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1 **Homogenisation of carnivorous mammal ensembles caused by global range reductions of**
2 **large-bodied hypercarnivores during the late Quaternary**

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7 **Abstract**

8 Carnivorous mammals play crucial roles in ecosystems by influencing prey densities and
9 behaviour, and recycling carrion. Yet, the influence of carnivores on global ecosystems has
10 been affected by extinctions and range contractions throughout the Late Pleistocene and
11 Holocene (~130 000 years ago to the current). Large-bodied mammals were particularly
12 affected, but how dietary strategies influenced species' susceptibility to geographic range
13 reductions remains unknown. We investigated 1) the importance of dietary strategies in
14 explaining range reductions of carnivorous mammals ($\geq 5\%$ vertebrate meat consumption), and
15 2) differences in functional diversity of continental carnivore ensembles by comparing current,
16 known ranges to current, expected ranges under a present-natural counterfactual scenario. The
17 present-natural counterfactual estimates current mammal ranges had modern humans not
18 expanded out of Africa during the Late Pleistocene and were not a main driver of extinctions
19 and range contractions, alongside changing climates. Ranges of large-bodied hypercarnivorous
20 mammals are currently smaller than expected, compared to smaller-bodied carnivorous
21 mammals that consume less vertebrate meat. This resulted in consistent differences in
22 continental functional diversity, whereby current ensembles of carnivorous mammals have
23 undergone homogenisation through structural shifts towards smaller-bodied insectivorous and
24 herbivorous species. The magnitude of ensemble structural shift varied among continents, with
25 Australia experiencing the greatest difference. Weighting functional diversity by species'
26 geographic range sizes caused a three-fold greater shift in ensemble centroids than when using
27 presence-absence alone. Conservation efforts should acknowledge current reductions in the
28 potential geographic ranges of large-bodied hypercarnivores and aim to restore functional roles
29 in carnivore ensembles, where possible, across continents.

30 **Keywords:** *carnivores, global-change, macroecology, community disassembly, extinctions*

31 **1. Introduction**

32 In the coming century, anthropogenic extinctions are predicted to shift global mammal
33 assemblages towards small-bodied insectivores [1]. Yet, mammal extinctions influenced by
34 humans are not only a future, or recent, phenomenon but began during the Late Pleistocene
35 (130 000 to 11 700 years ago) and continued throughout the Holocene (11 700 years ago to the
36 current) [2–4], henceforth collectively referred to as the late Quaternary. During the Late
37 Pleistocene, modern humans expanded out of Africa in waves [5] and colonised the inhabited
38 continents, which, in combination with changing climates [6–8], caused globally widespread
39 mammal range modifications and extinctions [9–12]. Mammal assemblages were further
40 modified by direct human-induced range contractions of extant species during the Holocene
41 [13,14]. Large-bodied mammals on continents were particularly susceptible to range reductions
42 (extinctions and range declines, collectively) throughout the late Quaternary [15], which
43 reduced ecological processes such as nutrient and seed dispersal [16,17]. However, knowledge
44 is limited on whether certain dietary strategies influenced species' susceptibility to late
45 Quaternary range reductions. Here, we address this knowledge gap for carnivorous mammals
46 by investigating whether late Quaternary range reductions were biased towards
47 hypercarnivorous species (those consuming $\geq 70\%$ vertebrate meat [18,19]), and how
48 continental ensembles of carnivorous mammals were modified since modern humans expanded
49 out of Africa. We refer to continental ensembles as pools of species in specified geographic
50 areas (i.e. continents) consuming a shared resource (vertebrate biomass) and are
51 phylogenetically restricted (Mammalia) [20].

52 Diet is a crucial ecological trait, which interacts with body mass to influence behaviour [21]
53 and ecological function [22]. Mammals with carnivorous diets consume animal biomass
54 following hunting or scavenging [23]. Ecological effects of predatory carnivores include the
55 potential to influence the behaviour and populations of their prey [24]. Indirectly, these
56 interactions can influence vegetation consumption rates and patterns [25], and prevent
57 mesopredator release [26]. Scavengers contribute to nutrient cycling by consuming carrion,
58 which can stabilise food webs [23]. However, carnivore extinctions [27] and widespread range
59 contractions of extant carnivores [13,28] have occurred in response to anthropogenic pressures,
60 including habitat fragmentation [29,30], prey depletion [31,32], and direct persecution [33].
61 Such recent effects of modern humans on carnivorous mammals may mirror prehistorical ones,
62 particularly, the reduction of prey diversity and abundance [32].

