1   **Scavenging in the Anthropocene: human impact drives vertebrate scavenger**

2   **species richness at a global scale**

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4   **Running head:** Scavenging in the Anthropocene

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83

84 **Abstract**

85 Understanding the distribution of biodiversity across the Earth is one of the most

86 challenging questions in biology. Much research has been directed at explaining the

87 species latitudinal pattern showing that communities are richer in tropical areas;

88 however, despite decades of research, a general consensus has not yet emerged. In

89 addition, global biodiversity patterns are being rapidly altered by human activities.

90 Here, we aim to describe large-scale patterns of species richness and diversity in

91 terrestrial vertebrate scavenger (carrion-consuming) assemblages, which provide key

92 ecosystem functions and services. We used a worldwide dataset comprising 43 sites,

93 where vertebrate scavenger assemblages were identified using 2,485 carcasses

94 monitored between 1991-2018. First, we evaluated how scavenger richness (number

95 of species) and diversity (Shannon diversity index) varied among seasons (cold vs.

96 warm, wet vs. dry). Then, we studied the potential effects of human impact and a set

97 of macroecological variables related to climatic conditions on the scavenger

98 assemblages. Vertebrate scavenger richness ranged from species-poor assemblages to

99 species-rich (4 - 30 species). Both scavenger richness and diversity also showed some

100 seasonal variation. However, in general, climatic variables did not drive latitudinal

101 patterns, as scavenger richness and diversity were not affected by temperature or

102 rainfall. Rainfall seasonality slightly increased the number of species in the

103 community, but its effect was weak. Instead, the human impact index included in our

104 study was the main predictor of scavenger richness. Scavenger assemblages in highly

105 human-impacted areas sustained the smallest number of scavenger species, suggesting

106 human activity may be over-riding other macroecological processes in shaping

107 scavenger communities. Our results highlight the effect of human impact at a global

108   scale. As species-rich assemblages tend to be more functional, we warn about

109   possible reductions in ecosystem functions and the services provided by scavengers in

110   human-dominated landscapes in the Anthropocene.

111

112   **1. INTRODUCTION**

113   Scientists have long tried to disentangle the processes driving the latitudinal

114   biodiversity gradient showing that species diversity is greatest in the tropics and

115   decreases towards the poles (e.g., Hawkins *et al.,* 2003; Schluter, 2016). In a review,

116   Willig, Kauffman & Stevens (2003) listed several hypotheses proposed to explain this

117   pattern. For example, species diversity is expected to be higher in areas with more

118   available environmental energy, in accordance with the Productivity Hypothesis

119   (Pianka, 1966; Willig *et al.,* 2003). This hypothesis posits the amount of energy

120   available to plants and water availability limit productivity of an ecosystem, affecting

121   all species within trophic chains (Wright, 1983). Similarly, the Physiological

122   Tolerance Hypothesis suggests diversity is limited by the number of species able to

123   tolerate local conditions (Currie *et al.,* 2004). For example, extinction rates in tropical

124   climates are low compared to temperate regions because of climatic stability

125   (Dynesius & Jansson, 2000). The Evolutionary Speed Hypothesis posits that

126   speciation rates are higher in warmer (tropical) environments because generation

127   times are shorter, mutation rates are higher, and interspecific competition and

128   selection pressures are stronger (Allen, Brown & Gillooly, 2002; Currie *et al.,* 2004).

129   Because of the strong effect of latitude on climate, most hypotheses (such as those

130   above) suggest climatic conditions are the main drivers of variation in species

131   richness, and this is supported by several empirical studies. For example, an increase

132   in the number of vertebrate species has been related to annual potential

133 evapotranspiration, a measure of the energy available in the ecosystem (Currie, 1991).

134 Similarly, productivity, rainfall and temperature explained broad scale vertebrate

135 richness patterns (Hawkins *et al.,* 2003). In the Anthropocene, however, human-

136 related factors in addition to climate are expected to influence global species

137 distribution patterns, due to the multitude of effects that humans impose on the

138 ecosphere. Because of its pervasiveness, human impact may directly (e.g., by hunting,

139 Benítez-López *et al.,* 2017) and indirectly (e.g., by altering the habitat and amount of

140 food available to species) affect the number of species in a community and their

141 interactions. For example, human factors drive global avian species loss (Jetz,

142 Wilcove & Dobson, 2007), affect macroecological patterns of seed-dispersal

143 assemblages (Sebastián-González, Dalsgaard, Sandel & Guimarães, 2015), and

144 restrict local and regional movements of terrestrial mammal species (Tucker *et al.,*

145 2018). Thus, assessing the contribution of human impact on species richness and

146 diversity is a pressing ecological challenge in an increasingly humanized world.

