

Learning from the past to prepare for the future: felids face continued threat from declining prey richness

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1 **Learning from the past to prepare for the future: Felids face continued threat**
2 **from declining prey richness**

3
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26
27

28 **Abstract**

29 Many contemporary species of large-felids (≥ 15 kg) feed upon prey that are
30 endangered, raising concern that prey population declines (defaunation) will further
31 threaten felids. We assess the threat that defaunation presents by investigating a late
32 Quaternary (LQ), 'present-natural' counterfactual scenario. Our present-natural
33 counterfactual is based on predicted ranges of mammals today in the absence of any
34 impacts of modern humans (*Homo sapiens*) through time. Data from our present-
35 natural counterfactual are used to understand firstly how megafauna extinction has
36 impacted felid communities to date and secondly to quantify the threat to large-felid
37 communities posed by further declines in prey richness in the future. Our purpose is
38 to identify imminent risks to biodiversity conservation and their cascading
39 consequences and, specifically, to indicate the importance of preserving prey
40 diversity.

41

42 We pursue two lines of enquiry; first, we test whether the loss of prey species richness
43 is a potential cause of large-felid extinction and range loss. Second, we explore what
44 can be learnt from the large-scale large-mammal LQ losses, particularly in the
45 Americas and Europe, to assess the threat any further decline in prey species presents
46 to large-felids today, particularly in Africa and Asia.

47

48 Large-felid species richness was considerably greater under our present-natural
49 counterfactual scenario compared to the current reality. In total, 86% of cells recorded
50 at least one additional felid in our present-natural counterfactual, and up to 4-5 more
51 large-felids in 10% of the cells. A significant positive correlation was recorded
52 between the number of prey species lost and the number of large-felids lost from a
53 cell. Extant felids most at risk include lion and Sunda clouded leopard, as well as
54 leopard and cheetah in parts of their range. Our results draw attention to the
55 continuation of a trend of megafauna decline that began with the emergence of
56 hominins in the Pleistocene.

57

58 **Introduction**

59 Between ~100,000 and 1,000 years ago humans played an important role in the
60 extinction of at least 166 large continental mammal species (≥ 10 kg) and the
61 continental extirpation of a further 11 (Sandom et al. 2014). With the loss of aurochs
62 (*Bos primigenius*) in 1627 (Tikhonov 2008), bluebuck (*Hippotragus leucophaeus*) in
63 1799 (IUCN 2008) and thylacine (*Thylacinus cynocephalus*) in 1936 (McKnight
64 2008, Ripple et al. 2015) amongst many others (IUCN 2013), it is clear that this
65 anthropogenic extirpation of large mammals continues. The outlook for future
66 mammal species is troubling, with 60% of large herbivores (≥ 100 kg) and 61% of
67 large carnivores (≥ 15 kg) classified as threatened, vulnerable or worse, by the IUCN
68 (Ripple et al. 2014, Ripple et al. 2015). The conservation of large mammals presents a
69 particular set of challenges (Macdonald et al. 2014), and although there are numerous
70 conservation success stories that are slowing this decline (Hoffmann et al. 2010),
71 there is little prospect of completely stemming this long-standing tide of extinction.

72

73 Prioritising taxa for conservation is technically, operationally and ethically difficult.
74 However, there are arguments that the conservation of large carnivores is important
75 for ecosystem function (Ripple et al. 2014) and because they attract public attention
76 through their charisma (Macdonald et al. 2015). Here, we focus on large-felids (≥ 15
77 kg) because they are hyper-carnivorous, highly endangered and make potent
78 ambassadors for conservation (Macdonald et al. 2010). We use past relationships
79 between prey and felid decline to assess the threat further declines in prey species
80 (defaunation) pose to extant felids (Wolf and Ripple 2016). We do this by comparing
81 and contrasting a Late Quaternary (LQ) ‘present-natural’ counterfactual (Peterken
82 1977) to the present reality. Counterfactuals are alternative scenarios to reality (e.g.
83 Bull et al. 2014), which, in our case, could have occurred in the absence of modern
84 human (*Homo sapiens*) intervention. Our present-natural counterfactual is based on
85 the predicted ranges of mammals today in the absence of past and present human
86 impacts, but taking climate change into account (Faurby and Svenning 2015). It is
87 hypothetical representation of what present day felid distributions might look like,
88 had modern humans not expanded out of Africa; for simplicity, we hereafter refer to
89 this concept by the term ‘natural counterfactual’. We see this as a technical term
90 unrelated to discussions of whether humans should be considered within or separate
91 from nature.

92

93 We use data from this natural counterfactual to understand firstly how megafauna
94 extinction impacted felid communities to date, and, secondly, to quantify the threat to
95 large-felid communities posed by further declines in prey richness in the future. Our
96 purpose is to use these scenarios to highlight the imminent risks that defaunation
97 poses to biodiversity conservation. Specifically, we highlight the importance of
98 preserving prey diversity to conserve charismatic large carnivores.