63 Diets are typically variable, and it is uncommon for species to be true dietary specialists with
64 only 23.7% of mammals primarily consuming a single food type (e.g. vertebrate meat or fruit)
65 [34]. However, hypercarnivores, like Felidae, are true specialists of vertebrate meat [18,19].
66 Throughout mammalian evolution large-bodied, hypercarnivorous clades have evolved and
67 subsequently disappeared, likely unable to adapt to ecological disturbances because of intrinsic
68 traits including specialised resource requirements and slow life-histories [35,36]. Dietary and
69 behavioural specialism determine a species' ecological niche and influence its ability to
70 respond to disturbances and fluctuation in resource availability [37,38]. In stable environments
71 dietary specialists are thought to thrive while preferred resources are abundant, whereas
72 generalists thrive in unpredictable environments with varied resource availability [39].

73 Disturbance events can create selection pressures that can be neutral or selective with respect
74 to species' ecological traits [40,41], and can be represented by changes in the structure of
75 multidimensional functional trait space [41]. Extinctions of large-bodied mammals, in response
76 to modern human arrival [10,11,42,43] and changing climates [6–8], was a filtering process
77 that led to functional diversity reduction in North American mammals [44], as well as for
78 Carnivora above 10kg worldwide [27]. In Africa, carnivore functional groups have been largely
79 retained [27]. Yet, previous estimates of continent-wide changes in late Quaternary functional
80 diversity have considered extinctions without considering geographic range contractions of
81 extant species [e.g. 33], and so functional diversity declines may be underestimated.

82 Here, we investigated whether current geographic ranges of hypercarnivorous mammals are
83 more restricted than those of less carnivorous mammals, and consequently how functional
84 diversity of continent-wide ensembles have been affected. We compared the current, known
85 geographic ranges of mammals in response to widespread human presence and changing
86 climates throughout the late Quaternary, to a present-natural counterfactual scenario [45]. The
87 present-natural represents current, expected ranges of mammals had modern humans not
88 expanded out of Africa and, alongside changing climates, contributed to late Quaternary range
89 reductions. Comparing current and present-natural ranges provides insights into how
90 prehistoric and historic effects of modern humans, alongside changing climates, influenced the
91 current geographic ranges of carnivorous mammals (Fig. S1). We assessed if (i) mammals with
92 more carnivorous diets have larger differences between current and present-natural ranges than
93 mammals with less carnivorous diets, (ii) differences in continental functional diversity of
94 carnivorous mammal ensembles between current and present-natural are consistent and

95 suggestive of trait filtering, and (iii) differences in functional diversity is underestimated when
96 excluding the lost geographic ranges of extinct and extant species.

97 **2. Methods**

98 **2.1. Species selection and functional traits**

99 The Phylogenetic Atlas of Mammals database (Phylacine) was used for species selection [46].
100 Carnivorous mammals were selected as those reported to consume $\geq 5\%$ vertebrate meat, and
101 to be terrestrial (coded 1 in Phylacine) and not aerial, freshwater or marine (0). Humans (Genus:
102 *Homo*) were excluded from our analyses. These criteria returned 1081 species from 15 orders,
103 with 12% classed as hypercarnivorous (Fig. S2; those consuming $\geq 70\%$ vertebrate meat
104 [18,19]).

105 For each species, we extracted functional traits from Phylacine describing two key dimensions
106 of a species' ecological niche: body mass (g), averaged across sex and geographical location
107 (as previously defined [47]), and diet, expressed as the average percentage of food consumed
108 from three resource categories: vertebrate, invertebrate, or plant (for details, see [46]).
109 Although diets vary across time and space [48], the available species-specific diet information
110 is sufficient for macroecological analyses [46].

111 **2.2. Continental ensemble species pools**

112 We used two geographic ranges for mammals from Phylacine: current and present-natural (Fig.
113 S1), both provided as rasters in Behrmann equal-area projection with raster cell resolution of
114 9000 km^2 , 1° wide. The current ranges included rasterized native ranges from the IUCN Red
115 List Version 2016-3 [49]. The present-natural ranges, created by Faurby & Svenning [45],
116 included counterfactual estimates of current, expected ranges for all mammals that have existed
117 during the past 130 000 years, assuming late Quaternary range reductions had not occurred (for
118 methods see [45]). To create present-natural ranges, all mammals were systematically reviewed
119 for range reductions, except for non-threatened, small-bodied species ($< 1\text{kg}$), assuming these
120 species were not impacted by humans. In total, 51% of species included in our analyses were
121 systematically reviewed. To assess potential bias in our results because of the uneven review
122 of species' range changes, all analyses were performed for all species, and only for species that
123 were systematically reviewed.

124 Species range rasters were clipped, using 'mask' from the 'raster' package [50] using R Version
125 3.5.1 [51] to an estimated Late Pleistocene land map (Fig. S3) to remove species ranges from
126 islands not connected to continental mainland by land bridges during the last glacial maximum.

