

Anthropogenic predictors of varying Holocene occurrence for Europe's large mammal fauna

Judith M. Ament^{1,2}, Chris Carbone², Jennifer J. Crees³, Robin Freeman² and Samuel T. Turvey^{2,*}

¹Centre for Biodiversity and Environment Research, University College London, London WC1E 6BT, UK

²Institute of Zoology, Zoological Society of London, London NW1 4RY, UK

³Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK

Corresponding author: samuel.turvey@ioz.ac.uk

Abstract. Understanding how species respond to different anthropogenic pressures is essential for conservation planning. The archaeological record has great potential to inform extinction risk assessment by providing evidence on past human-caused biodiversity loss, but identifying specific drivers of past declines from environmental archives has proved challenging. We used 17,684 Holocene zooarchaeological records for 15 European large mammal species together with data on past environmental conditions and anthropogenic activities across Europe, to assess the ability of environmental archives to determine the relative importance of different human pressures in shaping faunal distributions through time. Site occupancy probability showed differing significant relationships with environmental covariates for all species, and nine species also showed significant relationships with anthropogenic covariates (human population density, % cropland, % grazing land). Across-species differences in negative relationships with covariates provide ecological insights for understanding extinction dynamics: some mammals (red deer, aurochs, wolf, wildcat, lynx, pine marten, beech marten) were more vulnerable to past human-environmental interactions, and differing single and synergistic anthropogenic factors influenced likelihood of past occurrence across species. Our results provide new evidence for pre-industrial population fragmentation and depletion in European mammals, and demonstrate the usefulness of historical baselines for understanding species' varying long-term sensitivity to multiple threats.

Keywords: environmental archives, extinction filter, extinction risk, historical baselines, Quaternary extinction, zooarchaeology

1. Introduction

Identifying specific anthropogenic activities that are responsible for population declines and past extinctions, and determining how different species respond to the same pressures, are essential components of evidence-based conservation. Establishing a mechanistic understanding of biodiversity loss can be challenging in systems where humans interact with ecosystems in multiple direct or indirect ways, including hunting, habitat loss and introduction of invasive species, which have varying ecological impacts and selectivity [1,2]. However, identifying key threats is crucial for taxa such as large-bodied mammals that are particularly vulnerable and have already experienced high levels of extinction [3,4].

Although most extinction risk assessments only consider modern baselines, humans have driven biodiversity loss for millennia, with the most vulnerable taxa already lost and different landscapes having experienced varying histories of modification [5]. Modern inferences about risk may therefore be both incomplete and biased due to this 'extinction filter' [6]. Rich long-term environmental archives, notably the Late Quaternary archaeological and fossil records, are available for many systems to permit reconstruction of past species diversity and ecological conditions. These archives have also enabled systematic reconstruction of past human densities and major land-use activities across continental scales [7]. Inclusion of historical baselines into assessment of human-caused biodiversity loss has led to important new insights on extinction risk, dynamics, and ecological impacts [8,9]. However, the use of environmental archives to identify specific drivers of past declines has proved more challenging, and even assessing the relative importance of human versus climatic factors in Late Quaternary mammal extinctions remains contentious [10].

Europe has experienced a long history of human occupation and environmental modification through the climatically stable Holocene (~11,700 years ago to present), and has a rich regional archaeological record that provides evidence of past human activities and locally occurring faunas [11]. Its diverse postglacial large mammal fauna has been progressively impacted by anthropogenic activities, with some species becoming globally extinct but others showing no evidence of pre-modern population change [12]. Previous investigations of past human impacts on Europe's large mammals have reconstructed spatiotemporal range shifts and intrinsic extinction risk predictors [12,13], but the relationship between species persistence and specific anthropogenic pressures through time remains uncertain for this system. Understanding species sensitivities to different threats is crucial because many European mammals are highly threatened today [14], or are related to other threatened species that are expected to show similar vulnerabilities [1,15]. We therefore assessed the ability of long-term environmental archives to determine the relative importance of different human activities in shaping the distribution of Europe's large mammal fauna through time, in order to identify key threats associated with past species losses from Holocene landscapes, and make predictive recommendations for current-day conservation management.

