading to a Type 2 error, a problem that has also
21
22 436 been noted in previous large-scale analyses of fossil mammal assemblages [66]. The
23
24 437 disproportionately higher abundance of large-bodied mammals in the
25
26 438 zooarchaeological record probably reflects preferential human hunting of these species.
27
28 439 The likelihood that larger-bodied vertebrates have been a primary focus of prehistoric
29
30 440 human hunting effort is supported by the pattern of terrestrial and insular extinctions
31
32 441 following human arrival or technological change across the globe during the late
33
34 442 Quaternary [7,67], and wild megafaunal vertebrates continue to be overharvested for
35
36 443 consumption in many regions today [68]. Whilst the increased vulnerability of large-
37
38 444 bodied mammals to humans is also strongly related to their slower reproductive life
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40 445 histories, these species are highly detectable and non-arboreal and tend to be diurnal,
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42 446 and so are likely to have come into contact with humans relatively frequently [17].
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50 447 However, the abundance-body mass relationship observed in our zooarchaeological
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52 448 dataset was also confounded by trophic level, which was the only consistently
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54 449 significant predictor of zooarchaeological abundance across all models, with herbivores
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56 450 more abundant than carnivores. This almost certainly reflects the increased likelihood
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58 451 of prehistoric humans to hunt herbivores for subsistence, as well as the higher available
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3 452 biomass of large herbivores in ecosystems compared to carnivore biomass.
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6 453 Interestingly, the scaling of abundance and body mass in the zooarchaeological record
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8 454 also differs between trophic groups; small herbivores were more abundant than larger
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10 455 herbivores, a pattern shown in natural populations, whereas large carnivores were
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12 456 more abundant than smaller carnivores, which is significantly different from the pattern
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15 457 seen in natural populations [35]. This unexpected finding may reflect the fact that
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17 458 because herbivores were more heavily exploited overall for subsistence, humans were
18
19 459 less discriminate and hunted all body size classes opportunistically, leading natural
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21
22 460 patterns of relative abundance to be reflected in the zooarchaeological record. The
23
24 461 particular dominance of species such as red deer and wild boar (*Sus scrofa*) in Europe's
25
26 462 zooarchaeological record may also be partly due to forest laws that afforded protection
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28
29 463 to these 'noble game' species for recreational hunting, e.g. in medieval Britain [69]. By
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31 464 contrast, humans were less likely to come into contact with smaller carnivores and
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33 465 more likely to see large carnivores as competitors for both wild prey and domestic
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35 466 livestock, and so might have disproportionately targeted these species. Indeed, large
36
37 467 carnivores are more likely to be involved in human-wildlife conflict than smaller
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39 468 carnivores for these reasons today [70]. Large carnivores such as wolf (*Canis lupus*) and
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41 469 brown bear (*Ursus arctos*) were also the focus of recreational hunting in medieval
42
43 470 Europe [69].

47
48 471 Although the spatial spread of zooarchaeological data was uneven across Europe,
49
50 472 we found that the relative wealth of a country did not influence research output across
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52 473 European countries once geographic size was taken into account. This pattern may
53
54 474 partly reflect the fact that archaeology is a fairly international endeavour and therefore
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56 475 academics will often fund, carry out, or collaborate on excavations in countries other
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58 476 than their own. For example, within our study area there is a strong international

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3 477 academic presence in Anatolian archaeology [71] and parts of the Caucasus [72].
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5 478 Furthermore, even where research funds are reduced, countries can nonetheless have
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8 479 strong traditions of academic research and achieve relatively high research outputs
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10 480 through the efforts of only a few researchers. A final reason may be that the literature
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12 481 searches carried out to compile the database included grey literature in numerous
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14 482 European languages as well as research published in international journals, and
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16 483 therefore reached a range of research repositories beyond those dependent on or linked
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18 484 to higher levels of funding [29,73]. This finding is therefore a strong argument for
19
20 485 employing exhaustive and thorough data collection protocols when compiling species
21
22 486 occurrence datasets based on zooarchaeological assemblages in order to minimise
23
24 487 sources of researcher bias. There is also increasing availability of large, open-access
25
26 488 databases of zooarchaeological and palaeontological records that will continue to
27
28 489 facilitate the incorporation of long-term archives into biodiversity assessments [74].
29
30 490 However, as these datasets are usually derived from multiple and often secondary
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32 491 sources, great care is needed in auditing and curating in order to minimise the use of
33
34 492 erroneous or poor-quality data [75]. We also found no elevational bias in the spatial
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36 493 spread of zooarchaeological data across Europe. This may be due to the fact that many
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38 494 prehistoric human populations are known to have lived at high altitudes in Europe (and
39
40 495 elsewhere globally), and that archaeological research is increasingly conducted in
41
42 496 remote and hard-to-access landscapes including at higher elevations [76].

49
50 497 The precision of dating for zooarchaeological records, represented by the length of
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52 498 available date ranges, also varied across the Holocene, providing a further source of bias
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54 499 in our zooarchaeological dataset and influencing its ability to make inferences about
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56 500 past biodiversity baselines and human impacts. This temporal variation partly reflects
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58 501 the mix of absolute and relative methods used to date records; whereas the majority of

