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28 **Functional traits driving species role in the structure of terrestrial vertebrate scavenger**
29 **networks**

30

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116

117 **Abstract** Species assemblages often have a non-random nested organization, which in
118 vertebrate scavenger (carrion-consuming) assemblages is thought to be driven by facilitation in
119 competitive environments. However, not all scavenger species play the same role in maintaining
120 assemblage structure, as some species are obligate scavengers (i.e., vultures) and others are
121 facultative, scavenging opportunistically. We used a database with 177 vertebrate scavenger
122 species from 53 assemblages in 22 countries across five continents to identify which functional
123 traits of scavenger species are key to maintaining the scavenging network structure. We used
124 network analyses to relate ten traits hypothesized to affect assemblage structure with the ‘role’ of
125 each species in the scavenging assemblage in which it appeared. We characterized the role of a
126 species in terms of both the proportion of monitored carcasses on which that species scavenged, or
127 scavenging breadth (i.e., the species ‘normalized degree’), and the role of that species in the nested
128 structure of the assemblage (i.e., the species ‘paired nested degree’), thus identifying possible
129 facilitative interactions among species. We found that species with high olfactory acuity, social
130 foragers, and obligate scavengers had the widest scavenging breadth. We also found that social
131 foragers had a large paired nested degree in scavenger assemblages, probably because their
132 presence is easier to detect by other species to signal carcass occurrence. Our study highlights
133 differences in the functional roles of scavenger species and can be used to identify key species for
134 targeted conservation to maintain the ecological function of scavenger assemblages.

135
136 **Keywords** Assemblage nestedness, carrion, facilitative interaction, normalized degree, obligate
137 scavenger, olfactory acuity, social foraging, vulture

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139

140 **INTRODUCTION**

141 How natural communities organize has interested ecologists for decades (Elton 1966).
142 Understanding the structure of communities may reveal critical insights on their functioning, such
143 as understanding the role of keystone species, ecological engineers, and interactions among
144 species (Hooper et al. 2005). The species in an assemblage, however, differ in their contribution to
145 community structure. Ecologists have recently realized that the most important species for
146 network structure may share several key functional traits (Coux et al. 2016). For instance, in seed-
147 dispersal assemblages, frugivorous birds play the most important network roles at a global scale
148 (Schleuning et al. 2014). Functional traits, regarded as any property of organisms that influence

149 performance (McGill et al. 2006), offer an ideal framework to better understand the mechanisms
150 driving assemblage structure and how different geographic areas may be characterized by
151 functionally similar species. This trait-based approach is especially useful in the current scenario
152 of global environmental change, with different areas experiencing different levels of species
153 extinction (Mouillot et al. 2013).

154 Scavenging is an important ecological process that facilitates the removal of carrion from the
155 landscape (Beasley et al. 2019), thereby contributing to the recycling of nutrients and ultimately
156 stabilizing food-webs (Wilson and Read 2003, Wilson and Wolkovich 2011). In addition, by
157 decreasing the time that carrion persists in the field, scavengers are regarded as pest and disease
158 regulators (Hill et al. 2018, Ogada et al. 2012a), leading to tangible benefits to humans (Moleón et
159 al. 2014). Among all scavenger species, terrestrial vertebrates are especially relevant because they
160 can consume large amounts of carrion over short periods of time (DeVault et al. 2003, Mateo-
161 Tomás et al. 2017, Morales-Reyes et al. 2017). Therefore, insights into the organization of
162 vertebrate scavenging assemblages around carrion resources are critical to understanding their
163 broader contribution to ecosystem processes linked to decomposition.

164 Scavenging assemblages can be organized following a nested structure, meaning that the
165 species feeding on carcasses visited by few consumers are subsets of those species feeding on
166 carcasses visited by more consumers (Selva and Fortuna 2007). Sebastián-González et al. (2016)
167 found that vultures (i.e., obligate scavengers) can promote nestedness in scavenging communities
168 where competition for carrion resources is large. In turn, highly nested scavenging assemblages
169 are more efficient carrion-consumers (Sebastián-González et al. 2020). Vertebrate scavenging
170 assemblages exhibit nestedness primarily through facilitative processes, such as mammalian
171 scavengers using cues from vultures to locate carrion (Kane and Kendall 2017), vultures
172 benefitting from scavenging eagles by providing information on carcass location (Kane et al.
173 2014), mammalian predators (Jackson et al. 2020) and conspecifics (Cortés-Avizanda et al. 2014),
174 or larger species opening up carcasses and allowing access to smaller scavengers and specialists
175 like bone-eaters such as bearded vultures *Gypaetus barbatus* (Selva et al. 2003, Moreno-Opo et al.
176 2016). Interspecific facilitation is especially important in scavenger assemblages because carrion
177 is a relatively unpredictable and ephemeral food resource (Cortés-Avizanda et al. 2012, DeVault et
178 al. 2003). However, we lack information on the functional traits that drive this facilitation process
179 in nested vertebrate scavenger assemblages.