127 To measure a species' continental range size, we masked its geographic range raster to a
128 Behrman equal-area projected continental shapefile and summed the number of cells that fell
129 entirely within a continent's border [52]. For each species, geographic range difference was
130 calculated as the number of raster cells occupied in the current minus the present-natural ranges
131 (Fig. S4). Out of 1081 species, 14% had smaller ranges in the current compared to the present-
132 natural. As our focus was on range loss, four species with larger ranges in the current (coyotes,
133 North African white-toothed shrew, least weasel and lesser white-toothed shrew) were
134 classified as having unchanged geographic range.

135 **2.3. Functional diversity of continental ensembles**

136 We calculated functional diversity metrics from functional spaces for each continent and for
137 current and present-natural ranges separately, using the 'FD' package [53]. We scaled and
138 centred traits of \log_{10} -transformed body mass and the three dietary traits by subtracting the
139 means and dividing by the standard deviation. To calculate continental functional spaces, we
140 calculated a dissimilarity matrix for all species using Gower's distance because of unequal
141 weighting of traits (body mass: 1, each dietary trait: 1/3). Principal coordinate analysis (PCoA)
142 was performed on the dissimilarity matrix, using the 'dbFD' function which returns PCoA axes
143 to construct functional spaces. We incorporated the first four PCoA axes into our analyses, as
144 recommended by Maire *et al.* [54], which captured 73% of trait variation. The variance
145 explained by each axis was calculated by the sum of eigenvector values, divided by the value
146 of each axis. Each PCoA axis was explained by a combination of the original functional traits
147 (Fig. S5). A global functional trait space was calculated using all species (Fig. S6), with
148 continental functional spaces extracted as subsets of species present in a continental ensemble.

149 We calculated two functional diversity metrics, functional richness (FRic) [55] and functional
150 dispersion (FDis) [56] for the current and present-natural ensembles for each continent. FRic
151 was calculated as the minimum convex polygon for each continental functional space relative
152 to the global 4-D functional space, scaled from 0 (no functional space) to 1 (global functional
153 space). FRic is unaffected by range size weighting. FDis involves calculating the functional
154 space centroid, which can be weighted by a given metric (i.e. abundance). Here, FDis was
155 calculated first as the average distance of species from the centroid of the species functional
156 space without weighting (i.e. presence/absence) (Fig. S5), and second with weighting by each
157 species' continental geographic range, which shifts centroids towards species with larger
158 ranges (Fig. S7). Lower values of FDis indicate higher species similarity, whereas higher
159 values indicate higher species dissimilarity within an ensemble.

160 **2.4. Statistical analyses**

161 **2.4.1 Identifying traits influencing differences between current and present-natural**
162 **geographic ranges**

163 To investigate factors influencing differences between current and present-natural ranges of
164 carnivorous mammals, we fitted binomial Bayesian phylogenetic mixed models (BBPMMs)
165 accounting species' shared ancestry [57] using the 'MCMCglmm' package [58]. We used
166 phylogenetic trees from the Phylacine database and took average estimates (log-odds ratios)
167 and upper and lower 95% credible intervals from 100 sampled phylogenetic trees and BBPMM
168 models using the 'mulTree' package [59], to account for phylogenetic uncertainty. The
169 response variable was the proportional range reduction expressed as the number of lost and
170 currently occupied raster cells. We included all species in our models with extinct species ($n =$
171 26 species) coded as having a 100% range reduction. Scaled and centred predictor variables
172 included body mass ($\log_{10}(\text{g})$) and vertebrate consumption (%).

173 Each model was run for 200 000 iterations, with burn-in period of 10 000 and thinning interval
174 of 100. We checked model chain convergence using the Gelman-Rubin statistic, the potential
175 scale reduction factor (PSR), with all models having a PSR < 1.1 [60]. As recommended by
176 Hadfield [61], and as used by Healy et al. [62], we used an uninformative inverse-Wishart prior
177 distribution (variance, $V = 0.5$, and belief parameter, $nu = 1$). As in Healy et al. [62], we used
178 a hierarchical partitioning method for model selection by running models with each variable
179 individually and with interactions, to identify trait combinations best explaining proportional
180 range reduction. The model structure with the lowest average deviance information criteria
181 (DIC) value was selected as the best-supported model [63].

182 **2.4.2 Continental ensemble functional diversity and functional space structural change**