2. Material and Methods

Using a database of 17,684 georeferenced faunal records for Holocene archaeological sites, distributed across Europe (figure 1) and dating from 10,000 BCE to 1600 CE [11,12], spatiotemporal point locations were compiled for 15 native European large-bodied (≥ 1 kg) terrestrial mammal species: red deer *Cervus elaphus* (n=3927), roe deer *Capreolus capreolus* (n=2602), wild boar *Sus scrofa* (n=2551), red fox *Vulpes vulpes*

(n=1544), Eurasian beaver *Castor fiber* (n=1382), brown bear *Ursus arctos* (n=1267), aurochs *Bos primigenius* (n=1216), Eurasian elk *Alces alces* (n=862), wolf *Canis lupus* (n=681), European wildcat *Felis silvestris* (n=578), pine marten *Martes martes* (n=361), Eurasian lynx *Lynx lynx* (n=231), European bison *Bison bonasus* (n=225), European polecat *Mustela putorius* (n=181), and beech marten *Martes foina* (n=76) [16] (electronic supplementary material, figures S1-S2). Available archaeological site dates represent a combination of direct radiometric ages and indirect relative age estimates [11,12], and typically represent date intervals. Midpoints of estimated intervals were used to date species records, although we recognise that this standardisation approach is an approximation, as all values within reported age ranges may be equally probable (sites with midpoint dating before 0 CE: mean range = 1087 years, SD = 965; sites with midpoint dating after 0 CE: mean range = 388 years, SD = 284).

Environmental data known to mediate resource availability and constrain mammal distributions [17,18] were obtained across Holocene Europe: (1) five bioclimatic variables available across the Holocene (January minimum temperature, July maximum temperature, annual mean temperature, annual mean precipitation, annual mean relative humidity) [19]; (2) elevation and slope data [20], with slope data calculated in radians using the R “rgdal” package [21]. Indices of differing past human pressures across Europe (human population density, % cropland, % grazing land), extrapolated using ‘hindcast’ modelling and input with existing historical statistics, were obtained from ref. [7].

Data were analysed at 27 discrete 20-year intervals, in millennial time-steps from 10,000 BCE–0 CE (11 time-points) and centennial time-steps from 0–1600 CE (16 time-points) to match resolution of anthropogenic data; bioclimatic layers were generated at the same resolution. The resulting variables thus represent the anthropogenic and

mean climatic conditions in the 20-year window around each target time-point. All variables were resampled to 5-arcmin resolution using the R “raster” package [22]. Variable estimates were extracted for all spatiotemporal mammal locations. Collinearity was minimised by excluding variables displaying high correlation ($\rho > 0.8$; electronic supplementary material, figure S3), leading to removal of annual mean temperature. Remaining variables were transformed with the R “bestNormalize” package [23].

Site occupancy probability, a proxy for species’ ability to tolerate local environmental conditions and anthropogenic activities, was modelled for each species with Bayesian hierarchical inference using integrated nested Laplace approximation (R-INLA) [24,25]. The distribution of zooarchaeological sites is inherently biased towards past human presence, meaning that randomly generated pseudo-absence points might have different associations with human occupancy than species presence points. To account for this issue, pseudo-absence points for each species were instead selected from the distribution of presence points for the 14 other species, i.e. sites within the zooarchaeological database that have yielded other faunal remains (number of pseudo-absence points generated per species using this method: $n=13,757-17,608$). This approach binds pseudo-absence points to localities of past human occupancy in a similar manner to presence points, and controls for spatiotemporal bias in the distribution of archaeological sites across Europe [26]. Occupancy was modelled as a binomial response with logit-link function; covariates were considered significant if 95% credible intervals did not overlap zero. Forward stepwise model selection procedure was applied using uninformative prior hyperparameter estimates for all covariates ($n=10$) in separate models for all 15 species [27], to select optimal model structure for each species using the Watanabe-Akaike information criterion ($wAIC$) [28]. Univariate models were first fitted separately for each covariate, with the model with

lowest $wAIC$ chosen as the starting model; covariates ordered by univariate $wAIC$ values were added iteratively to the model structure and only retained if inclusion improved model fit by $>2 wAIC$ units. All models exited successfully. All analyses were performed in R v.3.5.1 [29] (electronic supplementary material, figures S4-S6, tables S1-S3).