99

100 The cause of predator decline in the LQ has largely been considered in the context of
101 the wider debate around the causes of the megafauna extinction. Thus, the primary
102 driver(s) of large mammalian predator extinction specifically remain unclear
103 (Barnosky et al. 2004, Koch and Barnosky 2006). With predator richness closely tied
104 to prey richness in a bottom-up direction at macro-scales (Sandom et al. 2013,
105 Sandom et al. in press), the loss of prey diversity may partly account for the extinction
106 of large carnivores, as postulated by Krantz (1970). However, in the opposite
107 direction, the role of predators as a cause of large herbivore extinction has also been
108 discussed. Ripple and Van Valkenburgh (2010) hypothesise that large carnivores
109 could have driven extinction through top-down pressure when combined with human
110 hunting. Alternatively, the loss of top-predators, through, for example, direct
111 persecution by humans, could have allowed stronger competitors amongst their prey
112 to dominate in the absence of their predators and exclude weaker competitors (Paine
113 1966). These hypotheses are not mutually exclusive; the arrival of modern humans to
114 rich large-carnivore communities increased top-down trophic pressures that may have
115 triggered the decline of large prey, the decline in prey availability and richness could
116 then have driven the decline in large carnivores, altering herbivore community
117 dynamics with potentially further cascading implications through the ecosystem
118 (Estes et al. 2011, Owen-Smith 1987).

119

120 Evidence for large carnivores being driven extinct as a result of the loss of prey
121 availability has been generated by the use of population simulation models directed at
122 determining whether modern humans could drive the megafauna extinct by over-
123 hunting (Koch and Barnosky 2006). Models that specified modern humans as
124 megafauna hunting specialists indicated that they were not capable of driving
125 megafauna extinct because human population density was tied to a boom and bust

126 cycle dependent on megafauna density (Koch and Barnosky 2006). However, more
127 realistic models, that specify humans as generalist omnivores, capable of maintaining
128 high population density at low megafauna density by switching to alternative smaller
129 prey and other food, did indicate humans could drive megafauna extinct. The latter
130 models successfully predicted the extirpation of megafauna in North America with
131 78% accuracy (Alroy 2001). While humans are adaptable and generalist omnivores,
132 large-felids are typically hyper-carnivores and are energetically constrained to predate
133 primarily on large prey (Carbone et al. 1999). For example, the fossil record indicates
134 that sabertooth cats did sometimes predate the largest prey available, proboscideans,
135 albeit their young (Marean and Ehrhardt 1995, Palmqvist et al. 2003, Ripple and Van
136 Valkenburgh 2010), and isotopic evidence suggests these felids preyed a variety of
137 large herbivores (Bocherens 2015, Coltrain et al. 2004). Therefore, models designed
138 to depict humans as megafauna specialists (e.g. Koch and Barnosky 2006) may better
139 reflect predation by large-felids that are more restricted to large-bodied prey. If so,
140 these models may explain why the large-felids could co-exist with the megafauna
141 prior to human arrival, and explain why they would, in turn, be susceptible to
142 extinction in the face of large herbivore declines following the arrival of humans.

143

144 The number of large mammals lost between 132,000 and 1,000 years ago varies
145 dramatically between biogeographic regions (Qian 2010; Fig. S1). The most severe
146 losses occurred in the Nearctic, Neotropics, western Palearctic and Australian
147 biogeographic regions, while in comparison, the Afrotropics and Indo-Malaya were
148 minimally affected (Sandom et al. 2014). Because most large herbivores have already
149 been lost in regions of high LQ extinction, most large herbivores and carnivores
150 currently threatened today are in Africa and Asia (Ripple et al. 2014, Ripple et al.
151 2015). Here, we pursue two lines of enquiry; firstly, we test whether the loss of prey
152 species richness is a potential cause of large-felid extinction and range loss. Secondly,
153 we explore what can be learnt from the large-scale large-mammal LQ losses,
154 particularly in the Nearctic and western Palearctic, to assess the threat any further
155 decline in prey species presents to large-felids today, particularly in the Afrotropics
156 and Indo-Malaya. We compare and contrast macro-scale predator-prey richness
157 relationships between the natural counterfactual and the present reality to infer how
158 predator-prey species richness relationships may have been altered (Hemmer 2004,
159 Morales and Giannini 2014). Finally, we use the relationship recorded between lost

160 prey and felid species richness to estimate the number of large-felids at risk of
161 extinction as a result of declining prey resources today.