180 Recent findings have shown scavenger species with large home-range sizes that are social

181 foragers remove carcasses at higher rates than other species (Gutiérrez-Cánovas et al. 2020).
182 These traits are shared by most vultures and some facultative scavengers, such as large
183 mammalian predators (e.g., lions *Panthera leo* and spotted hyaenas *Crocuta crocuta*; Gutiérrez-
184 Cánovas et al. 2020). These species are well known to be highly efficient scavengers (Mateo-
185 Tomás et al. 2017, Morales-Reyes et al. 2017, Sebastián-González et al. 2016). Vultures specialize
186 in the consumption of carrion (Cortés-Avizanda et al. 2014, Ruxton and Houston, 2004), and they
187 can outcompete other vertebrates for carrion resources (Byrne et al. 2019). Other species, such as
188 mesopredators, can also monopolize carcasses in human dominated landscapes devoid of large
189 mammalian predators (Buechley and Şekercioğlu 2016, DeVault et al. 2011), whereas bear species
190 *Ursus* spp. often monopolize carcasses in temperate and northern latitudes (e.g., Allen et al. 2014,
191 Krofel et al. 2012).

192 In addition to the amount of carrion that individuals of any species can consume (Gutiérrez-
193 Cánovas et al. 2020), each species can be important for its respective scavenger assemblage if it
194 contributes functionally towards maintaining or influencing the assemblage structure. Indeed, a
195 species with a driving influence on assemblage structure could make a disproportionately
196 important contribution to scavenging efficiency (i.e., carrion consumption rate), regardless of the
197 amount of carrion it consumes. For example, some scavengers are capable of finding and visiting
198 most available carcasses (e.g., Elbroch et al. 2015), thus potentially having a larger effect on the
199 structure of their assemblage and the regulation of the scavenging function. Moreover, approaches
200 using species-level network roles have already proven useful to link species function with their
201 ecological traits (Coux et al. 2016, Llopis-Belenguer et al. 2020, Stouffer et al. 2012). Thus,
202 network metrics can identify which functional traits of vertebrate scavengers maintain or influence
203 the structure of scavenging communities globally.

204 We used a global database consisting of 177 vertebrate scavenger species from 53 assemblages
205 across five continents. We identified relevant functional traits that characterize those species that
206 are critical to maintaining the structure of scavenger networks in terms of proportion of carcasses
207 visited (i.e., the scavenging breadth, or the so-called ‘normalized degree’ in network analyses) and
208 how good a species is in predicting the use of the carcass by another species (i.e., ‘paired nested
209 degree’, Almeida-Neto et al. 2008). We evaluated ten functional traits related to species biology
210 and foraging ecology that are hypothesized to affect assemblage structure (Table 1). In general, we
211 expected scavenger species with traits that enhance carcass detection and consumption, such as
212 having a keen smell ability or being highly mobile, to have the greatest effect on assemblage

213 structure, as they can find and exploit a larger proportion of available carcasses. We also expected
214 species with a large paired nested degree to have traits that facilitate carcass discovery or
215 consumption by other species, such as being vocal while foraging or being a social forager.