147   Given that global consensus on the species latitudinal processes has not emerged

148 (e.g., Hillebrand, 2004), large-scale investigations of understudied communities are of

149 particular interest. Scavenger assemblages, or species that include carrion in their

150 diets (DeVault *et al.,* 2003; Wilson & Wolkovich, 2011), have received comparatively

151 little attention from the scientific community. Scavengers play pivotal roles in

152 ecosystems by stabilizing food webs (Moleón *et al.,* 2014; Wilson & Wolkovich,

153 2011), providing regulating services for organic food waste (O'Bryan *et al.,* 2018),

154 accelerating nutrient recycling (Wilson & Read, 2003), and removing potential

155 sources of infectious disease transmission (Ogada, Torchin, Kinnaird & Ezenwa,

156 2012). Among all scavenger species, vertebrate scavengers in general and obligate

157 scavengers in particular, are especially important in terrestrial ecosystems because

158 they are able to consume large amounts of carrion in short time periods (DeVault *et*

159 *al.,* 2003; Morales-Reyes *et al.,* 2017; Sebastián-González *et al.,* 2016). There is some

160 evidence that vertebrate scavenger diversity is lower in biomes with more extreme

161 climatic conditions (e.g., desert or tundra; Mateo-Tomás *et al.,* 2015), and a major

162 impact of human disturbance on the ecosystem functions supported by vertebrate

163 scavenger assemblages has been suggested (Mateo-Tomás *et al.,* 2017). However, a

164 comprehensive study evaluating macroecological patterns in scavenger assemblages

165 is lacking, especially in the context of the human drivers that make current

166 (Anthropocene) conditions unique in evolutionary history.

167   The goals of our study were twofold. First, we aimed to describe large-scale

168 patterns of species richness (number of species) and diversity (Shannon diversity

169 index) in terrestrial vertebrate scavenger assemblages. We know from previous

170 studies that scavenger communities have a different structure in warm and cold

171 seasons (Selva & Fortuna, 2007) and that season plays a critical role in how long

172 carcasses are available to be scavenged (e.g., Turner *et al.,* 2017). Also, several

173 scavenger species are migratory, which also calls for the consideration of different

174 seasons. Thus, we also explored the effect of season (cold vs. warm and wet vs. dry)

175 in shaping the patterns of scavenger richness and diversity. We expected to have

176 seasonal differences in the number and diversity of scavenger species. Second, we

177 aimed to identify the main macroecological factors driving terrestrial vertebrate

178 scavenger richness and diversity and tested five climatic, scavenging, and human-

179 related hypotheses (Table 1). We expected scavenger species richness and diversity to

180 be higher in areas that are wetter (Productivity Hypothesis), more stable and thus with

181 lower seasonality (Physiological Tolerance Hypothesis), and warmer (Productivity

182   Hypothesis, Physiological Tolerance Hypothesis, and Evolutionary Speed

183   Hypothesis).

184   Alternatively, vertebrate scavengers compete with microorganisms and

185   invertebrates for carrion. The latter species may benefit from warm and wet climatic

186   conditions, reducing the temporal window of carcasses consumption, and

187   outcompeting vertebrates (DeVault, Brisbin & Rhodes, 2004; Ray, Seibold &

188   Heurich, 2014). Under this hypothesis, termed "competitive hypothesis", richness of

189   the vertebrate assemblage would be reduced in the most warm and wet environments.

190   Moreover, modern human-mediated factors may over-ride evolved latitudinal or

191   ecological patterns, and affect scavenger richness and diversity in both positive and

192   negative ways. On the one hand, humans may increase the availability of carrion from

193   hunting, livestock or roadkills (Lambertucci, Speziale, Rogers & Morales, 2009; Oro,

194   Genovart, Tavecchia, Fowler & Martínez-Abraín, 2013), as well as the predictability

195   of carcasses available through wild harvesting (Read & Wilson, 2004), or artificial

196   feeding stations (Cortés-Avizanda *et al.,* 2016), ultimately benefitting scavengers. On

197   the other hand, habitat modification and loss, or direct persecution may reduce the

198   population viability of many scavenger species, reducing community diversity and

199   richness (Mateo-Tomás, Olea, Selva & Sánchez-Zapata, 2018). Here, we used the

200   largest compilation of vertebrate scavenging studies to date to identify the major

201   drivers of scavenger richness and diversity at a global scale.

202

203

204   **2. METHODS**

205   **2.1 Carcass monitoring and scavenger diversity**

206   We assembled a global dataset consisting of 43 study sites from 17 countries

207   across five continents (average number of studies by continent ± SD: 8.6 ± 6.8; range:

208   2-18) describing the vertebrate scavenger assemblages, comprised of species observed

209   consuming carrion. Data originated from studies performed between 1991 and 2018

210   when carcasses were located in the field (Figure 1; Supporting Information Appendix

211   S1). Carcass monitoring in all study sites met some minimum requirements to be

212   included in the analyses. All carcasses were either fresh or had been frozen while

213   fresh prior to placement in the field. Only studies using herbivore carcasses (e.g.,

214   terrestrial ungulates, rodents, and lagomorphs) were included (see Moleón *et al.,*

215   2017). Carcasses were monitored either by camouflaged automatic camera traps, from

216   observatories that were far enough to minimize scavenger avoidance, or from indirect

217   signs of scavenger presence at carcass sites. Carcasses were continuously monitored

218   until scavenging ended (only bones and/or skin remained) or the carcass disappeared

219   because a scavenger took it. We only included information on species that were

220   detected consuming carrion. When consumption was suspected, but not clearly

221   recorded, we assumed consumption if that species had already been detected

222   consuming other carcasses in each particular study site. See details on the specific

223   monitoring procedures for each site in the references listed in Supporting Information,

224   Appendix S1.

225   For each study site, we collected information on vertebrate scavenger richness

226   (measured as the total number of scavenger species documented at monitored

227   carcasses at each study site), and the coordinates of the center of the study site.