162

163 **Methods**

164 *Species Distribution Data*

165 To contrast the current reality with our present-natural counterfactual, we used two
166 sets of mammal species distribution data. For the current distribution we used global
167 species distribution maps for all terrestrial mammal species (IUCN 2013), however, to
168 avoid zero inflated data Australia and Antarctica were excluded because they have no
169 felids. For the natural counterfactual, mammal distributions were taken from Faurby
170 & Svenning (2015), representing the distribution of each mammal as it could have
171 been today in the absence of modern humans.

172

173 Current and counterfactual polygonal distribution maps were converted to rasters on a
174 Behrmann projection (a cylindrical equal area projection) with a resolution of 2
175 degree equivalents at the equator (~220 km). A species was counted as present in a
176 cell if any part of the cell was covered by the species' range polygon. Further, grid
177 cells missing data and grid cells with <50% land area were excluded, resulting in
178 3250 cells in our analysis. All data handling and plotting was performed in the R
179 statistical program, version 3.3.2 (R Core Development Team 2016), using the raster
180 (Hijmans 2015), rgdal (Bivand et al. 2015), and maptools (Bivand and Lewin-Koh
181 2015) packages (see Sandom et al. 2013 for further details).

182

183 *Felid Diet Data*

184 Data on extant felids were taken from the felid diet database FelidDIET (Sandom et
185 al. in press). Of the 10 large extant felids that primarily prey on mammals, nine (the
186 exception being snow leopard *Panthera uncia*) are recorded to have larger ranges in
187 the natural counterfactual than in the present, with cheetah recording the greatest
188 difference with its current range covering 16% of its natural range. The felid diet data
189 recorded in FelidDIET are based on the felid and prey extant ranges, but prey
190 availability will be greater under the natural counterfactual. To correct for this, the
191 dietary preferences and mass characteristics recorded in FelidDIET were used to
192 predict each felid's primary prey in the natural counterfactual ranges of all mammals.
193 The procedure followed the prey extrapolation method used in Sandom et al. (in

194 press), but using natural species' ranges for the felids and all other mammals (see
195 supplementary methods for further details). We focus here on primary prey but we
196 recognise the potential for felids to switch to secondary prey if available, seemingly
197 as jaguar (*Panthera onca*) has done in response to the loss of larger prey species in its
198 range (Hayward et al. 2016), which warrants further examination.

199

200 In the absence of empirical data, diet for the seven extinct large-felids was
201 extrapolated from taxon substitutes using phylogenetically close relatives that have
202 similar ecological traits. American lion (*Panthera atrox*) and the cave lion (*Panthera*
203 *spelaea*) were considered functionally equivalent to the extant lion (*Panthera leo*)
204 (Barnett et al. 2009), although the degree to which cave lion was social has been
205 questioned (Bocherens 2015), also calling into question the sociality of America lion
206 as well. Although the American cheetah (*Miracinonyx trumani*) was a closer relative
207 of puma it was considered functionally equivalent to the extant cheetah (*Acinonyx*
208 *jubatus*) (Donlan et al. 2006a) and so this was used. For these three species the taxon
209 substitute's diet data were used to predict the mammals likely to be preyed upon their
210 extinct functionally equivalent species following the extrapolation method in Sandom
211 et al. (in press; see supplementary material). For the four sabertoothed cats
212 (*Homotherium latidens*, *Homotherium serum*, *Smilodon fatalis*, *Smilodon populator*),
213 the lion was selected as the closest functionally equivalent species because it is large
214 and social, and isotopic analyses support these species predated similar species to
215 American and cave lion, albeit with a considerable degree of individual variation in
216 behaviour within and between species (Anton et al. 2005, Bocherens 2015, Coltrain et
217 al. 2004). However, there must have been niche differences among these taxa to have
218 allowed their long-term coexistence (Anton et al. 2005). An important factor here is
219 whether these extinct felids were social or not, as sociality increases the range of prey
220 body masses that can be taken (Van Valkenburgh et al. 2015). Van Valkenburgh et al.
221 (2015) suggest that determining sociality from the fossil record is difficult if not
222 impossible, although Antón (2013), Carbone et al. (2009) and McHorse et al. (2012)
223 make the case for sociality in these extinct sabertooths, proposing that high
224 competition in felid communities of the Late Pleistocene would promote group living.
225 Certainly, group size is an important factor in determining which group of large
226 predators successfully competes for a carcass in Africa (Cooper 1991), which drives
227 the evolution of social behaviour, although clearly not all African extant felids are

228 social and smaller felids may be disrupted from social living by larger felids (Mosser
229 et al. 2015).