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2
3 502 our zooarchaeological records were indirectly dated, direct radiocarbon dates are
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5 503 generally associated with shorter ranges. However, in general we found that
6
7 504 zooarchaeological records were assigned increasingly specific dates nearer to the
8
9 505 present. This finding probably reflects the fact that archaeologically-defined time
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11 506 periods (e.g. Mesolithic, Neolithic, Bronze Age) tend to denote changes in human
12
13 507 technology and subsistence, and so become narrower towards the present due to the
14
15 508 general acceleration of technological change through time, with archaeologists
16
17 509 increasingly confident in constructing chronologies and assigning dates to
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19 510 archaeological material nearer the present. Ideally zooarchaeological records would be
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21 511 directly radiocarbon dated to ensure that chronologies for investigating faunal turnover
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23 512 and extinction were comparably accurate and consistent across datasets. However,
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25 513 given the sheer quantity of data generated from archaeological sites and the costs
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27 514 involved in absolute dating, this is unfortunately still rarely a realistic option.
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33 515 Our results also reveal periods of increased accumulation of Holocene
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35 516 zooarchaeological records over time. This pattern might reflect periods of prehistoric
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37 517 human population increase. For example, there is a notable increase in our
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39 518 accumulation curve from ~AD 500 to AD 1200, coincident with the Medieval period,
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41 519 during which there was an estimated six-fold increase in human population in Europe
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43 520 and evidence for associated large-scale forest clearance [77]. Increased pressure on
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45 521 wildlife populations could therefore potentially have led to increased numbers of
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47 522 zooarchaeological records found within these sites. Conversely, it has been
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49 523 demonstrated that younger components will always be more abundant than older
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51 524 components in the archaeological record, due to increased taphonomic destruction of
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53 525 older faunal remains and greater detectability of stratigraphically higher samples [78].
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55 526 These temporal trends therefore indicate that we have more abundant and precise
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3 527 records of faunal occurrence nearer the present, with important implications for using
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5 528 zooarchaeological datasets of faunal records through time to reconstruct biodiversity
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8 529 change.

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11 12 531 **5. Disentangling bias from reality in the Holocene faunal record**

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15 532 Our combined analyses demonstrate that bias is widespread, with sources and patterns
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17 533 of bias varying across taxonomic, spatial and temporal scales in the Holocene faunal
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19 534 record. Size bias is a particularly complex issue to resolve, especially when using the
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21
22 535 recent faunal record to investigate species population dynamics and extinctions at both
23
24 536 local and global scales. For example, large mammals tend to be well-identified and
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26 537 overrepresented in the Holocene fossil and zooarchaeological records relative to their
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28 538 status in natural source populations, whereas our knowledge of many small mammals is
29
30 539 generally more incomplete or even altogether unknown, providing a biased
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32 540 understanding of extinction risk across different taxa. In contrast, modern-day
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34 541 abundance has been shown to be a strong predictor of abundance in the Holocene
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36 542 faunal record for other vertebrate groups [18]. Sources and patterns of bias in Holocene
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38 543 faunal datasets therefore need to be carefully identified and quantified on a case-by-
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41 544 case basis, particularly accounting for potential variation in bias between different
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43 545 taxonomic or ecological groups, and considering appropriate spatial extents, timescales,
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45 546 and types of faunal data that are most relevant to the specific parameters of different
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48 547 research questions.

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51 548 However, whilst this study has addressed potential limitations associated with the
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53 549 use of recent fossil and zooarchaeological data “at face value”, we also recognise that
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55 550 Holocene faunal data can be a reliable and important indicator of biodiversity change
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57
58 551 when bias is accounted for. Indeed, we have previously used the zooarchaeological

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3 552 dataset studied above to reconstruct mammalian range change across the Holocene in
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5 553 Europe, and by controlling for sample size variation across time and between different
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8 554 species we were able to reconstruct the dynamics of range declines and identify
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10 555 taxonomic variation in vulnerability or resilience to human impacts over time [4]. These
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12 556 data provide the only available insights into a wide range of important questions
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14 557 surrounding past environmental and ecological conditions and how they have changed
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17 558 through time in response to different stressors or drivers, and so must remain an
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20 559 essential component of the toolkit available for biodiversity research.
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24 561 **Data accessibility.** The datasets supporting this paper are available in the
25
26 562 supplementary materials.

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28
29 563 **Authors' contributions.** J.J.C. and S.T.T. designed the research and coordinated data
30
31 564 collection; J.J.C. and B.C. analysed the data; and J.J.C. and S.T.T. wrote the manuscript.

32
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34
35
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42
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44
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46
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51 52 573 **REFERENCES**

- 53
54 574 1. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014 Defaunation in the
55
56 575 Anthropocene. *Science* **345**, 401–406. (doi:10.1126/science.1251817)

- 1
2
3 576 2. Ceballos G, Ehrlich PR, Dirzo R. 2017 Biological annihilation via the ongoing sixth
4
5 577 mass extinction signaled by vertebrate population losses and declines. *Proceedings*
6
7 578 *of the National Academy of Sciences* **114**, E6089–E6096.
9
10 579 (doi:10.1073/pnas.1704949114)
11
12
13 580 3. Faurby S, Svenning J-C. 2015 Historic and prehistoric human-driven extinctions
14
15 581 have reshaped global mammal diversity patterns. *Diversity and Distributions* **21**,
16
17 582 1155–1166. (doi:10.1111/ddi.12369)
18
19
20
21 583 4. Fritz SA, Bininda-Emonds ORP, Purvis A. 2009 Geographical variation in predictors
22
23 584 of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* **12**,
24
25 585 538–549. (doi:10.1111/j.1461-0248.2009.01307.x)
26
27
28
29 586 5. Turvey ST, Fritz SA. 2011 The ghosts of mammals past: biological and geographical
30
31 587 patterns of global mammalian extinction across the Holocene. *Philosophical*
32
33 588 *Transactions of the Royal Society B: Biological Sciences* **366**, 2564–2576.
34
35 589 (doi:10.1098/rstb.2011.0020)
36
37
38
39 590 6. Martin PS, Klein RG. 1989 *Quaternary Extinctions: A Prehistoric Revolution*.
40
41 591 University of Arizona Press.
42
43
44
45 592 7. Turvey ST. 2009 *Holocene Extinctions*. OUP Oxford.
46
47
48
49 593 8. Benecke N. 1999 *The Holocene history of the European vertebrate fauna: modern*
50
51 594 *aspects of research : workshop, 6th to 9th April 1998, Berlin*. Verlag Marie Leidorf
52
53 595 GmbH.
54
55
56
57
58
59
60

