#Nowhere to run, nowhere to hide: carnivoran extinction in the Holocene

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# Abstract

# Introduction

Carnivoran evolution and extinction - general

Mammalian extinction in the Holocene zoning into carnivorans

Why carnivores are a good model?

Variables used in the context of carn extinction (diet vs locomotion, brain, body size, longevity, abundance, home range etc)

Hypotheses

# Materials and Methods

## Data availability

All data, code and phylogenetic trees used for the analyses in this manuscript are available as electronic supplement and on Github at <https://github.com/orlinst/Carnivores-ext> [still not public]

## Sample

We collated a sample of 114 carnivoran species available in the Ecoregister (http://ecoregister.org). Five variables of interest were obtained by averaging the observed values per species for 934 observations over 195 sites from all continents - body mass, home range, basal metabolic rate (BMR), diet and extinction status. All sites were dated from Xya to Xya (covering the late Pleistocene and Holocene) and the final sample contained 19 species (16.7%) extinct, and 95 species (83.3%) extant carnivorans – a coverage of ~40% of all extant species in the order (excluding Pinnipedia).

Additionally, we collated data on brain size, EQ, locomotor type and litter size from literature sources (see TABLE X for details and sources) and calculated abundance, and Shannon and Simpson indices of diet diversity based on primary data (scat and camera-traps) from the Ecoregister. Scat categories in the Ecoregister include traces of vertebrates (mammals, birds, reptiles), invertebrates (arthropods, arachnids, insects), fruit, plant, aquatic (annelid, mollusc) and fungi. They were obtained from 134 observations from 103 different sites, based on the composition of between 12 and 3878 scats per site. Scat composition was subsequently recategorized using k-means clustering, resulting in 6 different diet categories: 1-6…[describe]

Shannon and Simpson indices of diet (diversity of food sources in the scat) were calculated using the package vegan (see Table X). Species’ abundance was calculated using data from camera-traps available in the Ecoregister using the following formula:

(count - number) / (count/ count per day) [CHECK THIS]

Furthermore, we obtained the first principal component (PC) derived from a principal component analyses (PCA) based on the following variables obtained from Noonan et al. (2015): social class, natal den, hibernaculum, predation, food storage, residence, fossorial propensity, primary, secondary, occupant, and burrowing class (for detailed description of these variables see Noonan et al. (2015)). The so obtained PC is related to burrowing behaviour and fossoriality as indicated by the highest positively loaded variables - fossorial propensity (0.68) and burrowing class (0.53). We chose only the first PC explaining ~53% of the variance, as there was a steep decline in explained variance into the subsequent principal components (PC2 – 23% proportion of variance explained, PC3 - 12%, and PC4 – 5%).

All continuous variables (except abundance) were natural-log transformed (abundance was Yeo-Johnson transformed due to many 0 values) and min-max normalised before imputation.

Detailed description of all variables used, including sources, distribution (along with distribution of the imputed datasets) is available in Table X.

Table X – data sources and detailed description of variables, including histograms of the distribution of the original dataset, and density plots of the 20 imputed datasets (red lines) and the observed original data (blue line). NM = number of missing species (out of 114)

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Variable | Units | Description | Distribution | Imputation | Source | NM |
|  |  |  |  |  |  |  |
| Body mass | kg | Body mass |  |  | Ecoregister | 10 |
| Home Range | km2 | ? |  |  | Ecoregister | 45 |
| Brain | mm3 | Endocranial volume |  |  | (Michaud et al., 2022) | 28 |
| EQ | Index | Derived using CEQ formula |  |  | (Chambers et al., 2021) | 49 |
| PC | PC score | See methods for details |  |  | (Noonan et al., 2015) | 46 |
| BMR | ml O2 hr-1 |  |  |  | Ecoregister | 0 |
| Litter size | number | Number of offspring per litter |  |  | (Noonan et al., 2015) | 34 |
| Shannon index of diet | Index |  |  |  |  | 46 |
| Simpson index of diet | Index |  |  |  |  | 46 |
| Abundance | Frequency of camera trap observation | See methods for details |  |  |  | 34 |
| Longevity | years | Maximal longevity |  |  | (Noonan et al., 2015) | 49 |
|  |  |  |  |  |  |  |
| **CATEGORICAL** |  |  |  |  |  |  |
| Extinct or Extant | 0 – extinct, 1 - extant |  |  |  | Ecoregister | 0 |
| Locomotor mode | 6 categoris | A – arboreal  R – semiarboreal  SA – semiaquatic  SC – scansorial  SF – semifossorial  T - terrestrial |  |  | (Gálvez-López & Casinos, 2022) | 0 |
| Diet | 6 Categories | Based on k-means clustering of scat data |  |  | Ecoregister | 46 |