230

231 The species recorded on each extinct felid's potential prey list were categorised
232 according to likely importance based on the relationships observed between felid
233 body mass and prey body mass in Sandom et al. (in press). For all extinct felids, the
234 minimum and maximum mass categories for primary prey and secondary prey (diet
235 Categories 1 and 2, for definitions see Sandom et al. (in press)) were multiplied by the
236 proportion by which the extinct felid was larger than the taxon substitute, to give a
237 best estimate of primary and secondary prey (see supplementary material for
238 sensitivity analysis). The predicted prey species of all large-felids under the natural
239 counterfactual are recorded in Appendix 1, where Category 1 = primary prey, 2 =
240 secondary prey, 3 = occasional prey, and 4 = non-prey. Finally, extinct potential prey
241 species, that are likely to have been excluded as prey by this approach because they
242 do not have close living relatives, were added to a felid's primary diet if that species
243 was of the appropriate mass. Mammal body masses were derived from a previously
244 compiled dataset (Faurby and Svenning 2016).

245

246 *Data Analysis*

247 Both felid and prey species richness were calculated per grid cell for the current and
248 the natural counterfactual mammal distributions. Current prey species richness was
249 calculated in two ways: 1) a species was counted if a felid that preyed upon this
250 species was also present in the cell using the present reality distribution maps for prey
251 and felids, 2) a prey species was counted if a felid that preyed upon this species was
252 present in the cell using the felids' natural counterfactual distributions. The latter
253 calculation of prey species richness provides an estimate of the loss of prey richness
254 ignoring the decline in felid distribution and diversity. Generalised linear models
255 (GLMs), with a poisson error distribution using a log link function, were used to test
256 if prey species richness was a significant predictor of felid species richness in the
257 present and the natural counterfactual structured by biogeographic realm which was
258 included to account for the differing biogeographic histories in the different realms
259 (Qian 2010; Fig. S1). To assess the degree of spatial autocorrelation, we computed
260 correlograms of GLM model residuals using the 'ncf' package in R (Bjornstad 2012),
261 with distance classes of 1000 km and used Spatial Autoregressive (SAR) models to

262 account for spatial autocorrelation.

263

264 The difference (as a percentage) in prey species richness between the natural
265 counterfactual and present was calculated for each cell for each felid. These data were
266 used to map whether the felids that lost the greatest proportion of prey species
267 richness corresponded with the felids that were lost from the cell. The difference
268 between the prey species richness in the natural counterfactual and the present was
269 used to predict the difference in felid species richness, using a GLM, with a poisson
270 error distribution using a log link function. This model was used to predict how many
271 felids would be lost under a future scenario where all large-felid prey currently
272 classified as vulnerable or worse by the IUCN (2013) were to go functionally extinct
273 and thus no longer provide a viable prey resource.

274

275 We carried out two sensitivity analyses, firstly to determine the sensitivity of our
276 results to the multiplication factor used to estimate the minimum and maximum
277 primary prey masses of the extinct felids, and secondly, to determine the sensitivity of
278 our results to removing *Homotherium latidens*, which is of uncertain presence in the
279 LQ in the Palaeartic.

280

281 **Results**

282 Felid species richness was considerably greater under the natural counterfactual
283 compared to the current reality, with 86% of cells recording at least one additional
284 felid in the natural counterfactual (Fig. 1a,c,e). The Nearctic and Palearctic indicate
285 the greatest difference between the large-felid communities of the two scenarios, with
286 up to five fewer felids in the present reality (Fig. 1e). In the Nearctic, under the
287 natural counterfactual, there were as many as six large-felids in some cells, and a
288 community of five large-felids is predicted to have been typical across much of the
289 western side of the region. This compares to just one large-felid in this region today,
290 puma. In the western Palearctic, the natural counterfactual recorded at least four
291 large-felids over much of the region, in comparison there is a maximum of one large-
292 felid today, the Eurasian lynx (*Lynx lynx*). In Indo-Malaya, large-felid losses have
293 been high in the west and east, while the community in the centre of Indo-Malaya
294 remains relatively intact (with as many as 5 large felids; Fig. 1a,c,e). In the

295 Neotropics there is at least one fewer large-felid over 95% of the region now
296 compared with the natural counterfactual (Fig. 1e). In the Afrotropics, the natural
297 counterfactual records three large-felids over 88% of the region, whereas 20% of the
298 region currently supports these three felid species (Fig. 1a,c).

299

300 Large-felid primary prey richness is highest in the eastern Afrotropics, eastern Indo-
301 Malaya, western Neotropics in the current reality (Fig. 1b), as it was, together with
302 most of the Neotropics, under the natural counterfactual (Fig. 1d). The southern
303 Neotropics, small areas of southern and western Afrotropics, the Nearctic, and to a
304 lesser extent European Palearctic, recorded the biggest differences in prey species
305 richness between the two scenarios with the maximum difference being 59, 41, 40 and
306 21 respectively (Fig. 1f).