- 1
2
3 596 9. Monjeau JA, Araujo B, Abramson G, Kuperman MN, Laguna MF, Lanata JL. 2017 The
4
5 597 controversy space on Quaternary megafaunal extinctions. *Quaternary International*
6
7 598 **431**, 194–204. (doi:10.1016/j.quaint.2015.10.022)
9
10
11 599 10. Stuart AJ. 2015 Late Quaternary megafaunal extinctions on the continents: a short
12
13 600 review. *Geological Journal* **50**, 338–363. (doi:10.1002/gj.2633)
15
16
17 601 11. Roberts N. 2013 *The Holocene: An Environmental History*. John Wiley & Sons.
18
19
20 602 12. Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000 Taphonomy and Paleobiology.
21
22 603 *Paleobiology* **26**, 103–147.
24
25
26 604 13. Reitz EJ, Wing ES. 2008 *Zooarchaeology*. Cambridge University Press.
27
28
29 605 14. Behrensmeyer AK, Western D, Boaz DED. 1979 New perspectives in vertebrate
30
31 606 paleoecology from a recent bone assemblage. *Paleobiology* **5**, 12–21.
32
33 607 (doi:10.1017/S0094837300006254)
35
36
37 608 15. Lyman RL, Lyman C. 1994 *Vertebrate Taphonomy*. Cambridge University Press.
38
39
40 609 16. Carbone Chris, Maddox Tom, Funston Paul J, Mills Michael G.L, Grether Gregory F,
41
42 610 Van Valkenburgh Blaire. 2009 Parallels between playbacks and Pleistocene tar
43
44 611 seeps suggest sociality in an extinct sabretooth cat, *Smilodon*. *Biology Letters* **5**, 81–
45
46 612 85. (doi:10.1098/rsbl.2008.0526)
47
48
49
50
51 613 17. Johnson C. N. 2002 Determinants of loss of mammal species during the Late
52
53 614 Quaternary ‘megafauna’ extinctions: life history and ecology, but not body size.
54
55 615 *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**, 2221–
56
57 616 2227. (doi:10.1098/rspb.2002.2130)
58
59
60

- 1
2
3 617 18. Turvey ST, Blackburn TM. 2011 Determinants of species abundance in the
4
5 618 Quaternary vertebrate fossil record. *Paleobiology* **37**, 537–546.
6
7
8
9 619 19. Barker P. 2003 *Techniques of Archaeological Excavation*. Routledge.
10
11
12 620 20. Alroy J. 2003 Taxonomic Inflation and Body Mass Distributions in North American
13
14 621 Fossil Mammals. *J Mammal* **84**, 431–443. (doi:10.1644/1545-
15
16 622 1542(2003)084<0431:TIABMD>2.0.CO;2)
17
18
19
20 623 21. Stuart AJ, Kosintsev PA, Higham TFG, Lister AM. 2004 Pleistocene to Holocene
21
22 624 extinction dynamics in giant deer and woolly mammoth. *Nature* **431**, 684–689.
23
24 625 (doi:10.1038/nature02890)
25
26
27
28 626 22. Dale Guthrie R. 2006 New carbon dates link climatic change with human
29
30 627 colonization and Pleistocene extinctions. *Nature* **441**, 207–209.
31
32 628 (doi:10.1038/nature04604)
33
34
35
36 629 23. Russell N. 2011 *Social Zooarchaeology: Humans and Animals in Prehistory*.
37
38 630 Cambridge University Press.
39
40
41
42 631 24. Jones KE *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and
43
44 632 geography of extant and recently extinct mammals. *Ecology* **90**, 2648–2648.
45
46 633 (doi:10.1890/08-1494.1)
47
48
49
50 634 25. Alroy J. In press. Small mammals have big tails in the tropics. *Global Ecology and*
51
52 635 *Biogeography*. (doi:10.1111/geb.12912)
53
54
55
56
57
58
59
60

- 1
2
3 636 26. Robuchon M, Faith DP, Julliard R, Leroy B, Pellens R, Robert A, Thévenin C, Véron S,
4
5 637 Pavoine S. 2019 Species splitting increases estimates of evolutionary history at risk.
6
7 638 *Biological Conservation* **235**, 27–35. (doi:10.1016/j.biocon.2019.03.041)
8
9
10
11 639 27. Faurby S, Davis M, Pedersen RØ, Schowanek SD, Antonelli1 A, Svenning J. 2018
12
13 640 PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology* **99**,
14
15 641 2626–2626. (doi:10.1002/ecy.2443)
16
17
18
19 642 28. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018 *caper*:
20
21 643 *Comparative Analyses of Phylogenetics and Evolution in R*. See [https://CRAN.R-](https://CRAN.R-project.org/package=caper)
22
23 644 [project.org/package=caper](https://CRAN.R-project.org/package=caper).
24
25
26
27 645 29. Crees JJ, Carbone C, Sommer RS, Benecke N, Turvey ST. 2016 Millennial-scale faunal
28
29 646 record reveals differential resilience of European large mammals to human impacts
30
31 647 across the Holocene. *Proceedings of the Royal Society B: Biological Sciences* **283**,
32
33 648 20152152. (doi:10.1098/rspb.2015.2152)
34
35
36
37 649 30. Sommer RS, Benecke N, Lõugas L, Nelle O, Schmölcke U. 2011 Holocene survival of
38
39 650 the wild horse in Europe: a matter of open landscape? *Journal of Quaternary Science*
40
41 651 **26**, 805–812. (doi:10.1002/jqs.1509)
42
43
44
45 652 31. Sykes NJ, Baker KH, Carden RF, Higham TFG, Hoelzel AR, Stevens RE. 2011 New
46
47 653 evidence for the establishment and management of the European fallow deer (*Dama*
48
49 654 *dama dama*) in Roman Britain. *Journal of Archaeological Science* **38**, 156–165.
50
51 655 (doi:10.1016/j.jas.2010.08.024)
52
53
54
55
56
57
58
59
60