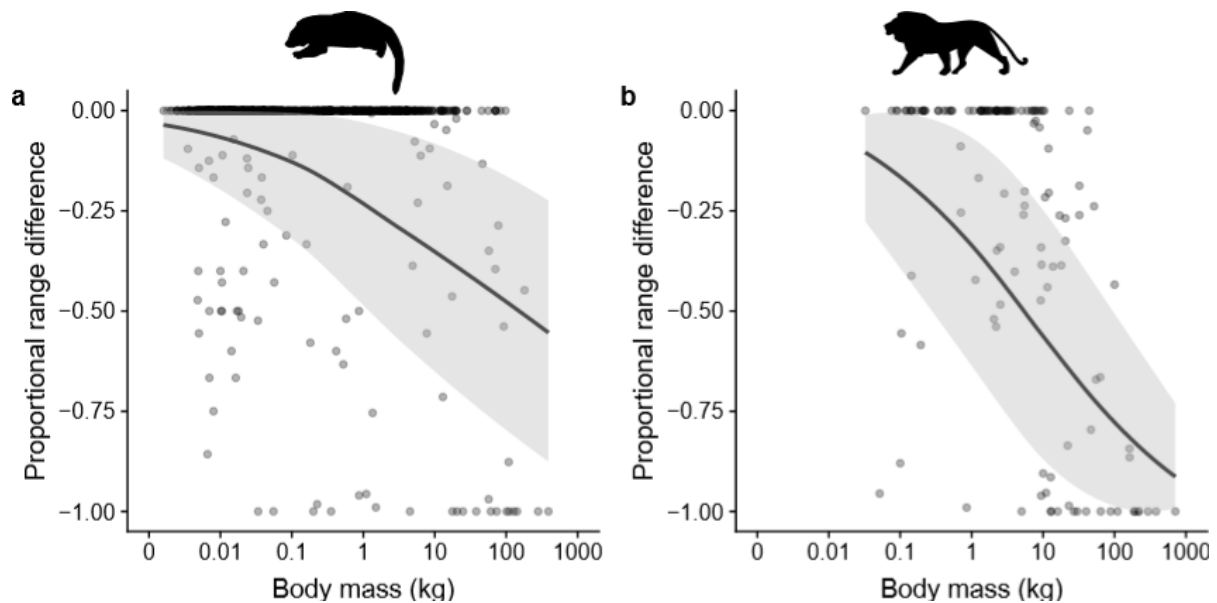
183 To test for differences in FDis and FRic between current and present-natural ensembles, we
184 performed non-parametric Wilcoxon signed-rank tests, using each continent as an independent
185 observation. Differences in continental functional space between current and present-natural
186 were investigated by assessing magnitude and directional shift of the ensemble centroids. To
187 assess directional difference in functional space, we calculated centroid shifts along each of the
188 four principal coordinate axes from the current to present-natural for each continent. We used
189 Kruskal-Wallis tests to test for differences in the magnitude of centroid shifts between axes for
190 both weighting methods separately. Post-hoc Dunn-tests identified pairwise differences. Mann-
191 Whitney tests were used to investigate differences in magnitude of centroid shifts within each

192 of the four functional space axes when calculating FDis as unweighted (presence-absence) and
193 weighted (geographic range size).

194 3. Results

195 3.1. Traits influencing differences between current and present-natural geographic 196 ranges

197 After controlling for phylogenetic relatedness, the best supported model for predicting species
198 geographic range differences (Table S1) included an interaction between body mass and
199 vertebrate consumption (Table S2). Increases in body mass resulted in greater geographic
200 range differences (BBPMM; body mass: log-odds ratio estimate [E] = 9.11, credible intervals
201 [CI]: 6.58-11.97), the effect of which increased with higher vertebrate consumption (Fig. 1;
202 interaction term: E = 1.52, CI: 0.13-2.97). In re-analyses including only systematically
203 reviewed species, the best supported model was the same (Table S3), although the significant
204 interaction between body mass and diet was lost, with body mass being the only significant
205 predictor (Table S4; Fig. S8).