228   Carcass size ranged from rodents (e.g., 20 g, mice) to large ungulates (e.g., 900 kg,

229   bison). For 37 of the 43 datasets for which quantitative information was available, we

230   computed the scavenger relative abundance as the maximum number of

231   unequivocally different individuals of each species detected at a single carcass. This

232   was calculated by identifying the highest number of individuals of a scavenger

233   species simultaneously observed or appearing in a picture (e.g., Mateo-Tomás *et al.,*

234   2017; Moleón, Sánchez-Zapata, Sebastián-González & Owen-Smith, 2015). For some

235   species (e.g., lions *Panthera leo* and Andean condors *Vultur gryphus*), different

236   individuals visiting the same carcass were counted using identifying features like skin

237   patterns, injuries, and sexual dimorphism. As a measure of scavenger diversity, we

238   calculated the Shannon diversity index for each study site based on scavenger relative

239   abundance using the *vegan* package (Oksanen *et al.,* 2017).

240   Because one of our goals was also to study seasonal differences in the scavenger

241   community, we assigned each carcass to one season depending on the main climatic

242   changes in the region. We calculated scavenger richness and diversity separately for

243   each season for those study sites monitored across seasons. For most study sites we

244   considered two seasons: cold (fall and winter, N = 23) vs. warm (spring and summer,

245   N = 31). However, for those areas where the main climatic seasonal changes are

246   driven by rainfall, we divided them in wet (N = 8) vs. dry (N = 8).

247

248   **2.2 Macroecological drivers**

249   We explored the proposed hypotheses on how climatic, scavenging-related, and

250   human-related factors were associated with scavenger richness and diversity (Table

251   1). For each site, we extracted five variables linked to one or several of the hypotheses

252   that explained the latitudinal diversity gradient: 1) mean annual temperature (ºC); 2)

253   annual temperature seasonality, calculated as the standard deviation (SD) of mean

254   daytime temperature during the year; 3) mean of the total annual rainfall (mm); 4)

255   annual rainfall seasonality, calculated as the coefficient of variation (SD/mean) of the

256   monthly rainfall during the year; 5) Human Footprint (HF, Venter *et al.,* 2016).

257   Mean and SD of temperature (ºC) between 2001 and 2015, with spatial resolution of ~

258   5 km, were obtained from Oxford Daytime Land Surface Temperature (Weiss *et al.,*

259   2014). The dataset for this temperature product is Moderate Resolution Imaging

260   Spectroradiometer (MODIS) land surface temperature data (MOD11A2), which was

261   gap-filled to eliminate missing data caused by factors such as cloud cover (see Weiss

262   *et al.,* 2014). Mean annual and SD of rainfall (mm/year) between 2001 and 2015 were

263   obtained from the Climate Hazards Group InfraRed Precipitation with Station data

264   (CHIRPS; Funk *et al.,* 2015), which is a quasi-global gridded rainfall time series with

265   0.05° spatial resolution. Where CHRIPS data were not available (latitudes higher than

266   50°), we used Global Land Data Assimilation System (GLDAS; Rodell *et al.,* 2004),

267   with 0.25° spatial resolution, to calculate mean annual and SD rainfall (mm/year)

268   between 2001 and 2015. We calculated the mean annual rainfall by adding up all the

269   rainfall in a pixel throughout the year and then averaging this total annual rainfall

270   across years. HF is an index available in a global dataset of 1-km grid cells, created

271   from global data layers indicating human population pressure (population density),

272   human land use and infrastructure (built-up areas, night-time lights, land use/land

273   cover), and human access (coastlines, roads, railroads, navigable rivers). HF was

274   downloaded from https://datadryad.org/resource/doi:10.5061/dryad.052q5. This

275   database provides information with the HF at two years: 1993 and 2009, so we

276   assigned to each study site, the HF value closest to the date when the study was

277   performed.

278   We calculated the average of all these variables within a spatial extent of 20 km

279   buffer radio around the center of the coordinates at each study site. This buffer area

280 was selected to represent: 1) local conditions in the area where most of the

281 experimental carcasses were located, 2) regional conditions aiming to account for the

282 landscape heterogeneity in the surroundings of the study site and 3) to reflect the

283 habitat characteristics of the study sites at the biogeographical scale without dilution

284 from nearby areas with different land uses. Because the climatic variables are derived

285 from a model and have a large spatial resolution (5km), we did not expect them to

286 change significantly with different spatial extents. However, we also calculated all the

287 variables using a 10 and 30 km buffer to understand the spatial consistency of our

288 results, and found that the results were similar at all buffer scales (Appendix S2,

289 Tables S2.5-2.6).

290   We also calculated other covariates that could influence scavenger richness and

291 diversity, including: 1) carcass size, 2) sample size, or number of carcasses monitored

292 and 3) spatial autocovariance, which is a term accounting for the spatial

293 autocorrelation in the data. Scavenger richness and diversity may depend on available

294 carcass size, with large carcasses providing higher carrion biomass, a greater diversity

295 of distinct food types (e.g., meat, viscera, bone) and feeding opportunities (e.g.,

296 tearing, picking, bone-crushing, stealing), as well as carrion availability for longer

297 periods of time (Moleón *et al.,* 2015; Turner, Abernethy, Conner, Rhodes & Beasley,

298 2017). Carcass size was categorized as: small (<2 kg), medium (2-10 kg) and large

299 (>10 kg) adapted from Moleón *et al.,* (2015). Sample size was included because

300 higher numbers of carcasses are expected to contain larger numbers of scavengers,

301 until the community is completely sampled. To account for the spatial autocorrelation

302 in the structure of the scavenger communities, we added a spatial autocovariate (AC)

303 term. AC was computed from the weighted average distance of all neighboring

304 samples, indicating the degree of spatial clustering among dependent variables. We

305 used the *autocov_dist* function from the *spdep* library (Bivand, 2015).