307

308 A significant positive correlation was recorded between prey and large-felid species
309 richness, structured by bioregion, in both the natural counterfactual (Fig. 2; Table A1;
310 $\text{Chi}^2 = 859.72$, D.F. = 9, $p < 0.001$) and current reality (Fig. 2; Table A2; $\text{Chi}^2 =$
311 1770.5 , D.F. = 9, $p < 0.001$). For the natural counterfactual, the relationship was
312 strongest in the Nearctic, where felid species richness was greatest, with a maximum
313 of six felids in any one cell (Fig. 2). A strong relationship was also evident in the
314 Palearctic (Fig. 2, Table A1). There is a correlation between prey species richness and
315 felid species richness in all bioregions in the current reality (Fig. 2, Table A2). Spatial
316 correlation was found to be minor (Fig. A2a,b), but to make sure that it did not bias
317 our results, we also analysed the results using a SAR model and got similar results
318 (Table A4 & A5).

319

320 In the Neotropics, Nearctic, and Palearctic, the felid species that have experienced the
321 greatest loss of primary prey between the natural counterfactual and the current reality
322 are the felids that were lost from the same cells, with 80% of cells recording a 100%
323 match (Figs. 3 and 4). By contrast, only 17% of cells in the Afrotropics and Indo-
324 Malaya lost the felids that lost the greatest proportion of their primary prey species
325 between the current reality and the natural counterfactual (Figs. 3 and 4). The seven
326 extinct large-felids experienced high prey species losses between the natural
327 counterfactual to the present reality over their entire ranges, except for *Panthera*

328 *spelaea* that had some areas of minimal prey loss (Fig. 4), while all extant species had
329 regions of their range that had comparatively low prey species richness losses (Fig. 4).

330

331 A significant positive correlation was recorded between the number of prey species
332 lost and the number of large-felids lost from a cell, structured by bioregion (Table A3;
333 $\text{Chi}^2 = 1381.4$, D.F. = 9, $p < 0.001$). The relationship was clearest in the Nearctic and
334 Palearctic, but all regions indicated a positive correlation (Fig. 5). Spatial correlation
335 was again found to be minor (Fig. A2c) and a SAR regression reported similar results
336 (Table A6).

337

338 In the present reality, the primary prey species of large-felids are particularly
339 threatened in eastern and central Afrotropics, Indo-Malaya, and western and central
340 Neotropics (Fig. 6a). The model explaining the relationship between the number of
341 prey species lost and the number of felids lost indicates that between one and five
342 large-bodied felids are at risk in any one cell as a result of defaunation (Fig. 6). The
343 threat is particularly acute in Indo-Malaya, but also in East Africa and to a slightly
344 lesser extent in the Neotropics (Fig. 6). The magnitude of the threat varies by
345 biogeographic realm; losses are predicted to be most severe under the Palearctic
346 relationship (Fig. 6e) and least severe under the Neotropics relationship (Fig. 6d).

347

348 If all currently threatened prey species become functionally unavailable for extant
349 felids, then the two worst affected species would be the lion and Sunda clouded
350 leopard (*Neofelis diardi*), which would, on average, lose 61% and 63% of their prey
351 base respectively in each of their cells compared to currently available prey richness
352 (Table 1; Fig. 4).

353

354 The sensitivity analyses indicate our results are robust to variation in the
355 multiplication factor used to estimate extinct felid prey and the inclusion of *H.*
356 *latidens* (Figs. A3 & A4).

357

358 **Discussion**

359 The counterfactual comparison of species richness points to a severe impoverishment
360 of large-felid communities between the current reality and the natural counterfactual,

361 and confirms this is likely to get worse under a business-as-usual scenario. We predict
362 that under a natural counterfactual there would be at least one additional large-felid
363 over 86% of the world's continental terrestrial surface, excluding Australia and
364 Antarctica, and up to 4-5 more large-felids over 10% of the area. Whether the loss of
365 large-felids was primarily caused by direct or indirect conflict with modern humans is
366 an important question in understanding part of the LQ megafauna extinction, and one
367 to which the answer may shed light on the magnitude of current threats to large-felid
368 communities. We find that only a small fraction (<41%) of the primary prey species
369 available to extinct felids' under the natural counterfactual, would still be available in
370 the current reality; in comparison, the prey base of the extant felids is relatively intact
371 (Fig. 4, Table 1). The relationship between loss of prey species richness and the loss
372 of felids also holds for extant lion, in terms of range contraction; millennia ago the
373 lion lost large swathes of its range (Sommer and Benecke 2006) from which its prey
374 has also been lost (Fig. 4), for example. Using these relationships recorded between
375 the natural counterfactual and the current reality to project forward, the trend suggests
376 large-felid communities are threatened everywhere. However, felids in Indo-Malaya
377 and eastern Afrotropics are at particular risk in the future, as defaunation levels could
378 match the levels already reached in the Palearctic, Nearctic, and Neotropics (Fig. 6).
379