206

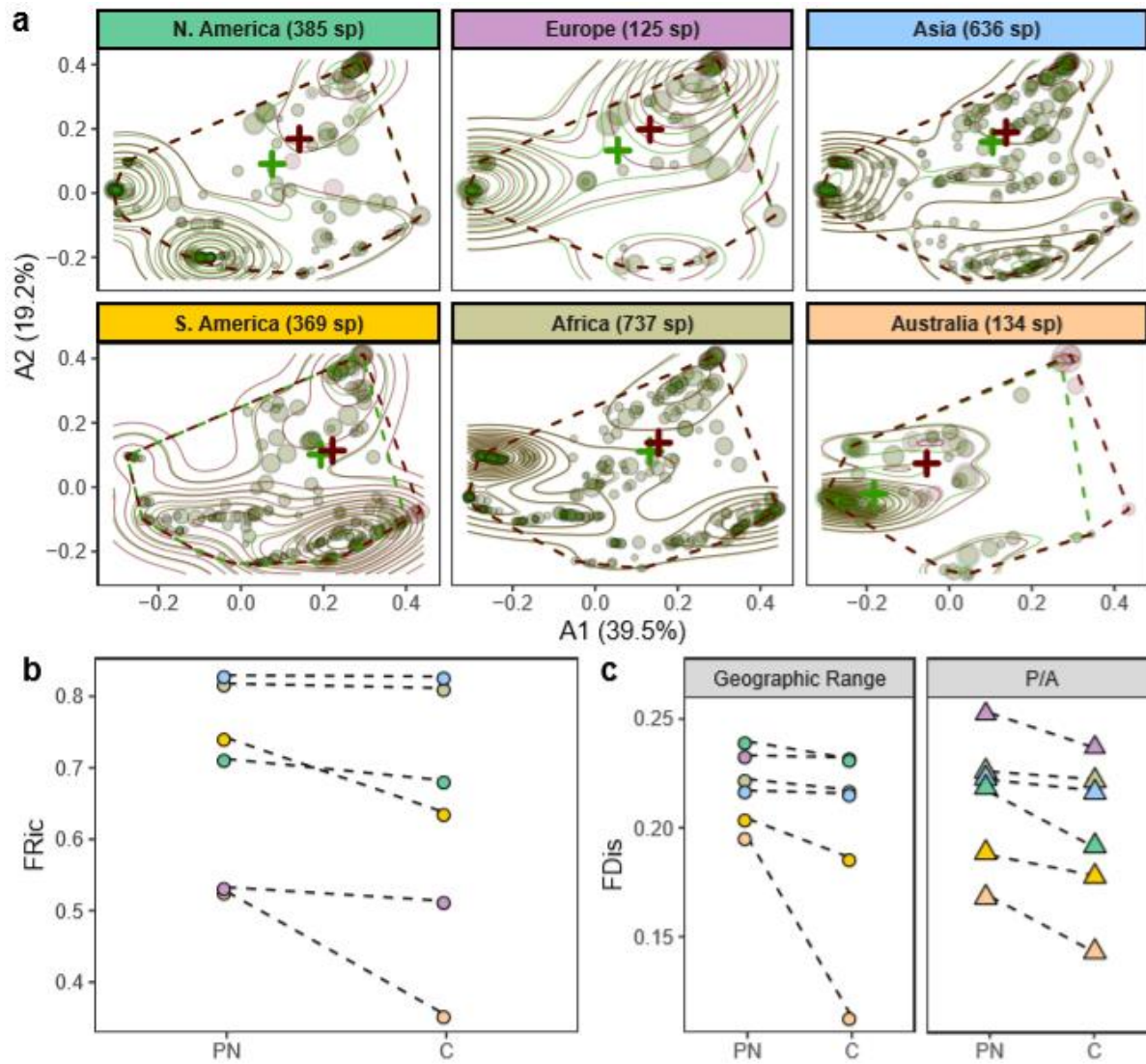
207 **Figure 1.** Proportional difference between current and present-natural species' geographic
208 ranges (points with equal transparency) increased with greater body masses ($\log_{10}(\text{kg})$ for
209 interpretability). The effect was greater for species with increased vertebrate meat
210 consumption, shown for illustration for (a) non-hypercarnivores (5-69% vertebrate meat, e.g.
211 binturong), and (b) hypercarnivores ($\geq 70\%$ vertebrate meat, e.g. African lion). Average
212 BBPMM estimate (black line), accounting for shared ancestry, is shown with upper and lower
213 95% credible intervals (shaded area).

214

215 **3.2. Continental ensemble structural shifts for carnivorous mammals**

216 All continents experienced similar structural shifts in functional diversity when comparing
217 current to present-natural ensembles when weighted (Fig. 2a) by geographic range and
218 unweighted (Fig. S9). Current FRic was lower across continents, indicating loss of species with
219 the most extreme traits (median relative decline: -3.9%, lower quartile (Q2): -1.5%, upper
220 quartile (Q4): 11.7%; Wilcoxon signed-rank test, $W = 21$, $p < 0.05$; Fig. 2b). The relative
221 magnitude of FRic difference varied from 32.9% for Australia to 0.1% for Asia. Current FDis
222 was consistently lower across continents, indicating increased similarity in species functional
223 traits; FDis was lower both weighted by geographic range (-2.8%, Q2: 7.5%, Q4: 1.1%; $W =$
224 21 , $p < 0.05$; Fig. 2c) and unweighted (-5.6%, Q2: 10.3%, Q4: 2.9%; $W = 21$, $p < 0.05$; Fig.
225 2c). The largest relative difference in FDis when weighted by geographic range occurred in
226 Australia (42.2%). However, on average, we detected a near two-fold relative increase in FDis
227 decline between the current and present-natural for the unweighted compared to weighted
228 analysis. The reason for this was that the FDis-weighted centroids in the present-natural
229 occurred in a species-rich location of trait space (causing a lower average distance from
230 species) and shifted towards less species-rich locations. Alternatively, unweighted centroids
231 began in less species-rich locations (a higher average distance from species) and shifted to
232 more species-rich locations of trait space, causing a greater negative difference in the FDis
233 metric for the current ensemble. Analysis with systematically reviewed species showed similar
234 trends (supplementary results), except for FDis difference in Europe, which increased when
235 using unweighted FDis (Fig. S10), likely because almost all small insectivores were not
236 systematically reviewed.