306   Finally, because of the different sample sizes among study sites, we calculated the

307 sample coverage as the number of scavenging species recorded at each site by using

308 both presence/absence and individual-based abundance data (Chao *et al.,* 2014). With

309 the sample coverage, we estimated the number of species in each site under a

310 complete survey (i.e., when all the species present in an area are surveyed), and we

311 then compared the observed with the estimated species richness to evaluate if we had

312 monitored most of the species present.

313

314 **2.3 Statistical analyses**

315   We first used Generalized Linear Models (GLMs) to test if there was a latitudinal

316 pattern in scavenger richness and diversity, by relating them with the latitude of each

317 study site.

318   We then evaluated the relationships between scavenger richness and diversity and

319 macroecological variables critical to our hypotheses using GLMs. To do so, we first

320 calculated Variance Inflation Factors (VIF) for the macroecological predictor

321 variables using the *car* package (Fox & Weisberg, 2011) to assess collinearity.

322 Variables exhibiting VIF values exceeding three (temperature for scavenger richness

323 and rainfall for scavenger diversity, Zuur *et al.,* 2010) were eliminated from the

324 model. In each model, predictor variables were standardized to the same scale

325 (meaning that they were transformed to have a mean of 0 and standard deviation of 1)

326 and sample size (the number of experimental carcasses used in the study) was log-

327 transformed prior to analyses to improve normality.

328   As the relationships between scavenger richness or diversity and our predictor

329   variables could be non-linear, we first compared linear and quadratic one-predictor

330   models for latitude and for each macroecological variable and our dependent variables

331   using an AIC-based model selection. We used this information to decide whether each

332   macroecological predictor variable should be included as linear or quadratic in the

333   models for scavenger richness and scavenger diversity.

334   Finally, we fitted all the possible combinations and subsets of the predictor

335   variables for scavenger richness and scavenger diversity separately. We selected the

336   model with the lowest AICc, but when there was more than one model with a delta

337   AICc <2 with respect to the first ranked model, we implemented a model-averaging

338   function in the *MuMIn* package (Barton, 2013). This function averages parameter

339   estimates across all considered models for each dependent variable where the

340   respective parameter appeared, weighted by the relative importance of each model.

341   We used a Poisson distribution for modeling scavenger richness and a Gaussian

342   distribution for scavenger diversity in all GLM analyses. All analyses were repeated

343   using a database that included only those studies that used camera traps instead of

344   signs or direct observations in the scavenging monitoring (N=38), to account for the

345   imperfect detection of the latter methods. Finally, we calculated the percent of

346   explained deviance (i.e., the amount of variability explained by the model) of each

347   model.

348   To evaluate if carcass size, sample size and spatial autocovariance affected

349   scavenger richness and diversity, we fitted one-predictor GLMs relating them (see

350   results of this analysis in Supporting Information Appendix S2, Table S2.1). We

351   included the variables that were significantly related ($P <0.05$) to scavenger richness

352   and diversity as covariates in the multivariate models relating them with latitude and

353   the macroecological variables. Therefore, the most complicated model tested included

354   the significant covariates (carcass size and sample size for scavenger richness, and

355   carcass size for scavenger diversity, see results) and the five macroecological

356   variables. All analyses were performed in R version 3.4.1 (R Development Core

357   Team 2017).

358

359   **3. RESULTS**

360   **3.1 Global scale diversity patterns in scavenger communities**

361   Our global dataset included information from 2,485 carcasses in 43 study sites

362   (Figure 1, Supporting Information Appendix S1). We found high variability in

363   scavenger richness and diversity depending on the study site (Table 2). For example,

364   scavenger richness ranged from 4 (in developed areas in UK and Australia) to 30

365   vertebrate species (in a Polish temperate old-growth forest) from a total of 174

366   different species (7 reptiles, 79 mammals and 88 birds; Supporting Information

367   Appendix S3).

368   The scavenger assemblage also changed depending on the season when the study

369   was performed. We found higher scavenger richness and slightly higher scavenger

370   diversity in cold compared to warm seasons, but these variables did not differ

371   between dry and wet seasons (Figure 2). Finally, when all the assemblages were

372   standardized to an equal sample coverage (0.95), the estimated species richness was

373   highly correlated to the observed richness for both the abundance (Spearman's

374   correlation $rs = 0.68$, $p < 0.001$) and the incidence data ($rs = 0.84$, $p < 0.001$,

375   Supporting Information Appendix S4).

376

377   **3.2 Macroecological trends in scavenger diversity**

378   Contrary to our expectations, scavenger richness and diversity did not show any

379   latitudinal trends and were not affected by most of the climatic variables (Tables 2 &

380   3, Supporting Information Appendix S2, Table S2.3-2.4 & Figure S2.1). However, the

381   best models for scavenger richness included the variable describing human impact.

382   HF was the main factor influencing scavenger richness in an assemblage, showing a

383   quadratic relationship. When HF was lower than 7, we found more species-poor than

384   species-rich assemblages, which were found more frequently with HF values between

385   7 and 15; contrastingly, scavenging assemblages at very high HF values (>15)

386   exhibited low scavenger richness (Table 3, Figure 3a, Supporting Information

387   Appendix S2, Tables S2.3-2.4). There also seems to be a reduction in the variability

388   of scavenger richness values around the mean, with an increase of HF (Appendix S2,

389   Figure S2.2). Rainfall seasonality was also included in the averaged model for species

390   diversity, but, as for species richness, its effect was not significant (Figure 3b). The

391   results were similar at the other two spatial extents (10 and 30 km, Supporting

392   Information Appendix S2, Tables S2.5-2.6), supporting our alternative hypothesis that

393   human impact overrides other patterns.