380 Felid species richness, then and now, correlates with prey species richness, as might
381 be expected, but the relationship differs between biogeographic realms. The
382 relationship is particularly strong in the Nearctic where large-felid richness under the
383 natural counterfactual is greatest. It is striking that in both the Nearctic and European-
384 Palearctic, large-felid richness exceeds that of the Neo- and Afro-tropics, despite the
385 higher primary prey species richness in these tropical regions (Fig. 1). This might be
386 the result of earlier felid extinctions in the Afro-tropics. Low diversity in the
387 Neotropical realm may reflect restricted dispersal opportunity from North America
388 into South America, particularly for open-habitat species such as American lion,
389 American cheetah and *Homotherium serum*. Alternatively, there may be a taphonomic
390 bias between the regions. In the Afrotropics there is no evidence of *Homotherium*
391 surviving beyond ~1.4 Ma (Werdelin and Lewis 2005), while a species of *Dinofelis*
392 persisted until ca. 1 Ma (Werdelin and Lewis 2001), leaving a surprisingly limited
393 large-felid community of three species. Furthermore, all three species are relatively
394 small compared to those in the Nearctic and Palearctic, despite the high prey

395 availability for large-felids in the Afrotropics (Kitchener et al. 2010). Sabertoothed
396 cats (Felidae: Machairodontinae) from three different tribes were found in the
397 Afrotropics in the Plio-Pleistocene, creating a more diverse large-felid assemblage,
398 but did not survive through to the Late Pleistocene, likely as a result of increased
399 competition for prey with early hominins (Werdelin and Lewis 2013).

400

401 The natural counterfactual species ranges are estimates based on a number of
402 assumptions, as described in Faurby and Svenning (2015). Extinct species ranges
403 were typically based on fossil co-occurrences. As reported in Faurby and Svenning,
404 this may lead to overestimates of species ranges. *Homotherium latidens*, amongst
405 other the non-felid species that were included as potential prey in our analysis, is
406 particularly noted as a species that may have an overestimated range. The validity of
407 *H. latidens* presence in the region for this period has been debated (see Barnett 2014,
408 McFarlane and Lundberg 2013), but a sample of *H. latidens* from the North Sea has
409 been dated to ca. 28,000 BP, supporting its inclusion (Reumer et al. 2003). In either
410 case, the very limited fossil evidence suggests *H. latidens* was exceedingly rare in the
411 landscape, possibly as a result of a prolonged decline triggered by climate change,
412 competition with other large predators and competition with hominins (Anton et al.
413 2005). Overestimations of species ranges would increase the diversity scores in those
414 regions, with the potential of inflating the number of felids and prey lost between the
415 two scenarios. However, our macroscale approach and the fact that our results are
416 robust to the removal of *H. latidens* (Fig. A4) suggest that any overestimations of
417 species natural range have a minimal impact on our results and conclusions.

418

419 Predicting the primary prey for extinct felids is challenging, but our estimates, which
420 are conservatively broad and comparable to surviving felids (Table 5), clearly suggest
421 that the extinct felids would have very few of their likely primary prey available today
422 compared to surviving felids (Fig. 4). Johnson (2002) highlights that species of the
423 family Felidae went extinct if they had low reproductive rates, and that this
424 relationship is consistent with all mammalian families, suggesting the cause of
425 extinction was consistent among mammalian families. Johnson (2002) also indicates
426 that this extinction pattern across families is consistent with modern human causes,
427 including increased direct exploitation or persecution of species or through
428 competitive exclusion. Because large-felids are energetically constrained to prey upon

429 large species (Carbone et al. 1999), a reduction of, or reduced access to, large prey
430 could cause a protracted decline and final extinction of large-felids. Our results,
431 supported by large prey specialist predator-prey interaction modelling (Koch and
432 Barnosky 2006), suggest that the decline and loss of large prey species as a result of
433 the arrival of modern humans (Sandom et al. 2014) would have driven large-felids to
434 extinction even without direct killing. There are a number of interesting examples
435 from the fossil record that indicate large-predators can be susceptible to prey decline.
436 For example, a recorded bottle-neck of the cave lion population has been linked to the
437 decline in European bison, thought to be a primary prey species, ~ 50,000 years BP
438 (Barnett et al. 2009). Other examples include, the extinction of a North American
439 wolf ecomorph, thought to have been particularly specialised on megafauna, when
440 other wolf populations survived (Leonard et al. 2007). California condors
441 (*Gymnogyps californianus*) are now artificially fed livestock carcasses because of the
442 loss of terrestrial and marine megafauna during and since the Late Pleistocene
443 (Chamberlain et al. 2005). Other factors, such as direct conflict between modern
444 humans and large-felids, would have exacerbated the problem.