237

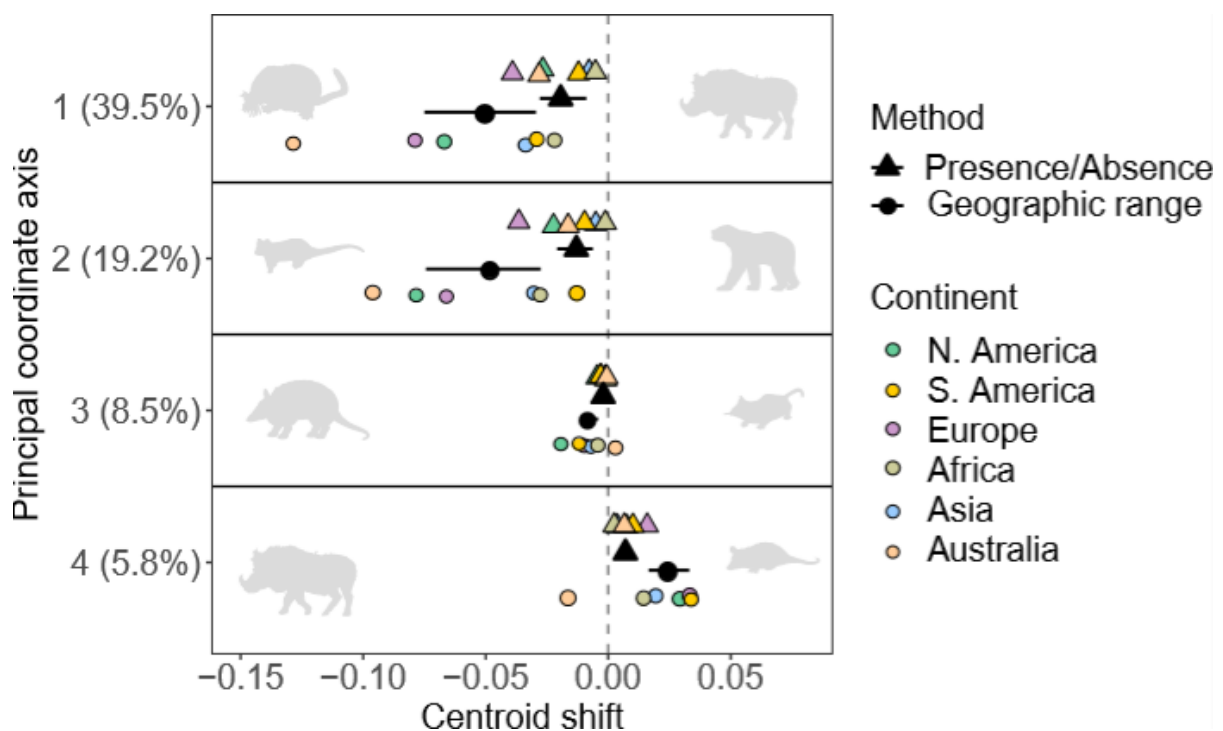


238

239 **Figure 2.** Functional diversity differences between present-natural and current ensembles for
 240 each continent. (a) Continental functional trait spaces (species richness in parentheses) shown
 241 using the first two PCoA axes with species represented by points (size scaled to geographic
 242 range size) for present-natural (PN; brown) and current (C; green) ensembles. For simplicity,
 243 only the first two axes of change in functional richness are shown here by minimum convex
 244 polygons (dashed lines) for PN and C ensembles for each continent, explaining 59% of the
 245 variance, despite it being calculated from the first four axes. Functional dispersion is
 246 represented by the distance of all species from the ensemble centroids (crosses) representing
 247 the weighted centres of the functional hypervolumes, with the weight being species' geographic
 248 range size. (b) Differences in the 4-dimensional functional richness (FRic) for each continent
 249 between the PN and C ensembles. (c) Difference in functional dispersion (FDis) between
 250 current and present-natural ensembles for each continent, calculated using two weighting

251 methods: geographic range-weighted (left, circles) and presence-absence (P/A) only (right,
 252 triangles). Colours in b & c represent continents, colours as in a.

253 Comparing between present-natural and the current, continental ensemble centroids displayed
 254 similar directional shifts along axes in functional space (Fig. 2a & Fig. 3). The centroid shift
 255 magnitude was significantly different between the four functional trait axes for unweighted
 256 (Kruskal-Wallis: $\chi^2 = 18.75$, $df = 3$, $p < 0.001$) and weighted analyses ($\chi^2 = 17.62$, $df = 3$, $p <$
 257 0.001). Continental ensembles shifted towards smaller-bodied and more insectivorous species,
 258 and away from hypercarnivorous species towards more herbivorous species, as indicated by
 259 shifts on A1 and A2, respectively.