- 1
2
3 656 32. Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren
4
5 657 PH. 2005 Body size in ecological networks. *Trends in Ecology & Evolution* **20**, 402–
6
7 658 409. (doi:10.1016/j.tree.2005.04.005)
8
9
10
11 659 33. Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA,
12
13 660 Brown JH, Haskell JP. 2003 Body Mass of Late Quaternary Mammals. *Ecology* **84**,
14
15 661 3403–3403. (doi:10.1890/02-9003)
16
17
18
19 662 34. Linden MJM. 2019 *AICcmodavg: Model Selection and Multimodel Inference Based on*
20
21 663 *(Q)AIC(c)*. See <https://CRAN.R-project.org/package=AICcmodavg>.
22
23
24
25 664 35. Damuth J. 1987 Interspecific allometry of population density in mammals and other
26
27 665 animals: the independence of body mass and population energy-use. *Biol J Linn Soc*
28
29 666 **31**, 193–246. (doi:10.1111/j.1095-8312.1987.tb01990.x)
30
31
32
33 667 36. Blackburn TM, Gaston KJ. 1997 A Critical Assessment of the Form of the Interspecific
34
35 668 Relationship between Abundance and Body Size in Animals. *Journal of Animal*
36
37 669 *Ecology* **66**, 233–249. (doi:10.2307/6025)
38
39
40
41 670 37. Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D. 2018 *MASS: Support*
42
43 671 *Functions and Datasets for Venables and Ripley's MASS*. See <https://CRAN.R->
44
45 672 [project.org/package=MASS](https://CRAN.R-project.org/package=MASS).
46
47
48
49 673 38. Bates D *et al.* 2019 *lme4: Linear Mixed-Effects Models using 'Eigen' and S4*. See
50
51 674 <https://CRAN.R-project.org/package=lme4>.
52
53
54
55 675 39. R Core Team. 2018 *R: The R Project for Statistical Computing*. Vienna, Austria: R
56
57 676 Foundation for Statistical Computing. See <https://www.r-project.org/>.
58
59
60

- 1
2
3 677 40. Panahi H. 2010 Size of a Country, Openness and the Economic Growth. *World*
4
5 678 *Academy of Science, Engineering and Technology* **42**, 686–692.
6
7
8
9 679 41. World Bank: GDP (Current US\$). See
10
11 680 <https://data.worldbank.org/indicator/NY.GDP.MKTP.CD?page=2> (accessed on 15
12
13 681 March 2013).
14
15
16
17 682 42. WorldClim - Global Climate Data | Free climate data for ecological modeling and GIS.
18
19 683 See <http://www.worldclim.org/> (accessed on 15 March 2013).
20
21
22
23 684 43. Reeder DM, Helgen KM, Wilson DE. 2007 *Global trends and biases in new mammal*
24
25 685 *species discoveries*. Lubbock, TX: Museum of Texas Tech University,
26
27 686 (doi:10.5962/bhl.title.156951)
28
29
30
31 687 44. Bebber Daniel P, Marriott Francis H.C, Gaston Kevin J, Harris Stephen A, Scotland
32
33 688 Robert W. 2007 Predicting unknown species numbers using discovery curves.
34
35 689 *Proceedings of the Royal Society B: Biological Sciences* **274**, 1651–1658.
36
37 690 (doi:10.1098/rspb.2007.0464)
38
39
40
41 691 45. Nabout JC, da Silva Rocha B, Carneiro FM, Sant'Anna CL. 2013 How many species of
42
43 692 Cyanobacteria are there? Using a discovery curve to predict the species number.
44
45 693 *Biodivers Conserv* **22**, 2907–2918. (doi:10.1007/s10531-013-0561-x)
46
47
48
49 694 46. Herrmann B, Hummel S. 2012 *Ancient DNA: Recovery and Analysis of Genetic*
50
51 695 *Material from Paleontological, Archaeological, Museum, Medical, and Forensic*
52
53 696 *Specimens*. Springer Science & Business Media.
54
55
56
57
58
59
60

- 1
2
3 697 47. Clason AT, Prummel W. 1977 Collecting, sieving and archaeozoological research.
4
5 698 *Journal of Archaeological Science* **4**, 171–175. (doi:10.1016/0305-4403(77)90064-
6
7
8 699 4)
9
10
11 700 48. Klein RG, Cruz-Uribe K. 1984 *The Analysis of Animal Bones from Archeological Sites*.
12
13 701 University of Chicago Press.
14
15
16
17 702 49. Burness GP, Diamond J, Flannery T. 2001 Dinosaurs, dragons, and dwarfs: The
18
19 703 evolution of maximal body size. *PNAS* **98**, 14518–14523.
20
21 704 (doi:10.1073/pnas.251548698)
22
23
24
25 705 50. Brace Selina, Turvey Samuel T., Weksler Marcelo, Hoogland Menno L. P., Barnes Ian.
26
27 706 2015 Unexpected evolutionary diversity in a recently extinct Caribbean mammal
28
29 707 radiation. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20142371.
30
31 708 (doi:10.1098/rspb.2014.2371)
32
33
34
35 709 51. Turvey S.T, Oliver J.R, Narganes Storde Y.M, Rye P. 2007 Late Holocene extinction of
36
37 710 Puerto Rican native land mammals. *Biology Letters* **3**, 193–196.
38
39 711 (doi:10.1098/rsbl.2006.0585)
40
41
42
43 712 52. Collen B, Purvis A, Gittleman JL. 2004 Biological correlates of description date in
44
45 713 carnivores and primates. *Global Ecology and Biogeography* **13**, 459–467.
46
47 714 (doi:10.1111/j.1466-822X.2004.00121.x)
48
49
50
51 715 53. Cardillo M. 2003 Biological determinants of extinction risk: why are smaller species
52
53 716 less vulnerable? *Animal Conservation forum* **6**, 63–69.
54
55 717 (doi:10.1017/S1367943003003093)
56
57
58
59
60

- 1
2
3 718 54. Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme
4
5 719 CDL, Purvis A. 2005 Multiple Causes of High Extinction Risk in Large Mammal
6
7 720 Species. *Science* **309**, 1239–1241. (doi:10.1126/science.11116030)
8
9
10
11 721 55. Johnson CN, Isaac JL. 2009 Body mass and extinction risk in Australian marsupials:
12
13 722 The ‘Critical Weight Range’ revisited. *Austral Ecology* **34**, 35–40.
14
15 723 (doi:10.1111/j.1442-9993.2008.01878.x)
16
17
18
19 724 56. Chisholm RA, Taylor R. 2010 Body size and extinction risk in Australian mammals:
20
21 725 An information-theoretic approach. *Austral Ecology* **35**, 616–623.
22
23 726 (doi:10.1111/j.1442-9993.2009.02065.x)
24
25
26
27 727 57. Hansford J, Nuñez-Miño JM, Young RP, Brace S, Brocca JL, Turvey ST. 2012
28
29 728 Taxonomy-testing and the ‘Goldilocks Hypothesis’: morphometric analysis of
30
31 729 species diversity in living and extinct Hispaniolan hutias. *Systematics and*
32
33 730 *Biodiversity* **10**, 491–507. (doi:10.1080/14772000.2012.748697)
34
35
36
37 731 58. Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ. 2017
38
39 732 Extinction risk is most acute for the world’s largest and smallest vertebrates.
40
41 733 *Proceedings of the National Academy of Sciences* **114**, 10678–10683.
42
43 734 (doi:10.1073/pnas.1702078114)
44
45
46
47 735 59. Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP. 2006 Tradeoffs of
48
49 736 different types of species occurrence data for use in systematic conservation
50
51 737 planning. *Ecology Letters* **9**, 1136–1145. (doi:10.1111/j.1461-0248.2006.00970.x)
52
53
54
55
56
57
58
59
60