445

446 Our results support the loss of prey diversity as a potentially important factor in the
447 extirpation and continental extirpation of the largest felids in the Neotropics, Nearctic
448 and Palearctic. Conversely, more recent felid range declines in the Afrotropics and
449 Indo-Malaya are not occurring in the species that have lost the greatest proportion of
450 their prey species (Fig. 3), and prey losses in general have been relatively modest in
451 comparison (Fig. 4). Direct persecution and habitat loss have been important drivers
452 of predator decline recently, and more and larger protected areas have been called for
453 as part of the solution to preserving these species (Ripple et al. 2014). However,
454 tracking forward, contemporary large-felids are likely to face an increasing threat
455 from loss of prey species, even in protected areas (Lindsey et al. 2013). Our results
456 suggest lion and Sunda clouded leopard could lose on average over 60% of their
457 primary prey in each cell, comparable to the extinct American cheetah (Fig. 4). The
458 Sunda clouded leopard appears to face as great a threat as did the extinct felids.
459 However, diet data for this species are extremely limited and this might influence the
460 results (Sandom et al. in press). While the risk prey loss presents to extant felids may
461 not be quite as severe as that experienced by their extinct relatives from the Late
462 Pleistocene (Fig. 4), extant felids face greater challenges from human-wildlife conflict

463 that are likely to be severely exacerbated by the loss of their wild prey. A particular
464 concern is felids switching to prey on livestock because of the loss of their wild prey,
465 which often leads to retaliatory killings (Kissui 2008). Furthermore, where prey
466 richness and availability is declining together with habitat loss and fragmentation
467 increased competition between felids will lead to greater pressure on smaller felids
468 (Hayward and Kerley 2008).

469

470 If a lasting and secure future for these felids is to be found, it will be important to
471 counter the threat posed by loss of their prey. From a large-felid perspective, further
472 defaunation is a particularly pressing issue due to prey declines because of bushmeat
473 hunting (Ripple et al. 2016). In Sarawak, Malaysia, 23,500 tons of bush meat are
474 estimated to be consumed annually (Bennett 2002), while in Tanzania around 2,000
475 tons are confiscated annually, although understanding what these estimates mean in
476 terms of defaunation rates is challenging (Lindsey et al. 2013). Interestingly, bush
477 meat exploitation in South America is also a serious problem (Peres 2000), but is not
478 predicted to impact South American felids as significantly because fewer large-felids'
479 prey species are classified as threatened by the IUCN in this region (Fig. 6a). Where
480 threatened prey species have or will become functionally extinct, it may lead to the
481 loss of at least one big cat species in the foreseeable future and potentially entire felid
482 communities (Fig. 5). Felids most at risk include lion, tiger, Sunda clouded leopard
483 and regions of leopard (*Panthera pardus*) and cheetah ranges. The magnitude of the
484 potential loss of primary prey species for tiger and lion is particularly alarming (Fig.
485 4), and our results draw attention to the continuation of an unhappy trend begun in the
486 Pleistocene perhaps as much as two or more million years ago.

487

488 We present these relationships as speculations, intending to illustrate the principle that
489 an understanding of the past can help in anticipating the future. If modern humans
490 contributed to the demise of the primary prey of large felids, it follows that their
491 impact would disadvantage these predators. Our point, therefore, is to emphasise that
492 the emptying of the Late Pleistocene larder, attributable to modern humans, has
493 reverberated through predator-prey systems to cause up to five fewer species of large
494 felid today than would otherwise have been the case. Unfortunately, it seems
495 continued losses of large prey are set to cause the loss of even more large felids in the
496 future. Of course, insofar as direct persecution of these same felids may extinguish

497 them before they are starved out of existence, we should already be alerted to their
498 peril. Alternatively, this long-term perspective offers an opportunity to consider a
499 rewilded future where felids and their prey could be restored to their natural ranges. In
500 terms of restoring prey species to support felid conservation, even exotic species can
501 be viewed positively in the absence of native prey. For example, non-native wild boar
502 (*Sus scrofa*) in Brazilian Atlantic Forest are being seen as an important prey species
503 for recovering jaguar populations (Verdade et al. 2016). In terms of restoring felids,
504 the Eurasian lynx is re-colonising and has been reintroduced to lost range in Europe
505 (Linnell et al. 2009) and range expansion through reintroduction has been proposed
506 for tigers in Asia (Hebblewhite et al. 2014, Hebblewhite et al. 2012, Qin et al. 2015,
507 Wikramanayake et al. 2011), Eurasian lynx to the United Kingdom (Hetherington et
508 al. 2006), leopard to the Russian Far East (Hebblewhite et al. 2011), and lions and
509 cheetah as taxon-substitutes for the American lion and cheetah in North America
510 (Donlan et al. 2006b). These efforts may not only be important for species
511 conservation, but also to the functioning of ecosystems through the re-establishment
512 of trophic cascades (Estes et al. 2011). Data presented in this paper offer an important
513 resource for taking a systematic approach to exploring rewilding opportunities going
514 forward.