394   The only variable that affected both species richness and diversity was carcass size

395   (Table 3, Figure 4a,b). Large carcasses were consumed by more scavenger species,

396   but scavenger diversity was greater at medium-sized carcasses. Finally, scavenger

397   richness also increased with sample size (number of experimental carcasses used in

398   each study, Table 3, Figure 4c). The results did not change when only studies using

399   camera traps were used for the analyses (N = 38, Supporting Information Appendix

400   S5).

401

402   **4. DISCUSSION**

403   Our results provide evidence that human impact is a dominant factor shaping

404   animal communities worldwide (Jetz *et al.,* 2007; Sebastián-González *et al.,* 2015;

405   Tucker *et al.,* 2018). The human-related factor was the only macroecological variable

406   included in the best models for scavenger richness. Our data (Fig. 3) clearly show that

407   regions with low human impact contained both species-rich and species-poor

408   vertebrate scavenger assemblages, while highly developed areas always had low

409   vertebrate scavenger species. HF combines information on human population density,

410   harvest, livestock, land use, land change and human accessibility. All of these factors

411   are known to affect vertebrates (e.g., Tucker *et al.,* 2018), to predict extinction risk

412   (Di Marco 2018), and to negatively affect particular scavenger species, at least at the

413   local scale (e.g., Bogoni *et al.,* 2016; Lambertucci *et al.,* 2009). However, this is the

414   first time that human impacts have been shown to be more important than the climatic

415   attributes in driving scavenger species richness at the global scale.

416

417   **4.1 Effect of human impact**

418   The loss of animal species, or defaunation, in humanized regions occurs at the

419   global scale (Dirzo *et al.,* 2014), and it also seems to be an important process shaping

420   the observed macroecological patterns in terrestrial vertebrate scavenger species

421   richness. Indeed, two of the main scavenger functional groups, obligate scavengers

422   and top predators, are among the most threatened species worldwide (IUCN, 2018).

423   More importantly, human impact (e.g., human population density, intensification in

424   land use, and land accessibility) is expected to increase, threatening the maintenance

425   of the ecosystem functions and services provided by scavengers (DeVault *et al.,*

426   2016). In areas where the most endangered species in the scavenger community (i.e.,

427   obligate scavengers and top predators) have become rare or absent, carrion may

428   remain in the field for longer periods of time, leading to an increase of generalist

429   scavengers that are less efficient at removing carcasses (Mateo-Tomás *et al.,* 2017;

430   Morales-Reyes *et al.,* 2017). This may have several consequences, such as increasing

431   the risk of pests and infectious disease transmission (Buechley & Sekercioglu, 2016;

432   Ogada *et al.,* 2012) or slowing down the cycling of nutrients (Moore *et al.,* 2004). For

433   example, the crash of vulture populations in the Indian subcontinent due to a

434   veterinary drug seemed to increase the population of feral dogs and consequently the

435   incidence of rabies (Markandya *et al.,* 2008). Such changes in vertebrate scavenger

436   guilds may also have consequences for ecosystem functioning as species-rich

437   communities are typically more efficient (Sebastián-González *et al.,* 2016), promoting

438   the stability of ecosystem processes and the services provided to humans (Moleón *et*

439   *al.,* 2014).

440   Moreover, we found a quadratic relationship between scavenger richness and

441   human footprint, so that the highest values of species richness were found in areas

442   with a certain level of human impact. The quadratic relationship suggests a decrease

443   in scavenger richness in areas with low to medium HF (<7). In some cases, moderate

444   human impact can increase availability of carcasses through roadkill, livestock, or

445   offcuts from wild harvests (Read & Wilson, 2004; Lambertucci *et al.,* 2009), thus

446   benefiting scavengers. For example, in Guinea-Bissau, hooded vultures *Necrosyrtes*

447   *monachus* were more frequently found in densely populated areas where there is a

448   higher garbage availability (Henriques *et al.,* 2018). Also, the highest values of

449   habitat suitability for the endangered Egyptian vulture *Neophron percnopterus* were

450   found in areas of intermediate livestock density (Mateo-Tomás & Olea, 2015).

451   However, highly human impacted areas become unavailable for many scavenger

452   species because of habitat reduction and fragmentation, pollution, or direct

453   persecution (e.g., Huijbers *et al.,* 2013; Lambertucci *et al.,* 2018). Combined, our

454   results suggest that scavenger communities may benefit from some degree of human

455   impact, but are sensitive to high human perturbation (Oro et al. 2013). From a

456   conservation and management perspective, finding that human factors are more

457   important than the climatic attributes for species richness at the global scale is yet

458   another reminder that human decisions may favor or reduce the capacity of

459   ecosystems to retain species richness and associated functions and services.

460

461   **4.2 Lack of support for latitudinal hypotheses**

462   In general, the hypotheses previously proposed to explain latitudinal patterns in

463   species richness were not supported by our data, as scavenger richness and diversity

464   were not affected by temperature or rainfall. Rainfall seasonality slightly increased

465   the number of species in the community, contrary to the predictions of the

466   Physiological Tolerance Hypothesis (Currie *et al.,* 2004). However, its effect was

467   overall very weak. Scavenging-related and human-related hypotheses seemed more

468   appropriate in explaining this pattern as human impact may be over-riding the effect

469   of environmental variables (e.g., Nogués-Bravo, Araújo, Romdal & Rahbek, 2008).