- 1
2
3 738 60. Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K, Mace GM.
4
5 739 2010 Distorted Views of Biodiversity: Spatial and Temporal Bias in Species
6
7 740 Occurrence Data. *PLoS Biology* **8**, e1000385. (doi:10.1371/journal.pbio.1000385)
8
9
10
11 741 61. Monsarrat S, Kerley GIH. 2018 Charismatic species of the past: Biases in reporting of
12
13 742 large mammals in historical written sources. *Biological Conservation* **223**, 68–75.
14
15 743 (doi:10.1016/j.biocon.2018.04.036)
16
17
18
19 744 62. Smith AB. 2007 Intrinsic versus extrinsic biases in the fossil record: contrasting the
20
21 745 fossil record of echinoids in the Triassic and early Jurassic using sampling data,
22
23 746 phylogenetic analysis, and molecular clocks. *Paleobiology* **33**, 310–323.
24
25 747 (doi:10.1666/06073.1)
26
27
28
29 748 63. Benton MJ, Dunhill AM, Lloyd GT, Marx FG. 2011 Assessing the quality of the fossil
30
31 749 record: insights from vertebrates. *Geological Society, London, Special Publications*
32
33 750 **358**, 63–94. (doi:10.1144/SP358.6)
34
35
36
37 751 64. Damuth J. 1981 Population density and body size in mammals. *Nature* **290**, 699–
38
39 752 700. (doi:10.1038/290699a0)
40
41
42
43 753 65. Cotgreave P. 1993 The relationship between body size and population abundance in
44
45 754 animals. *Trends in Ecology & Evolution* **8**, 244–248. (doi:10.1016/0169-
46
47 755 5347(93)90199-Y)
48
49
50
51 756 66. Jernvall J, Fortelius M. 2002 Common mammals drive the evolutionary increase of
52
53 757 hypsodonty in the Neogene. *Nature* **417**, 538–540. (doi:10.1038/417538a)
54
55
56
57 758 67. Smith FA, Smith REE, Lyons SK, Payne JL. 2018 Body size downgrading of mammals
58
59 759 over the late Quaternary. *Science* **360**, 310–313. (doi:10.1126/science.aao5987)
60

- 1
2
3 760 68. Ripple WJ *et al.* 2019 Are we eating the world's megafauna to extinction?
4
5 761 *Conservation Letters* **0**, e12627. (doi:10.1111/conl.12627)
6
7
8
9 762 69. Ashby SP. 2002 The role of zooarchaeology in the interpretation of socioeconomic
10
11 763 status: a discussion with reference to Medieval Europe. *Archaeological Review from*
12
13 764 *Cambridge* , 37–59.
14
15
16
17 765 70. Ripple WJ *et al.* 2014 Status and Ecological Effects of the World's Largest Carnivores.
18
19 766 *Science* **343**, 1241484. (doi:10.1126/science.1241484)
20
21
22
23 767 71. Zeder MA. 2006 Archaeozoology in Southwest Asia: A Status Report Based on the
24
25 768 Eighth Meeting of the Archaeozoology of Southwest Asia and Adjacent Areas
26
27 769 Working Group 2006 (Lyon, June 28 th -july 1 st 2006). *Paléorient* **32**, 137–147.
28
29
30
31 770 72. Chataigner C. 1995 La Transcaucasie au Néolithique et au Chalcolithique. British
32
33 771 Archaeological Reports International Series 624. Tempus Reparatum, Oxford.
34
35
36
37 772 73. Crees JJ. 2013 Dynamics of large mammal range shifts and extinction: evidence from
38
39 773 the Holocene record of Europe. Imperial College London; Zoological Society of
40
41 774 London.
42
43
44
45 775 74. Wolniewicz P. 2009 Easily-accessible digital palaeontological databases-a new
46
47 776 perspective for the storage of palaeontological information. *Geologos* **15**, 181–188.
48
49 777 (doi:10.2478/v10118-009-0002-1)
50
51
52
53 778 75. Lister AM, Stuart AJ. 2013 Extinction chronology of the woolly rhinoceros
54
55 779 *Coelodonta antiquitatis*: reply to Kuzmin. *Quaternary Science Reviews* **62**, 144–146.
56
57 780 (doi:10.1016/j.quascirev.2012.10.039)
58
59
60

- 1
2
3 781 76. Stirn M. 2014 Why All the Way Up There? *Mountain and High-Altitude Archaeology*.
4
5 782 *Special Issue of the SAA Archaeological Record* **14**, 7–10.
6
7
8
9 783 77. Williams M. 2000 Dark ages and dark areas: global deforestation in the deep past.
10
11 784 *Journal of Historical Geography* **26**, 28–46. (doi:10.1006/jhge.1999.0189)
12
13
14 785 78. Surovell TA, Brantingham PJ. 2007 A note on the use of temporal frequency
15
16 786 distributions in studies of prehistoric demography. *Journal of Archaeological Science*
17
18 787 **34**, 1868–1877. (doi:10.1016/j.jas.2007.01.003)
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789 **FIGURE LEGENDS**