3. Results

Site occupancy probability showed differing significant relationships with environmental covariates for all species, and showed significant relationships with anthropogenic covariates for nine species (figure 2). Human population density was associated with increased occupancy likelihood for red deer, roe deer and beech marten, and decreased likelihood for aurochs, wolf, wildcat and pine marten. Cropland was associated with decreased occupancy likelihood for red deer, wildcat and lynx. Grazing land was associated with increased occupancy likelihood for bison, and decreased likelihood for aurochs and beech marten.

4. Discussion

By combining a large zooarchaeological dataset with spatiotemporal extrinsic covariates, we provide a new conservation-relevant baseline for understanding how human activities have affected local persistence of European mammals. To investigate the effect of anthropogenic factors in shaping species distributions, it was necessary to also include environmental parameters available for the Holocene within our models, to control for the known effect that climatic and elevational characteristics have in determining mammalian occurrences [17,18] and past human-environmental interactions [30]. All species models are expected to show varying significant relationships with environmental covariates; indeed, these relationships might better

define mammalian fundamental niches compared to modern-only data, if species now persist in environmentally marginal refugia within human-occupied landscapes [31]. However, the fact that 60% of models also show significant relationships with anthropogenic covariates provides a new perspective on varying vulnerability to human activities.

Whereas macroecological analyses can be biased by excluding data from environmental archives, these archives themselves contain biases that prevent straightforward interpretation of past ecological conditions [26]. Our method for generating pseudoabsence data to model occupancy probability removes error associated with selecting pseudoabsence points where no archaeological excavations have taken place, and where species absence may therefore merely reflect lack of opportunity for detection rather than unsuitable environmental or anthropogenic conditions (i.e. omission error). However, this approach also means that species' associations with covariates in our models are relative to those of other species: significant associations with explanatory variables indicate higher sensitivity to those factors than for other species in the dataset that show non-significant associations. Positive model relationships between occupancy probability and anthropogenic covariates (population density, grazing land) also potentially reflect increased likelihood of exploitation of many species at sites with larger human populations (e.g. for deer [32]), with sites that supported larger human populations more likely to contain extensive zooarchaeological records, rather than this relationship representing increased natural abundance of species close to humans and human-modified landscapes (i.e. commission error). The likelihood for such commission error is removed when considering across-species differences in negative relationships with covariates, and so we focus on the ecological implications of these relationships for

understanding extinction dynamics. These results demonstrate that some mammals were more vulnerable to past human-environmental interactions, and identify specific activities influencing likelihood of local occurrence.

Wolf and pine marten only show negative relationships with human density; this metric represents a proxy for multiple human activities, but is decoupled from specific indices of habitat modification in our study, indicating these species were more sensitive to local human presence or were disproportionately persecuted (e.g. as pests). Red deer and lynx instead show negative relationships with past cropland extent, suggesting increased sensitivity to habitat conversion. Wildcat is negatively associated with both covariates, suggesting declines were driven by both persecution and habitat loss. Whereas several factors have been proposed to explain continent-wide decline of the globally extinct aurochs [15,33], it is negatively associated with both human density and extent of grazing land but not cropland in our models, indicating that continent-wide decline was likely driven primarily by overhunting and specific interactions with livestock (e.g. competitive exclusion or hybridisation with cattle, its conspecific domestic form) rather than habitat loss. Conversely, European bison shows a positive association with grazing land. Whilst this relationship might represent a commission error, it might also further demonstrate that the two co-occurring European wild cattle species had differing ecological sensitivities to human pressures. Although European bison are mixed feeders, they predominantly consume grasses and herbs and thus might have benefitted from increased habitat heterogeneity created by open grass-rich pasture, with their recent historical survival in closed forest habitat instead probably representing an ecologically marginal refuge [34]. The two marten species also show differing relationships with anthropogenic covariates; whereas pine marten is negatively associated with human density, beech marten is positively associated with

human density but negatively associated with grazing land, matching the latter species' known increased tolerance of urban areas but decreased tolerance of meadows in areas where they co-occur today [35].