## Missingness and Multiple imputation

We imputed 20 datasets following a recommendation for imputation of as many datasets as the percentage of missing data in the original dataset (~20% in our case) (White et al., 2011). The variable with the highest number of missingness was longevity (43% or 49 missing values) while locomotor type and BMR had no missing values. We analysed the phylogenetic signal in the missingness using the D statistic and additionally, the overall pattern of missingness was shown to not be missing completely at random (MCAR) (Little’s MCAR test = 713, df=554, p<0.0001 (Little, 1988)). All continuous variables (natural log transformed and min-max normalised) were imputed using Predictive Means Matching (PMM), and all categorical variables were imputed using Polytomous logistic regression (Polyreg) (Buuren & Groothuis-Oudshoorn, 2011; Rubin, 1987). Imputation was run over 100 iterations using the package mice (Buuren & Groothuis-Oudshoorn, 2011). Detailed description of the missingness pattern and imputation analyses can be found in the Supplementary material. The distribution of the 20 imputed datasets is shown in Table X.

## Phylogeny

We used the phylogeny provided by PHYLACINE (version 1.2.1) comprising 1000 trees of 111 of the 114 carnivoran species in our sample (Faurby et al., 2018). The 3 missing species were manually added to all 1000 trees as follows: *Martes caurina* as sister species to *Martes americana*, *Conepatus robustus* as sister to both *Conepatus chinga* *and Conepatus leuconotus*, and *Felis lybica* as sister to *Felis silvestris*.

## Statistical analysis

All statistical analyses were performed in R 4.2.1 (R Core Team, 2021) using RStudio 2022.07.1 Build 554. All packages used are listed in TABLE X. All phylogenetic analyses were conducted on the 20 imputed datasets and were run across all 1000 trees. The MCMCglmm results (20 datasets, 1000 trees, N chains) were pooled used Rubin’s rule (Barnard & Rubin, 1999).

Table X Packages used in the analyses and data processing.

|  |  |  |
| --- | --- | --- |
| **Package name** | **Version** | **Use** |
| ape (Paradis & Schliep, 2019) | 5.6.2 | Phylogenetic analyses |
| BAMMtools (Rabosky et al., 2014) | 2.1.10 | Tree manipulation |
| caper (Orme, 2012) | 1.01 | Estimation on D phy signal |
| dplyr (Wickham, 2020) | 1.0.10 | Various data manipulation |
| easystats (Lüdecke, 2022) | 0.5.2 | Descriptive statistics and plotting |
| ggplot2 (Wickham, 2016) | 3.3.6 | Plotting |
| ggtree (Yu et al., 2017) | 3.4.4 | Phylogenetic tree visualisations |
| lattice (Sarkar et al., 2015) | 0.20.45 | Plotting |
| lavaan (Rosseel et al., 2017) | 0.6.12 | Structural Equation Modelling |
| mice (Buuren & Groothuis-Oudshoorn, 2011) | 3.14.0 | Multiple imputation |
| MCMCglmm (Hadfield, 2010) | 2.34 | MCMCglmm |
| mulTree (Guillerme & Healy, 2014) | 1.3.7 | Incorporating multiple trees in MCMCglmm |
| naniar (Tierney et al., 2019) | 0.6 | Analyses of missing data |
| phylolm (Ho et al., 2016) | 2.6.2 | Phylogenetic logistic regressions |
| phytools (Revell, 2012) | 1.2.0 | Various phylogenetic data manipulation |
| psych (Revelle, 2015) | 2.2.9 | Descriptive statistics and plotting |
| semTools (Jorgensen et al., 2016) | 0.5.6 | Plotting SEM |
| vegan (Oksanen et al., 2013) | 2.6.4 | Calculating of Shannon and Simpson index |

## MCMCglmm

* Priors
* Parameters
* Chains, etc etc etc

## SEM

# Results

PCA for model selection

MCMCglmm (and phyloglm) – report models and posterior distributions

SEM – analyse causality

# Discussion

# References

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Supplement

Table XXX Phylogenetic signal in the missingness pattern (D statistic)

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable** | **D** | **Prob random (D ≠ 1)** | **Prob Brownian (D ≠ 0)** |
| Body mass | 0.2903328 | 0 | 0.236 |
| Brain size | 0.932837 | 0.267 | 0 |
| Home range | 1.047108 | 0.685 | 0 |
| PC | 0.6307042 | 0 | 0.001 |
| Litter size | 0.7311753 | 0.01 | 0 |
| Shannon | 0.8283136 | 0.044 | 0 |
| Simpson | 0.8282997 | 0.045 | 0 |
| Abundance | 0.9189907 | 0.231 | 0 |
| Longevity | 0.932138 | 0.253 | 0 |
| Diet Category | 0.8314431 | 0.052 | 0 |

The D statistic for all variables except for body mass is significantly different from 0 (0 indicating strong phylogenetic signal) and for body mass, PC and litter size it is also significantly different from 1 (random), assuming an alpha level of 0.01. This suggests, that there is no strong phylogenetic signal in the missingness pattern, except for body mass, where D is significantly < 1 but also not significantly different from the Brownian expectation (D = 0).