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29 791 Figure 1. Cumulative and decadal descriptions of extinct Holocene mammal species, AD
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31 792 1750 – AD 2012.
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36 794 Figure 2. The relationship between log body mass of extinct Holocene mammal species
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38 795 and description date, modified by whether they were described from modern or fossil
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40 796 specimens (top row) or whether they originated from continental or insular regions
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42 797 (bottom row). Slopes taken from linear regressions; see main text for regression
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44 798 information.
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48
49 800 Figure 3. Comparison of the abundance-body mass relationship between
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51 801 zooarchaeological and ecological datasets. **(a)** Relationship between proportion of
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53 802 occupied sites in which a species occurs in the zooarchaeological record and log body
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55 803 mass. **(b, c)** Relationship between population density and body mass in the orders
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57 804 Artiodactyla, Carnivora and Perissodactyla, within the body size range 0.5-700 kg from
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3 805 the ecological dataset published by Damuth (1987); data for North America (b) and all
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5 806 continents pooled together (c). Population density and body mass are log transformed.
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7 807 Closed circles represent herbivores, open circles represent carnivores. Dashed lines
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9 808 represent a simple linear regression for herbivore subsets, solid lines represent a
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11 809 simple linear regression for carnivore subsets; see main text for regression information.
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17 811 Figure 4. Map of Europe showing the density of mammalian Holocene zooarchaeological
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19 812 records (Azimuthal Equidistant projection, cell size: 1 x 1 degree).
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23 814 Figure 5. Plot showing (i) ranges of estimated dates for all zooarchaeological records
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25 815 through the Holocene (black bars), and (ii) the accumulation of records in the
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27 816 zooarchaeological record through time (red line). Grey slope denotes a theoretical
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29 817 linear rate of accumulation.
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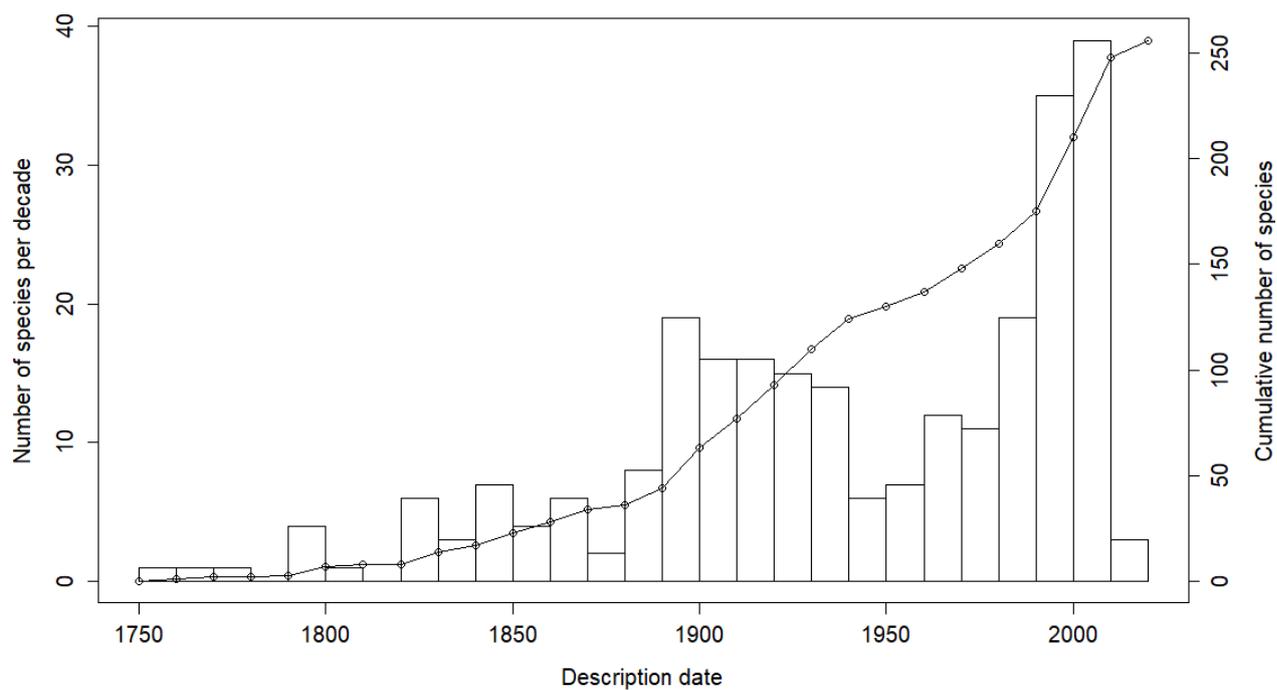


Figure 1. Cumulative and decadal descriptions of extinct Holocene mammal species, AD 1750 - AD 2012.