470   Additionally, high temperatures are linked to increased productivity or evolutionary

471   speed (Allen *et al.,* 2002; Currie *et al.,* 2004; Pianka, 1966; Willig *et al.,* 2003), which

472   may lead to higher scavenger richness. However, at the same time, high temperatures

473   may be enhancing the competitive interactions of vertebrates with microorganisms

474   and invertebrates, because the latter are benefitted from warm temperatures (DeVault

475   *et al.,* 2004; Ray *et al.,* 2014). These two forces may be affecting scavenger species

476   richness concurrently with opposite effects, thus counteracting each other and

477   preventing the appearance of an effect of temperature on scavenger species richness.

478

4.3 Effect of covariates

As expected, the size of the carcasses in each site affected the macroecological patterns described in this study. Carcass size has already been described as a major driver of scavenger assemblage richness and structure (Moleón *et al.,* 2015; Turner *et al.,* 2017). Larger carcasses are detected faster and consumed at higher rates, but the longer availability of the carrion resource permits its consumption by a larger number of scavenger species compared to smaller carcasses, which are usually consumed entirely by a single scavenger (Moleón et al., 2015). Moreover, large carcasses also allow niche specialization where different species utilize different carcass parts (e.g., lappet-faced vultures *Torgos tracheliotos* feeding on skin and Egyptian vultures eating remains on bones). Interestingly, in contrast to species richness, scavenger diversity reached the highest values in medium-sized carcasses, maybe because of the lower ability of large dominant scavengers (i.e., top predators and vultures) to gather at such carcasses and exclude other species (Moleón *et al.,* 2015, Pardo-Barquín *et al.,* 2018). Besides, top predators and vultures can frequently monopolize large carcasses, thus resulting in lower species richness and/or diversity (Pardo-Barquín *et al.,* 2018), while small carcasses are mainly used by mesopredators (Moleón *et al.,* 2015).

4.4 Seasonal changes

Our study also shows that species richness and diversity of terrestrial vertebrate scavenger assemblages vary among seasons. Several factors may be increasing the scavenger richness and diversity in the cold season. For example, the cold season typically has less food resources and harsher climatic conditions in temperate

503   ecosystems (e.g., Selva & Fortuna, 2007). This is reflected in greater availability of

504   carrion through natural deaths and a higher number of species adding carrion as a

505   food source (Turner *et al.,* 2017). In some areas, dominant scavengers known to

506   monopolize carcasses such as bears (*Ursus* spp.) hibernate during the cold seasons

507   (Allen, Elbroch, Wilmers & Wittmer, 2014), enabling other species to use carcasses

508   as a resource. Also, in highly seasonal areas, facultative scavengers may be more

509   predatory during the productive season because prey is more easily available (e.g.,

510   vulnerable neonates, migrating species), and so they may be less dependent on

511   scavenging (Pereira, Owen-Smith & Moleón, 2014). Finally, carrion decomposition

512   by invertebrates and microorganisms slows down when temperatures are low, and

513   carrion is therefore available over a longer time period (DeVault *et al.,* 2004).

514   Conversely, we did not find significant differences between the wet and dry season.

515   Carrion availability in warm regions tends to peak at the end of the dry

516   season (Pereira *et al.,* 2014). However, the differences in resource availability

517   between wet and dry seasons may be less extreme than in regions where the seasons

518   are characterized by cold and warm periods, especially in areas where long-distance

519   ungulate migrations are absent or artificially prevented.

520

521   **4.5 Caveats and future directions**

522   We only considered a species to be a scavenger in a region if it was documented

523   consuming carrion during one of the experimental studies used in our analyses

524   (Supporting Information, Appendix S1). Our approach thus ignores other species

525   known to be present in the areas that are likely scavengers, such as species that are

526   known from other studies to consume carrion. An alternative approach would be to

527   use lists of scavenger species present in different regions rather than only those

528   species documented to scavenge during our evaluations of carcass consumption. This

529   alternative approach might eliminate the potential bias of differences in the

530   experimental approach used in each empirical study, such as the differences in carcass

531   size or type. However, we chose not to pursue this alternative approach for two

532   reasons. First, lists of species present in a region, especially in under-studied regions,

533   are often incomplete and in some cases not available. Second, and perhaps more

534   importantly, even if a species has been documented as a member of the scavenging

535   community in one region it does not necessarily mean that is also scavenges in other

536   portions of its range due to changing dietary choices or competitive interactions (e.g.,

537   Sebastián-González *et al.,* 2016). Therefore, we chose to use only data from studies

538   that documented scavenging behavior under the conditions of the study site.

539   Relative scavenger abundance, and thus diversity, was calculated as the maximum

540   number of different individuals of each species detected at a single carcass. This is the

541   best measure of abundance we could get, but is unavoidably biased for solitary

542   species lacking skin patterns or sexual dimorphism because it is impossible to

543   differentiate among individuals, and so their relative abundances will always appear

544   low. An alternative method of measuring abundance would be to count the total

545   number of individuals of a given species in each photograph. However, this measure

546   may count the same individual several times and might bias towards species that visit

547   the carcasses for longer periods of time. More importantly, in our study, using the

548   total number of individuals of a species may be misleading because data were

549   collected using different experimental designs. For example, authors set camera traps

550   to have refractory periods from 30 second to 5 minutes. This may result in a large

551   variance in the number of individuals detected, which is related to the experimental

552   design instead of real biological differences. An alternative for estimating relative

553   species abundance for future studies would be to estimate the mean visit time of an

554   individual to a carcass and use this estimate to minimize re-counts of the same

555   individuals. Unfortunately, the information currently available is still scarce to do it

556   for most of the species studied. Moreover, data based on observations cannot be

557   measured using this approach, so we decided not to use it in our study. We also

558   acknowledge that the population and community metrics of abundance, richness and

559   diversity can often obscure considerable shifts within species assemblages (Read,

560   Parkhurst, & Delean, 2015) and hence non-significant effects of variables on

561   population metrics does not necessarily mean these same variables will not exert

562   profound influence on species composition and conservation status.