216

217 **METHODS**

218 ***Dataset***

219 We used information on 53 terrestrial vertebrate scavenger assemblages from 22 countries (see list
220 of assemblages in Appendix S1: Table S1). These datasets include information on 177 vertebrate
221 scavenger species (see a list of the species in Appendix S1: Table S2), including 95 birds, 75
222 mammals and 7 reptiles from 36 different families. The scavenger species consuming herbivore
223 carcasses were identified predominantly from the monitoring of carcasses using automatic camera
224 traps (47 studies), but also using direct sightings from a distance or from indirect signs of
225 scavenger interaction with the carcass (N=5, e.g., Selva and Fortuna, 2007). Carcasses were either
226 prey remains after predator kills, fresh meat or meat that had been frozen while fresh prior to
227 placement in the field. Each carcass was monitored continuously (24 h/day) until it was removed
228 by a scavenger or until its entire consumption, excluding bones and skin. Then, we identified all
229 the vertebrate species detected consuming each carcass. Data were collected between 1991 and
230 2019. The final dataset included a total of 2,629 herbivore carcasses ranging from 0.07 to 150 kg
231 in weight (mean \pm SD: 33.17 \pm 37.48 kg) and the vertebrate scavenger species feeding on each
232 monitored carcass. More details on the fieldwork methods and compilation of the dataset are
233 provided in Sebastián-González et al. (2019). All data used in this study can be found at Figshare
234 (doi: 10.6084/m9.figshare.14672250).

235

236

237 ***Characterizing species contribution to network structure***

238 For each scavenger assemblage, we created a network matrix where carcass i was represented by
239 rows and scavenging species j by columns. Each matrix cell a_{ij} indicated whether scavenger
240 species j had been detected consuming carcass i or not. Using these matrices, we calculated two
241 different network metrics that summarize different aspects of the contribution to network structure
242 by each scavenger species (see Fig.1 for a conceptual explanation of the network metrics). These
243 metrics are related to the role of the species in the assemblage. We calculated (1) scavenging
244 breadth as the normalized degree, defined as the proportion of realized interactions calculated as

245 k_j/S , where k_j (i.e., the species degree) is the total number of carcasses where a species was
246 detected scavenging and S is the number of surveilled carcasses in the network. Species with a
247 large normalized degree are important because they are present at most carcasses. We calculated
248 normalized degree with the ‘bipartite’ package of R (Dormann et al. 2009). Then, as most
249 scavenger networks are nested (see Appendix S1: Table S1), we calculated (2) species’ paired
250 nested degree as the average *paired overlap* of the matrix columns (i.e. species) described in
251 Almeida-Neto et al. (2008). For every pair of species in the matrix, the paired overlap is the
252 percentage of presences in a given column that are located at an identical row in another column.
253 The paired nested degree is the average of the paired overlaps between a focal species and all the
254 other species in the assemblage. In a perfectly nested network, when the degree of a species m
255 (i.e., k_m) is lower than the degree of another species n (i.e., k_n), the carcasses being consumed by m
256 are a subset of the carcasses consumed by n . Species with a high paired nested degree will follow
257 this pattern, whereas species that deviate from the pattern will have low paired nested degree
258 values. Species with a large paired nested degree are important because they appear in most of the
259 carcasses where other species appear. The paired nested degree was measured with the
260 ANINHADO software (Guimarães and Guimarães 2006). Although normalized degree and paired
261 nested degree are correlated (Spearman correlation coefficient = 0.67), we analyzed them
262 separately because they represent different ecological processes. The normalized degree identifies
263 species that are present at most carcasses, measuring in some way the niche breadth for a given
264 scavenger, i.e. on how many different carcasses can a species feed, independently of the presence
265 or not of other scavengers at that carcass. However, species with a large paired nested degree
266 consume most carcasses where other species with smaller paired nested degrees appear. Thus, the
267 paired nested degree also measures the overlap of a given species with others in the scavenger
268 community, e.g. how prone it could be to interact with others.

269

270 ***Scavenger functional traits***

271 We compiled information on ten functional traits that could affect the ability of a scavenger
272 species to detect, signal and consume carcasses (see the detailed description in Table 1): (1)
273 noisiness, (2) visual and (3) olfactory acuity, (4) mobility capacity, (5) mean home range size of
274 adults (km^2), (6) sociality in foraging behavior, (7) scavenging specialization (8), predatory
275 behavior, (9) main diet, and (10) mean adult body mass (kg). These variables may also influence
276 the role of a species in driving the network structure. Except for body mass and home range size,

277 we used categorical variables due to the limited information available for many species. The
278 classification of predatory behavior (top predator, mesopredator, non-predator) was made by
279 expert criteria of each contributing researcher in each respective study area, and thus could vary
280 by study system for any species. More information on how variables were defined can be found in
281 Table 1. Even though we looked for scientific information about all the traits for each species, our
282 database is not complete and there are some missing values. The total number of data obtained for
283 each variable can be found in Table 2 (column N). Information comes from published data.