260

261 **Figure 3.** The magnitude of continental ensemble centroid shifts between present-natural and
 262 current ensembles for each continent (coloured points) along the four PCoA axes of functional
 263 space (73% total variance). We used two different weighting methods: with geographic range
 264 (circles) and presence-absence only (triangles). Axis medians and interquartile ranges shown
 265 by black symbols and lines, respectively. Silhouettes highlight species at the extremes of
 266 functional space, including from high to low values: *Metridiochoerus compactus*[†] (extinct) to
 267 Alaska tiny shrew (A1), *Arctodus simus* (extinct) to long-tailed pygmy possum (A2), giant
 268 armadillo to montane African climbing mouse (A3), and gray four-eyed opossum to
 269 *Metridiochoerus compactus* (extinct) (A4). Negative shifts along A1 indicate shifts towards
 270 smaller species with more insectivorous diets. Negative shifts on A2 indicate shifts away from

271 more carnivorous to more herbivorous species. Positive shifts along A3 indicate shifts away
272 from larger-bodied insectivorous species. Positive shifts along A4 indicate shifts away from
273 large-bodied dietary specialists towards medium-bodied dietary generalists.

274 We detected a significant difference between the two weighting methods in the magnitude of
275 the centroid shift along A1 (Mann-Whitney: $U = 5$, $p < 0.05$), and A2 ($U = 5$, $p < 0.05$), with
276 geographic range weighting causing a 2.5-fold greater shift than using presence-absence only
277 on A1, and 3.6-fold greater shift on A2. For systematically reviewed species there were,
278 generally, shifts away from hypercarnivorous to more herbivorous species (A2). The exception
279 was South America where ensembles shifted slightly towards hypercarnivores when using
280 geographic range size as a weighting (Supplementary results; Fig. S11). A shift from larger-
281 bodied to smaller-bodied species (A1) is still detected, although no significant difference
282 between weighting methods. Similar results were seen on A3 and A4 compared to the full
283 dataset, with geographic range weighted centroid shifts being greater on A3.

284

285 **4. Discussion**

286 The global geographic ranges of carnivorous mammals are currently more reduced for species
287 with greater body mass and with higher specialisation on vertebrate meat, as a result of late
288 Quaternary extinctions and range contractions. This bias towards large-bodied,
289 hypercarnivorous clades following ecological disturbance has been a common occurrence
290 throughout mammalian evolution [64,65]. Trophic specialisation on large prey and intrinsic
291 traits, such as low population densities, likely increases vulnerability of large-bodied
292 hypercarnivores to ecological disturbances, such as the arrival of competitors [64,65]. This is
293 analogous to the effects of modern humans which have competed with carnivores through prey
294 exploitation [66], habitat modification [67], and direct persecution [68]. The loss of megafauna
295 around the world [15] has reduced the diversity of resources for both predators and scavengers
296 [32,69,70]. The selection against large, hypercarnivorous mammals is consistent with human-
297 induced niche filtering [41,71], resulting in functional homogenization of carnivore ensembles
298 globally [38]. Despite diet varying potentially across space [72] and time [79] for some taxa,
299 our study revealed continental ensembles have become increasingly ecologically similar as
300 smaller-bodied, less carnivorous mammals have been more resilient to disturbances in the late
301 Quaternary, a phenomenon predicted to continue into the future in response to anthropogenic
302 pressures [1].

303 Despite range reductions of large-bodied, hypercarnivorous mammals having occurred across
304 all continents, the magnitude of change varied. Australia suffered the largest relative decline in
305 its carnivorous mammal ensemble, primarily because of the originally low functional
306 redundancy of the continent's hypercarnivorous mammals. This was previously unreported
307 because of taxonomic focus of research on Carnivora [27]. Furthermore, the loss of functional
308 diversity for mainland Australia is likely underestimated because the only extant, native
309 hypercarnivorous (100% vertebrate meat) mammal, the Tasmanian devil, is restricted to
310 Tasmania. The native, highly-carnivorous tiger quoll, which still occurs on the mainland, also
311 consumes a relatively high (30%) proportion of invertebrates. However, the dingo, an apex
312 predator potentially introduced by humans, likely buffers the loss of functional diversity for
313 the Australian ensemble [74]. In North America and Europe, ensembles have also suffered
314 large structural shifts away from large-bodied and hypercarnivorous mammals, which was
315 reflected in loss of functional richness and consistent with previous research [75]. This may, in
316 part, be explained by generally more research on these continents [76] and greater knowledge
317 of species' range contractions. The South American ensemble experienced a large decline in
318 functional richness, influenced by the loss of large-bodied, and primarily herbivorous, short-
319 faced bears *Arctotherium tarijense* and *A. wingei*. The functional diversity and ensemble
320 structure of carnivorous mammals in Asia and Africa have been less affected by late
321 Quaternary extinctions. The large shift away from large-bodied hypercarnivorous species on
322 continents would likely be even greater with wider taxonomic inclusion. In Australia, large-
323 bodied, hypercarnivorous reptiles, including a large snake (*Wonambi naracoortensis*), monitor
324 lizard (*Megalania prisca*), and terrestrial crocodile (*Quinkana sp.*), went extinct shortly after
325 the arrival of modern humans [77]. Including large scavenging birds whose range reduction
326 was caused by the decline in megafauna carcasses in the landscape [73], would further
327 influence shifts in carnivorous species' functional diversity.