563   The spatial resolution of the climate (rainfall and temperature) datasets was low

564   and heterogeneous. Low spatial resolution and imbalanced scale in remote sensing

565   data can propagate noise into models and mask local-level effects of environmental

566   conditions, which may negatively impact the percentage of explained deviance in

567   model. Nevertheless, the value of these global remote-sensing datasets to

568   macroecology is well documented and their hyper-temporal availability provides

569   valuable insights into temporal oscillation of climate conditions.

570   Another consideration is that our metric of human impact (HF) is based on

571   information on human population density, land use, land change, and human access,

572   but not other specific factors that directly affect scavengers, such as animals killed

573   through vehicle collisions or the use of poisons. Thus, our analysis does not link the

574   HF with species-specific threats known to cause declines (i.e., Allan et al. 2019). The

575   HF metric combines several variables and we cannot separate the relative importance

576   and effect that each have on scavengers using only this variable. Thus, we encourage

577 further studies focusing on disentangling how the different aspects of human pressure

578 affect scavenger communities.

579   Finally, despite considerable effort invested in searching for data on scavenger

580 assemblages, our dataset is clearly unbalanced in space. There is an

581 overrepresentation of study sites in Western Europe and the USA, whereas other

582 regions such as Australia, Asia and South America contributed a small number of

583 studies (see Figure 1). Similarly, we lack study sites on large extents of the tropical

584 vegetation, deserts and boreal forests, so some particularities of these biomes may not

585 be considered here. For example, there are large areas such as the Sahel, for instance,

586 with light human footprints (low road and infrastructure densities) but high human

587 pressure on scavengers (Anadón, Sánchez-Zapata, Carrete, Donázar & Hiraldo,

588 2010). Finally, it is also important to notice that most of the regions assessed in this

589 study are located in human-dominated areas, and we lack sites from the most diverse

590 regions in the planet. Despite having an unbalanced sample distribution towards areas

591 in temperate latitudes, the importance of HF over climatic and latitudinal factors

592 could be expected to increase with a more balanced sample since most of the study

593 sites considered are located in regions with higher human pressure than

594 underrepresented regions (e.g., tropical and subtropical biomes). Thus, more complete

595 gradients of the environmental conditions should be investigated using new datasets

596 from understudied regions.

597

598 **4.6 Conclusion**

599   Our study highlights a novel consequence of the global changes driven by human

600 impact in the Anthropocene. Latitudinal or climatic patterns did not seem to be the

601 main drivers of the number of terrestrial vertebrate scavenger species in the

assemblages, but we found that scavenger species richness was low in highly human-impacted areas. This loss of scavengers may have detrimental consequences for the conservation and functioning of the ecosystems where these species live, reducing the quality and efficiency of the ecosystem services provided by scavengers. Thus, we urge for specific management and conservation actions to preserve scavengers and their functions worldwide.

Actions should include effective conservation plans of the most globally endangered scavengers (vultures, raptors and top predators) threatened by poisoning, veterinary drugs, persecution and mortality associated with infrastructures (power lines, wind farms, and roads) (e.g., Botha *et al.,* 2017). Furthermore, actions favoring traditional extensive farming systems and strengthening the link between farmers and nature can be a strategic tool for fostering positive perceptions of scavengers (Morales-Reyes et al. 2018), and promoting their conservation and the ecosystem services they provide. Both actions match within the strategic goals of UN Biodiversity Targets (https://www.cbd.int/sp/targets/, particularly those of strategies C & D) and should be addressed and reinforced on their upcoming renewal.

639

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880

TABLE 1 Climatic, scavenging- and human-related hypotheses explaining large-

scale patterns in vertebrate scavenger communities. We indicate their associated

predictions and the variables included in this study to evaluate hypothesis importance.

Hypothesis	Main associated variables	Main prediction
Climatic		
Productivity Hypothesis	Temperature Rainfall	Higher species richness and diversity in areas with higher available environmental energy
Physiological Tolerance Hypothesis	Temperature seasonality Rainfall seasonality	Larger species richness and diversity under more stable climatic conditions
Evolutionary Speed Hypothesis	Temperature	Larger species richness and diversity in warm environments where speciation rates are high
Scavenging-related		

Competitive Hypothesis	Temperature Rainfall	Lower vertebrate scavenger richness and diversity under warm and wet climatic conditions, as microorganisms and invertebrates may over-compete vertebrate scavengers

Human-related

Human impact over-rides other patterns	Human footprint (HF)	Reduced species richness and diversity in areas with higher HF

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888 **TABLE 2** Scavenger richness and diversity (Shannon diversity index) of vertebrate

889 scavenger communities. Mean, standard deviation (SD) and range (minimum-

890 maximum) values are provided. We also show the coefficients and p-values for the

891 generalized linear models relating these variables with latitude. The model for

892 scavenger richness included both carcass size (small, medium or large; see main text