Future studies could further explore the specific impacts of differing human activities on past species occurrence by reducing potential multicollinearity within our anthropogenic dataset (e.g. by regressing population density against indices of habitat modification and using the residuals as further independent predictors), and could also explore methods to reduce the potential for spatial autocorrelation (e.g. associated with incorporating faunal remains dating from multiple time-periods within the same site), which might influence variance of estimates in regression coefficients. However, the relationships with anthropogenic covariates we identify in our analyses are consistent with known post-1600 CE threats to European mammals [36,37]. Our incorporation of archaeological baselines also provides novel insights about species' long-term sensitivity to human-environmental interactions. Indeed, some sensitive species show little or no overall range contraction before the modern era [12], suggesting a pre-industrial trajectory of local-scale population fragmentation and depletion not detected in previous analyses. These findings have direct policy implications. Continental mammals are increasingly threatened by synergistic interactions between hunting and habitat loss [38], but although we demonstrate past threat synergies for some species, we also identify specific factors responsible for many past declines that represent continued risks to European mammals, and their threatened relatives such as Asian wild cattle [15]. More positively, in light of the continent-wide rewilding movement, our findings identify which species were historically impacted by habitat loss and thus most likely to benefit from returning abandoned agricultural land to nature [39]. We encourage further investigation of the conservation information-content of

environmental archives, to learn lessons from past biodiversity loss that can strengthen resilience in future systems.

Funding. This study was supported by a Natural Environment Research Council doctoral training programme studentship (NE/L002485/1) and Research England.

Acknowledgements. We thank Robert Sommer and Norbert Benecke for providing zooarchaeological data from the ‘Holocene History of the European Vertebrate Fauna’ project for analysis, and Richard Pearson for support.

References

1. Fritz SA, Purvis A. 2010 Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042-1051.
2. Munstermann MJ, Heim NA, McCauley DJ, Payne JL, Upham NS, Wang SC, Knope ML. 2022 A global ecological signal of extinction risk in terrestrial vertebrates. *Conserv. Biol.* **36**, e13852.
3. Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239-1241.
4. Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ. 2017 Extinction risk is most acute for the world’s largest and smallest vertebrates. *Proc. Natl Acad. Sci. USA* **114**, 10678-10683.
5. Turvey ST, Crees JJ. 2019 Extinction in the Anthropocene. *Curr. Biol.* **29**, R982-R986.

6. Balmford A. 1996 Extinction filters and current resilience: the significance for past selection pressures for conservation biology. *Trends Ecol. Evol.* **11**, 193-196.
7. Klein Goldewijk K, Beusen A, van Drecht G, de Vos M. 2011 The HYDE 3.1 spatially explicit database of human induced land use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* **20**, 73-86.
8. Turvey ST, Fritz SA. 2011 The ghosts of mammals past: biological and geographical patterns of global mammalian extinction across the Holocene. *Philos. Trans. R. Soc. B* **366**, 2564-2576.
9. Dietl GP, Kidwell SM, Brenner M, Burney DA, Flessa KW, Jackson ST, Koch PL. 2015 Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annu. Rev. Earth Planet. Sci.* **43**, 79-103.
10. Koch PL, Barnosky AD. 2006 Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* **37**, 215-250.
11. Benecke N (ed.) 1999 *The Holocene history of the European vertebrate fauna: modern aspects of research*. Rahden/Westf: Verlag Marie Leidorf.
12. Crees JJ, Carbone C, Sommer RS, Benecke N, Turvey ST. 2016 Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene. *Proc. Royal Soc. B* **283**, 20152152.
13. Crees JJ, Turvey ST, Freeman R, Carbone C. 2019 Mammalian tolerance to humans is predicted by body mass: evidence from long-term archives. *Ecology* **100**, e02783.
14. Temple HJ, Terry A. 2007 *The status and distribution of European mammals*. Gland: IUCN Species Programme.
15. Melletti M, Burton J (eds) 2014 *Ecology, evolution and behaviour of wild cattle: implications for conservation*. Cambridge: Cambridge University Press.