284

285 ***Statistical analyses***

286 Our aim was to relate the network metrics (normalized degree and paired nested degree, i.e.,
287 response variables) with the species' functional traits (i.e., predictor variables). To do so, we
288 created one database combining information from the 53 networks, where each row was a species
289 in a network, including information on the species traits and the species network metrics in each
290 network where the species appears. Due to some missing values describing the scavengers'
291 functional traits, we performed statistical analyses in two steps.

292 First, we identified the functional traits that characterized species with a high paired nested
293 degree and normalized degree using all data available. This allowed us to identify the importance
294 of each species trait using the maximum information available for each of them. We did so by
295 fitting Generalized Linear Mixed Models (GLMMs) for each of the ten predictor variables (one
296 model for each predictor) and two random terms: species and network ID. We modeled the two
297 network metrics separately. Normalized degree was log-transformed and modeled using a
298 Gaussian distribution. Paired nested degree was transformed by dividing the number by 100
299 before modeling and fitted using a Beta distribution with the *glmmTMB* package (Brooks et al.
300 2017). Also, zero and one values were transformed to 0.001 and 0.999, respectively, to fulfill the
301 Beta distribution requirements. The only two continuous explanatory variables (i.e., body mass
302 and home range) were log-transformed. Individuals that were not identified to species level (i.e.,
303 only identified to genus) were eliminated from the analyses. We considered that the effect of a
304 variable received statistical support when the 95% confidence interval (CI) did not overlap zero.
305 Then, we selected variables that received statistical support in the one-predictor models to be used
306 in the second step. Also, because these relationships may be non-linear for the two continuous
307 variables, we compared linear and quadratic one-predictor GLMMs for each variable using AIC-
308 based model selection and determined whether each continuous variable should be included as

309 quadratic in the models.

310 Second, we ran a model with all the variables with statistical support identified in the first step,
311 but with only the species for which we had complete information so that models were comparable
312 (i.e., they had the same degrees of freedom). We fitted all possible combinations and subsets of
313 the predictor variables using the same data transformations and distributions described above. We
314 selected all models with $\Delta AICc < 2$ and implemented a model-averaging function with the
315 *MuMIn* package (version 1.9.5; Bartoń 2013). This function averages parameter estimates across
316 all models for each dependent variable where the respective parameter appeared, weighted by the
317 relative importance of each model. We calculated Variance Inflation Factors (VIF) for all the
318 explanatory variables using the *car* package (Fox and Weisberg 2011) to assess collinearity.
319 “Mobility” for normalized degree and “scavenging specialization” for paired nested degree were
320 excluded from the models because they had VIF values > 5 . We also tested possible interactions
321 among predictor variables by running models with all the variables plus one pairwise interaction
322 (i.e., we run one separate model for each possible interaction). All analyses were performed in R
323 version 3.6.2 (R Development Core Team, 2019).

324 We also wanted to account for the potential effect of three site-specific environmental variables
325 that are known to affect the structure of scavenger assemblages (Sebastián-González et al. 2020):
326 (a) carcass weight (mean weight of the monitored carcasses, in kg), (b) Normalized Difference
327 Vegetation Index (NDVI), a proxy of the primary productivity and biomass; and (c) Human
328 footprint (HF), an indicator of human population pressure, human land use and infrastructure, and
329 human access (Venter et al. 2016). HF has been calculated for two years, so we assigned to each
330 study site the HF value closest to the date when the study was performed: 1993 (N=3) and 2009
331 (N=50). The NDVI was calculated from the MYD13Q1 V6 product (NASA Land Processes
332 Distributed Active Archive Center). We calculated these variables within a 20 km buffer radius
333 around the coordinates of each study site to represent site conditions where carcasses were located.
334 More details on the calculations of these variables and on the criteria used to select the buffer
335 radius are provided in Sebastián-González et al. (2020). The significance and inclusion of these
336 three variables followed the same two steps as the species traits. All continuous variables were
337 scaled in the model.