893 for further explanations) and sample size (log-transformed number of carcasses

894 monitored) as covariates, while the model for scavenger diversity included only

895 carcass size (see complete results for these models in Supporting Information

896 Appendix S2, Table S2.2).

897

	Mean ± SD	Range	Latitude Coefficient	Latitude p-value
Scavenger richness	12.4 ± 6.07	4 - 30	-0.001	0.536
Scavenger diversity	1.40 ± 0.49	0.43 - 2.29	0.002	0.317

898

899

900

901 **TABLE 3** GLMs relating scavenger richness and diversity (Shannon diversity index)

902 with the macroecological variables calculated at 20km buffer extent. We present the

903 model averaged coefficients of each variable for models with delta AICc <2, with

904 respect to the model with the lowest AICc. Significant P-values as follow: *** $p <$

905 0.001, ** $p < 0.01$, * $p < 0.05$ are highlighted in bold. We also show the % of

906 explained deviance of the model (i.e., the proportion of the variability explained by

907 the model) and the number of studies included in the analyses (n). Human Footprint^2

908 is the quadratic term of the human footprint variable.

909

	Scavenger richness	Scavenger diversity
Sample size (log)	**0.362***	-
Carcass size: small	**-0.804***	-0.361
Carcass size: medium	-0.182	**0.367***
Carcass size: large	**2.585***	**1.355***
Human footprint	-0.081	-
Human footprint^2	**-0.144**	-
Rainfall seasonality	0.054	0.090
n	43	37
% Explained deviance	57.53	19.86

910

911

912

913 **Figures captions**

914 **FIGURE 1** Map showing the location of the 43 study sites. Each point represents one

915 study site. The size of the point is related to scavenger richness in the assemblage. In

916 the lower left corner, we show a detail of the study sites conducted in the Iberian

917 Peninsula because of the high number of studies overlapping in this region. The map

918 in the background represents the values of the human footprint variable measured in

919 2009.

920

921 **FIGURE 2** Boxplot representing (a) scavenger richness and (b) scavenger diversity

922 (Shannon diversity index) by season. We show the significance of the tests comparing

923 wet vs. dry ($n = 16$) and cold vs. warm ($n = 54$) seasons by means of pairwise t-tests,

924 with significant p-values (<0.05) in bold.

925

926 **FIGURE 3** Relationships between scavenger richness and the two macroecological

927 variables included in the averaged model: (a) human footprint and (b) rainfall

928 seasonality. The plots show the relationships predicted by the averaged model (black

929 line) and the 95% confidence interval for scavenger richness (grey shade).
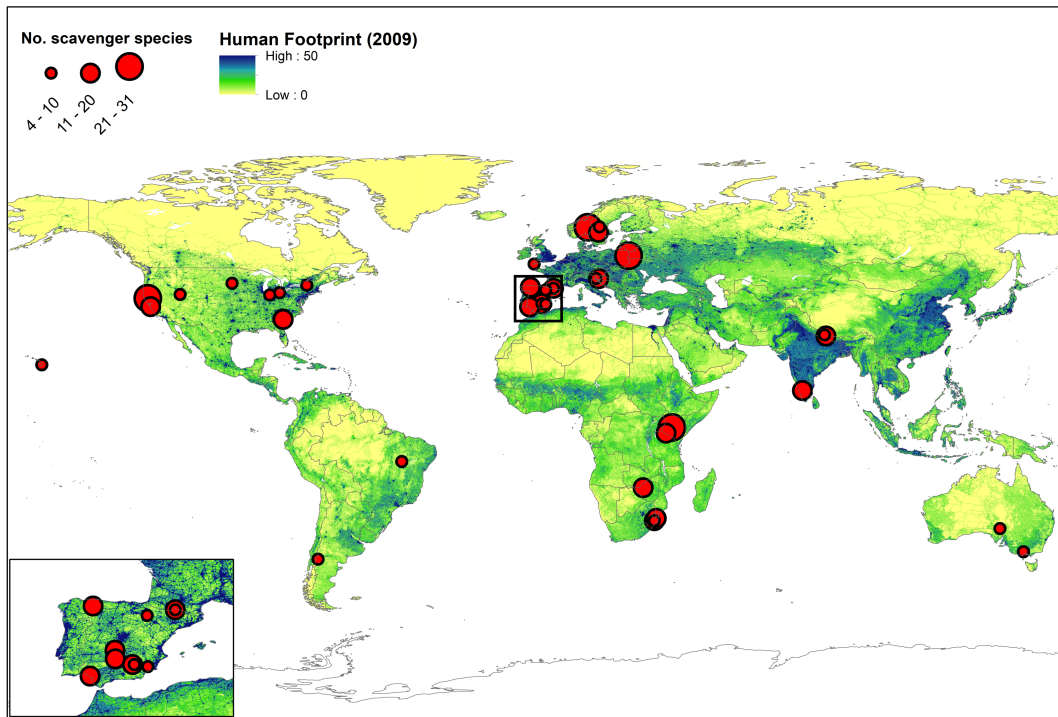
930

931 **FIGURE 4** Relationships between scavenger richness and diversity, and the

932 covariates, as inferred from generalized linear models averaging: (a, b) Carcass size,

933 (c) Sample size. For sample size, we also show the regression line for the

934 relationships. Note that the graph represents the pure relationships between the two

935 variables.

936

937

938   Figure 1

939

940

Figure 2

(a)

(b)

943   Figure 3

(a)

(b)

944

945

(a)

(b)

(c)