328 Geographic range contractions have been observed for a variety of taxa across the world [78],
329 with many extant carnivorous mammals having suffered large range contractions [13,28]. Our
330 findings demonstrate that only considering extinction events, and not including geographic
331 range size, likely leads to underestimates of ensemble structural changes at large spatial scales,
332 although not necessarily changes in functional diversity metrics. This was particularly evident
333 in the functional space axes relating to body mass and vertebrate consumption, which both had
334 a roughly three-fold greater shift in the ensemble centroid position when weighted by
335 geographic range compared to presence-absence alone. Shifts of this magnitude were expected

336 for body mass because of the correlation between range size and body mass [79]; however
337 hypercarnivory, alongside large body mass, was also another previously widespread functional
338 trait that is now severely geographically restricted across continents. This may, in part, be
339 influenced by the known, current range of large-bodied, hypercarnivorous species being
340 smaller as they tend to have been studied in more depth [80], resulting in increased
341 fragmentation and range loss (Supplementary methods, Table S5, and Fig. S12-13). However,
342 such species are likely to have comparatively highly fragmented ranges in reality in response
343 to anthropogenic pressures [30,81]. Although the lack of range reduction for small-bodied
344 species is influenced by many not being systematically reviewed, this likely reflects reality
345 because of the well described bias towards large body size extinctions during the Late
346 Quaternary [15].

347 The shift of ensembles away from hypercarnivorous species across continents likely has global
348 consequences for ecological processes. Predatory hypercarnivorous mammals have the
349 potential to exert top-down forcing on prey populations both directly and indirectly [74,82–
350 85], and influence the distribution of nutrients in ecosystems [86]. Removal of predators can
351 lead to increased herbivore densities [87] and cause mesopredator release [26]. In Australia,
352 removal of top-down forcing by apex predators has resulted in introduced mesopredators
353 becoming abundant [88], while the presence of apex predators has been shown to benefit native
354 biodiversity [89]. Reintroducing, or facilitating natural recolonization, of large predators may
355 counteract these effects, with top-down effects demonstrated through herbivore behavioural
356 changes in response to grey wolves in Yellowstone National Park [90] and Europe [91], the
357 effects of predator auditory and scent cues on bushbuck in Mozambique [25], and the influence
358 of dingoes on mesopredator populations in Australia [92]. In Australia, reintroduction of the
359 hypercarnivorous Tasmanian devil to the mainland could (re-)introduce top-down forcing on
360 non-native mesopredators [93], although, dingos are argued to already exert greater top-down
361 pressures on mesopredators [94] and capable of restoring the large predator guild [95]. While
362 these are active processes, restoring predator guilds could be achieved passively by promoting
363 natural recolonization of predators, as seen in Europe [96], and incorporating management
364 decisions to minimise human-carnivore conflict [97]. Although the range expansions of four
365 species were excluded here, future research could assess the effects of such range changes, and
366 include introduced species, to understand the full spectrum of continental ensemble functional
367 change related to human-impacts.

368 The interacting effects of humans and changing climates throughout the late Quaternary have
369 resulted in reductions in the current global ranges of large-bodied, hypercarnivorous mammals,
370 compared to a counterfactual scenario in which humans had not migrated out of Africa. Range
371 reductions have resulted in globally consistent structural shifts in continental carnivorous
372 mammal ensembles, with the greatest loss of native functional diversity having occurred in
373 Australia. While functional homogenization of carnivorous mammals will likely continue to
374 occur in the coming century [1], we show that this process is already underway as continental
375 ensembles have shifted towards smaller-bodied, less carnivorous species. We recommend
376 enhanced protection of large-bodied, hypercarnivorous mammals, as well as identifying
377 regions for reintroductions, facilitating natural recolonizations, and accepting already
378 introduced apex predators, to reverse past attritions and preserve trophic complexity of current
379 and future ecosystems.

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385 **7. Contributions**

386 OSM collated data, performed analyses and wrote the first manuscript draft. OSM, CJS and
387 JPWS contributed to the conception and development of analyses, interpretation of data, and
388 manuscript revision.

389 **8. Data accessibility**

390 All analyses were performed using data from the PHYLACINE database accessed through
391 Github (Version 1.2; https://github.com/MegaPast2Future/PHYLACINE_1.2).

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