338 Nestedness may be related to network size (Ulrich et al. 2009). Moreover, it is mathematically
339 more difficult to find a nested structure in very small networks. Therefore, we reran all the
340 analyses excluding those networks with less than 20 nodes (number of scavengers + number of

341 carcasses), or less than 7 scavenger species (all networks had more than 7 carcasses). We chose
342 this limit because almost all networks with more than 7 species were significantly nested (see
343 Appendix S1: Table S1).

344

345 **RESULTS**

346 The home range of the scavenger species ranged between 0.000001 and 165,514 km² (mean:
347 3,383.9, median: 8.12, SD: 16,784.4) and the mean body mass ranged between 0.01 and 500 kg
348 (mean: 11.9, median: 2, SD: 44.6). Most often, scavengers possessed good visual abilities (91%),
349 were solitary while foraging (76%), and were top predators (53%) in their respective study
350 systems (Appendix S1: Table S3). Species differed greatly in their network values for scavenging
351 breadth (mean: 0.25, SD: 0.25, range: 0.005-1) and paired nested degree (mean: 36.4, SD: 23.2,
352 range: 0-100).

353 The one-predictor GLMMs indicated that seven of the ten functional traits studied were related
354 to species' scavenging breadth (i.e., CI not overlapping with zero, Appendix S1: Table S4; Figure
355 2). Social species (i.e., species foraging in groups and/or families) had larger normalized degrees
356 than solitary species. Obligate scavengers, as well as terrestrial scavengers with good olfactory
357 abilities, large home ranges, and large body masses also presented higher values of scavenging
358 breadth, as did species with an omnivorous diet. When comparing all significant variables using a
359 model-averaging approach, obligate scavengers, social scavengers, and species with good
360 olfactory abilities were the taxa with highest scavenging breadths. None of the covariates (i.e.,
361 carcass weight, NDVI or human footprint; Appendix S1: Table S4) or interactions were
362 significant.

363 The paired nested degree was related to four functional traits by means of one-predictor
364 GLMMs: home range, sociality, predation and scavenging specialization. Solitary non-predators
365 with carnivorous diets and small home ranges showed lower paired nested degrees (Appendix S1:
366 Table S5). When modeling all these variables together, the most important trait affecting paired
367 nested degree was sociality, with solitary species showing the lowest degrees, species foraging in
368 family groups showing intermediate degrees, and social scavenger taxa having the highest degrees
369 (Table 2, Figure 2). Species with a large home range also contributed more than those with a small
370 home range, but the coefficient of this model overlapped zero. Sites with larger carcasses (i.e.,
371 higher carcass weight) also showed larger paired nested degree values (Table 2), but NDVI and
372 human footprint were not significant (Appendix S1: Table S5). We did not find any significant

373 interaction.

374 The results for normalized degree and paired nested degree were similar when excluding small
375 networks (Appendix S1: Table S6). Two additional variables (body mass for normalized degree
376 and home range for paired nested degree) affected the network role of the species. Also, there
377 were small changes in the effect of some covariates (i.e., NDVI and carcass weight).

378

379 **DISCUSSION**

380 Our study identifies the main functional traits that characterize vertebrate scavenger species with
381 important roles in maintaining different aspects of network structure at a global scale. Obligate
382 scavengers, as well as species with high olfactory acuity and social foraging behavior, had the
383 greatest scavenging breadth (largest normalized degree) and were, thus, the species foraging on
384 the highest proportion of available carcasses. As measured in this study, paired nested degree
385 identifies scavengers whose presence at a carcass is a good indicator of the presence of other
386 species consuming the same carcass. Thus, species with a high paired nested degree may compete
387 with other species for the resource, but they many also be involved in the facilitative processes
388 that promote nestedness in scavenging assemblages (Sebastián-González et al. 2016, 2019). Our
389 analyses show that paired nested degree increased with sociality, suggesting that social foragers
390 may facilitate carrion consumption by other species in scavenger assemblages (Sebastián-
391 González et al. 2016, 2019).

392 These results, based on the largest dataset compiled to date at a global scale, reinforce those of
393 previous studies showing that the presence in an assemblage of key species, such as vultures,
394 promote nestedness (Sebastián-González et al. 2016) and that scavengers with large home ranges
395 are more efficient carrion consumers (Gutiérrez-Cánovas et al. 2020). These functional traits can
396 be used to identify, in any scavenging assemblage, key species that should be managed or
397 protected to maintain or improve the ecological function of scavenging assemblages. At a local
398 scale, other species traits are known to affect scavenging patterns, such as being a top predator in
399 the Californian mountains (Allen et al. 2014), but the main assemblage roles can be replaced by
400 others when these species are absent from the community.