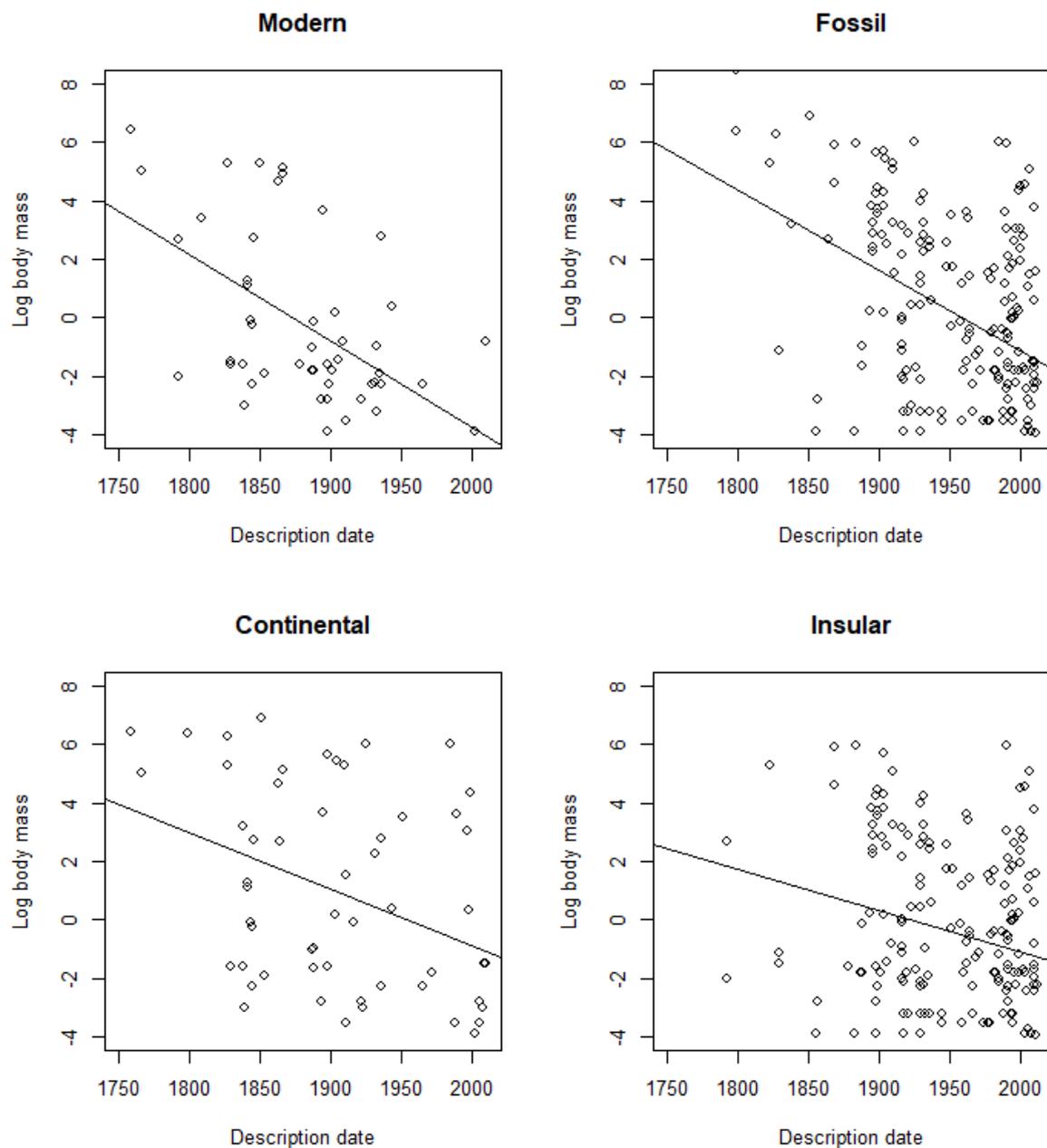
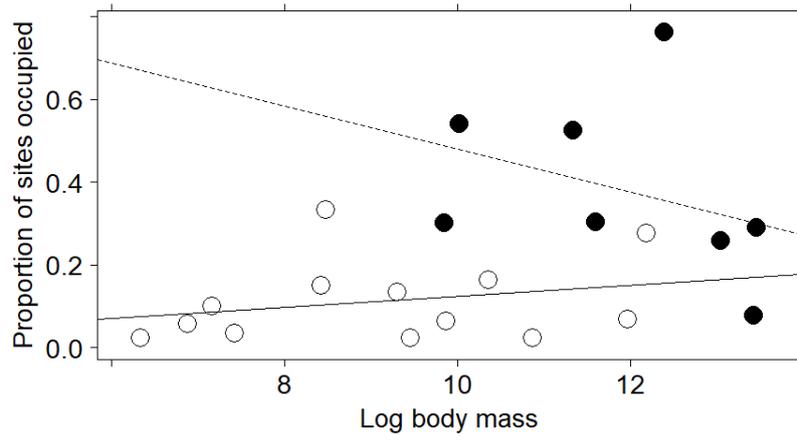


Figure 2. The relationship between log body mass of extinct Holocene mammal species and description date, modified by whether they were described from modern or fossil specimens (top row) or whether they originated from continental or insular regions (bottom row). Slopes taken from linear regressions; see main text for regression information.