515

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526

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Supplementary material ((Appendix EXXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.

Tables

Table 1: Average difference of prey richness per cell for each felid between the natural counterfactual, present reality and projected defaunated future.

Felid	Average percentage of prey lost from natural counterfactual to present (mean per cell)	Average percentage of prey lost from natural counterfactual to future loss of threatened prey (mean per cell)
<i>Panthera atrox</i>	84%	84%
<i>Panthera spelaea</i>	64%	64%
<i>Smilodon populator</i>	84%	91%
<i>Smilodon fatalis</i>	82%	82%
<i>Homotherium latidens</i>	75%	76%
<i>Homotherium serum</i>	78%	78%
<i>Panthera tigris</i>	28%	41%
<i>Panthera leo</i>	37%	61%
<i>Panthera onca</i>	17%	24%
<i>Miracinonyx trumani</i>	59%	59%
<i>Panthera pardus</i>	30%	40%
<i>Puma concolor</i>	23%	31%
<i>Acinonyx jubatus</i>	15%	43%
<i>Panthera uncia</i>	0%	11%
<i>Neofelis nebulosa</i>	14%	35%
<i>Neofelis diardi</i>	11%	63%
<i>Lynx lynx</i>	17%	30%

Table 2: Summary large-felid primary prey data. CF = Natural counterfactual.

Felid	Felid Mass (kg)	Max Prey Mass (kg)	Min Prey Mass (kg)	Felid Range Size Present (cells)	Felid Range Size CF (cells)	Total Mammal Richness in Range	No. of Primary Prey
<i>Panthera atrox</i>	433	1698.2	45	NA	319	545	37
<i>Panthera spelaea</i>	380	2943.2	43.8	NA	879	356	47
<i>Smilodon populator</i>	295	2000	32.2	NA	531	1483	72
<i>Smilodon fatalis</i>	219	1698.2	21.3	NA	350	552	40
<i>Homotherium latidens</i>	189	1417.5	22.5	NA	320	278	31
<i>Homotherium serum</i>	189	1587	21.3	NA	338	464	40
<i>Panthera tigris</i>	163	825	12	201	739	1249	51
<i>Panthera leo</i>	161	1417.5	15.0	339	877	1294	112
<i>Panthera onca</i>	100	62.4	1.2	402	631	1667	83
<i>Miracinonyx trumani</i>	88	372	3.4	NA	90	264	31
<i>Panthera pardus</i>	55	180.3	0.9	935	1663	2131	192
<i>Puma concolor</i>	52	420.1	0.3	749	998	1806	370
<i>Acinonyx jubatus</i>	47	213.5	1.6	183	1143	1410	105
<i>Panthera uncia</i>	44	130	3.3	216	216	578	12
<i>Neofelis nebulosa</i>	21	180.3	0.2	125	152	635	183

<i>Neofelis diardi</i>	21	180.3	0.8	58	68	413	59
<i>Lynx lynx</i>	18	180.2	1.5	849	1283	930	120

Figure Legends

Fig. 1: Maps of large-felid (≥ 15 kg) and primary, most important, felid prey species richness, comparing the present reality and a ‘natural’ scenario: (a) current felid species richness; (b) current felid primary prey species richness; (c) natural counterfactual felid species richness; (d) natural counterfactual felid primary prey species richness; (e) difference between natural counterfactual and current felid species richness; (f) difference between natural counterfactual and current felid primary prey species richness.

Fig. 2: Plot of the relationship between primary prey species richness and felid species richness in our natural counterfactual (left column) and the current reality (right column), across five biogeographic realms and collectively. Full statistical details are available in Tables A1 and A2.

Fig. 3: Map indicating whether the felids lost between the natural counterfactual and present reality were the felids that lost the greatest proportion of their prey, where 0 indicates none of the felids lost had lost the greatest proportion of their prey and 1 indicates all felids lost were the felids that had lost the greatest proportion of their prey.

Fig. 4: Proportion of the natural counterfactual prey species that are unavailable if prey species currently classified as threatened or worse by the IUCN become functionally unavailable if each felid occupied its predicted natural counterfactual range.

Fig. 5: Plots of the relationship between the number of primary prey species lost against the number of large-felid species lost between the natural counterfactual and the current reality. Black lines represent linear regression plots for each bioregion represented and collectively for all biogeographic realm. Full statistical details are available in Table A3.

Fig. 6: Maps predicting the number of felids threatened by defaunation: a) the number of primary large-felid prey species that are classified as vulnerable or worse by the IUCN, excluding data deficient species; b-e) the number of large-felids at risk per grid cell using the relationship reported between the number of prey species lost and the number of felids lost using the global relationship (b), the Nearctic (c), the Neotropics (d), the Palearctic (e).