16. Ament JM, Carbone C, Crees JJ, Freeman R, Turvey ST. 2023 *Records for 15 large-bodied mammal species across 17,684 European Holocene archaeological sites*.
<https://rdr.ucl.ac.uk/articles/dataset/Records_for_15_large-bodied_mammal_species_across_17_684_European_Holocene_archaeological_sites/22179931>
17. Hof AR, Jansson R, Nilsson C. 2014 The usefulness of elevation as a predictor variable in species distribution modelling. *Ecol. Modell.* **246**, 86-90.
18. Di Moreno M, Santini L. 2015 Human pressures predict species' geographic range size better than biological traits. *Glob. Chang. Biol.* **21**, 2169-2178.
19. Fordham DA, Saltré F, Haythorne S, Wigley TML, Otto-Bliesner BL, Chan KC, Brook BW. 2017 PaleoView: a tool for generating continuous climate projections spanning the last 21000 years at regional and global scales. *Ecography* **40**, 1348-1358.
20. Danielson JJ, Gesch DB. 2011 *Global multi-resolution terrain elevation data 2010 (GMTED2010)*. Reston, VA: US Geological Survey.
21. Bivand R, Keitt T, Rowlingson B. 2019 *rgdal: bindings for the "Geospatial" data abstraction library*. <<https://cran.r-project.org/web/packages/rgdal/index.html>>
22. Hijmans RJ. 2019 *raster: geographic data analysis and modeling*. <<https://cran.r-project.org/web/packages/raster/raster.pdf>>
23. Peterson RA. 2017 *bestNormalize: normalizing transformation functions*. <<https://mran.microsoft.com/snapshot/2018-04-19/web/packages/bestNormalize/bestNormalize.pdf>>
24. Martins TG, Simpson D, Lindgren F, Rue H. 2013 Bayesian computing with INLA: new features. *Comput. Stat. Data Anal.* **67**, 68-83.

25. Rue H, Martino S, Chopin N. 2009 Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc. B Stat. Methodol.* **71**, 319-392.
26. Crees JJ, Collen B, Turvey ST. 2019 Bias, incompleteness, and the “known unknowns” in the Holocene faunal record. *Philos. Trans. R. Soc. B* **374**, 20190216.
27. Redding DW, Lucas TCD, Blackburn TM, Jones KE. 2017 Evaluating Bayesian spatial methods for modelling species distributions with clumped and restricted occurrence data. *PLoS ONE* **12**, e0187602.
28. Gelman A, Hwang J, Vehtari A. 2013 Understanding predictive information criteria for Bayesian models. *Stat. Comput.* **24**, 997-1016.
29. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna: R Foundation.
30. Banks WE, Antunes N, Rigaud S, d’Errico F. 2013 Ecological constraints on the first prehistoric farmers in Europe. *J. Archaeol. Sci.* **40**, 2746-2753.
31. Kerley GIH, te Beest M, Cromsigt JPGM, Pauly D, Shultz S. 2020 The Protected Area Paradox and refugee species: the giant panda and baselines shifted towards conserving species in marginal habitats. *Conserv. Sci. Pract.* **2**, e203.
32. Baker K, Carden R, Madgwick R (eds) *Deer and people*. Oxford: Oxbow Books.
33. van Vuure C. 2005 *Retracing the aurochs: history, morphology and ecology of an extinct wild ox*. Sofia/Moscow: Pensoft.
34. Kerley GIH, Kowalczyk R, Cromsigt JPGM. 2012 Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? *Ecography* **35**, 519-529.

35. Wereszczuk A, Zalewski A. 2015 Spatial niche segregation of sympatric stone marten and pine marten—avoidance of competition or selection of optimal habitat? *PLoS ONE* **10**, e0139852.
36. Breitenmoser U. 1998 Large predators in the Alps: the fall and rise of man's competitors. *Biol. Conserv.* **83**, 279-289.
37. Yalden DW. 1999 *The history of British mammals*. London, UK: T & AD Poyser.
38. Bogoni JA, Ferraz KMPMB, Peres CA. 2022 Continental-scale local extinctions in mammal assemblages are synergistically induced by habitat loss and hunting pressure. *Biol. Conserv.* **272**, 109635.
39. Ceaușu S, Hofmann M, Navarro LM, Carver S, Verburg PH, Pereira HM. 2015 Mapping opportunities and challenges for rewilding in Europe. *Conserv. Biol.* **29**, 1017-1027.

Figure 1. Spatial distribution of records for 15 large-bodied mammal species across 17,684 European Holocene archaeological sites.

Figure 2. Posterior distributions of spatiotemporal covariates from best-fitting single-species models of site occupancy probability for 15 large-bodied European mammals. Each species plot shows mean posterior estimates (points) and 95% credible intervals (whiskers) for significant environmental (green) and anthropogenic (orange) variables derived from Bayesian hierarchical models.