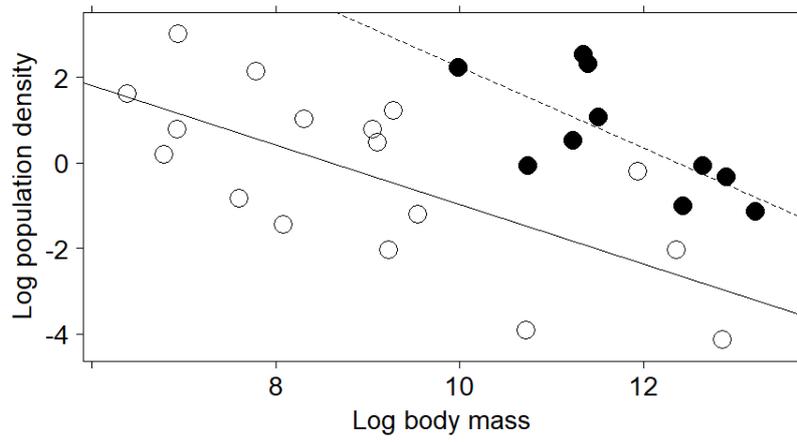
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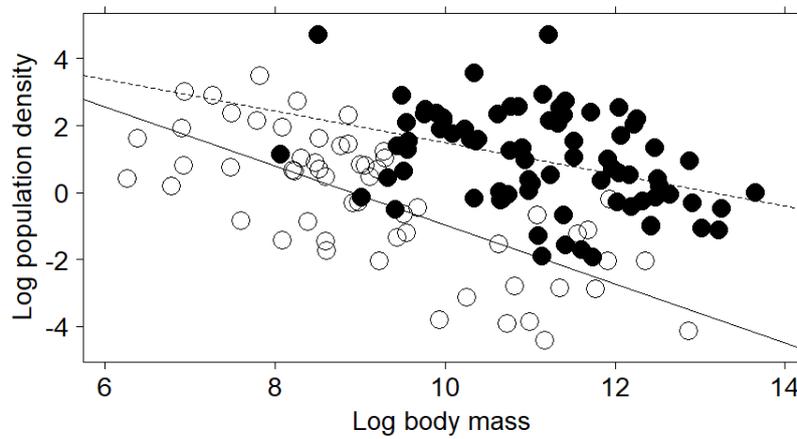
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5 zooarchaeological and ecological datasets. **(a)** Relationship between proportion of
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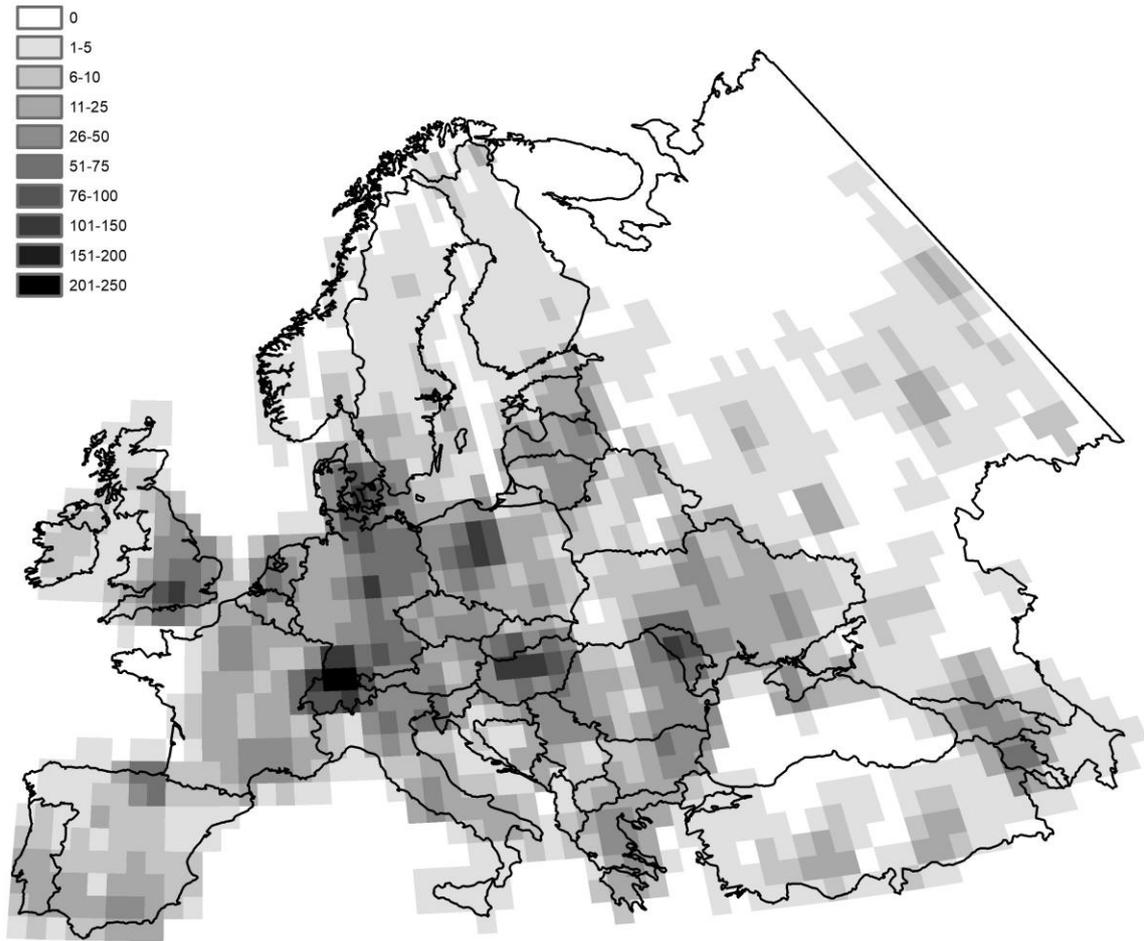


Figure 4. Map of Europe showing the density of mammalian Holocene zooarchaeological records (Azimuthal Equidistant projection, cell size: 1 x 1 degree).

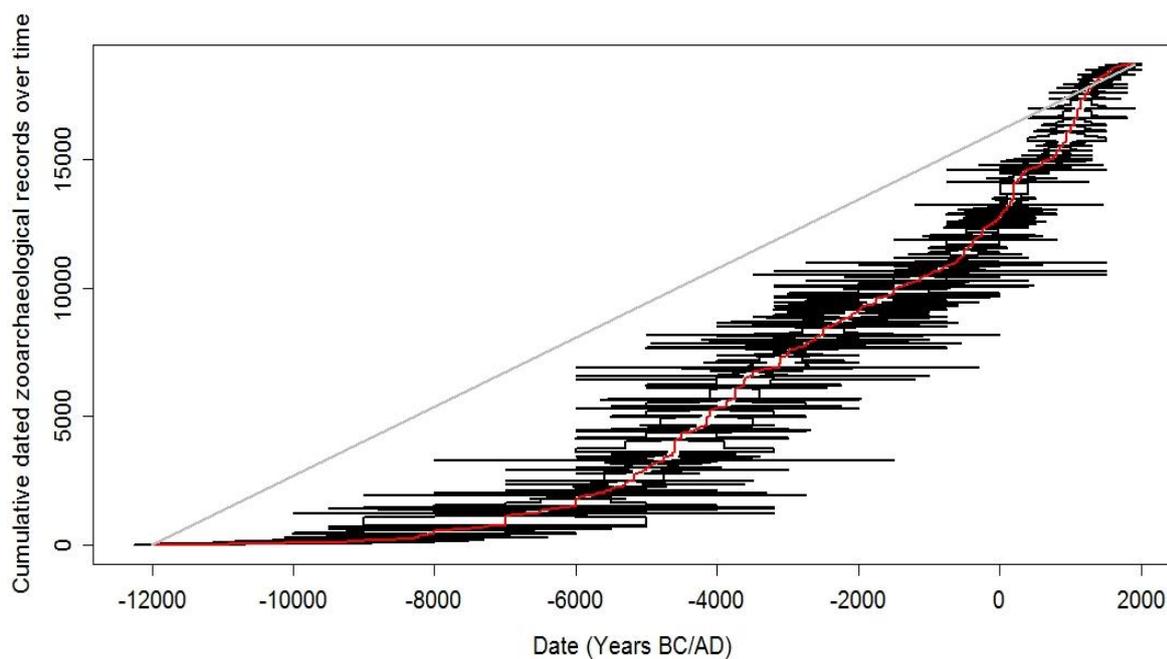


Figure 5. Plot showing (i) ranges of estimated dates for all zooarchaeological records through the Holocene (black bars), and (ii) the accumulation of records in the zooarchaeological record through time (red line). Grey slope denotes a theoretical linear rate of accumulation.