401 Being social while foraging was one of the main traits describing species frequently present at
402 many different carcasses (i.e., having a large scavenging breadth). Although it has been
403 traditionally assumed based on field observations that social scavengers are key species in the
404 assemblage (Selva et al. 2019), this is the first demonstration of their importance based on a large,

405 worldwide dataset. Social scavengers include mainly vultures, corvids and canids, and other
406 species such as spotted hyenas, lions and wild boars *Sus scrofa*. Even when social species compete
407 for carrion with conspecifics, this may be largely compensated by other positive effects emerging
408 from sociality. For example, social species tend to search for and defend food collaboratively and
409 use conspecifics as indicators of food presence (e.g., Dermody et al. 2011). When animals forage
410 in groups, there is a higher flow of social information and thus a higher chance of learning
411 efficient foraging techniques from more experienced individuals (Krause and Ruxton 2002).
412 Furthermore, group foraging may increase the dominance hierarchy, outcompeting other
413 scavenger species (Kendall, 2013). It also decreases the chances of being preyed upon, as larger
414 groups have higher chances of detecting potential predators (Krause and Ruxton 2002, Allen and
415 Krofel 2017). Social foraging behavior was also the most important trait of species with large
416 paired nested degrees, which was low for solitary foragers, intermediate for family groups, and
417 high for social species. This suggests social scavengers facilitate carrion use for other scavengers
418 by providing information that may be easiest to detect by other species to locate carrion. Given
419 that carrion is an ephemeral food resource, sharing might not be negative for a species, especially
420 when the carcass is large relative to the scavenger's body size. However, more studies are needed
421 to fully understand the facilitation processes among heterospecific scavengers.

422 Even though the statistical support was weak when using the entire dataset, species with large
423 home ranges had higher paired nested degree when excluding small networks. The differences in
424 the results between the two datasets may be related to small assemblages having fewer large
425 species with large home ranges. Large species are the first ones to be lost when an ecosystem is
426 defaunated (Dirzo et al. 2014). When these species are absent, the main network roles are taken by
427 other species. Overall, our results suggest that, when present, species with large home ranges play
428 an important role for the nestedness of the assemblage. These species have a greater capacity to
429 cover large areas, potentially allowing them to find and thus signal the presence of more carcasses
430 to other species (Ruxton and Houston 2004). As nestedness increases carrion consumption rates
431 (Sebastián-González et al. 2016, 2020), social species with large home ranges may be key in
432 providing scavenging functions to ecosystems (Gutiérrez-Cánovas et al. 2020). However, an
433 understanding of how scavenging rates by social species with large home ranges changes in
434 response to carrion availability would assist in determining their ability to influence food web
435 dynamics around carrion.

436 Vultures presented consistently high scavenging breadths, as expected from the strong selective

437 pressure for heightened food detection abilities to meet their energetic demands (Ruxton and
438 Houston 2004). Their soaring search strategy is energetically efficient, and their visual acuity
439 enables them to locate carrion from high altitudes, so they can forage effectively at a wider spatial
440 scale than all other scavengers (Byrne et al. 2019, Ruxton and Houston 2004). Many vulture
441 species also have strong beaks that can open thick-skinned carcasses, permitting access for other
442 species (Ruxton and Houston 2004). These features increase their ability to find and consume
443 carrion, promoting their widespread presence at the carcasses in assemblages where the species
444 are present.

445 Scavengers with high olfactory acuity also had high scavenging breadths, having been observed
446 at a relatively high proportion of carcasses. As carcass odor increases with time through
447 decomposition, olfaction is especially important for nocturnal scavengers and for locating
448 carcasses in densely vegetated areas. In general, mammals have high olfactory acuity and some
449 avian scavengers such as turkey *Cathartes aura*, lesser yellow-headed *C. burrovianus* and greater
450 yellow-headed vultures *C. melambrotus*, and southern caracaras *Caracara plancus* also use
451 olfaction for carcass detection (Poitier 2019, Poitier et al. 2019).

452 Our results highlight differences in the network role played by scavenger species depending on
453 their functional traits. However, scavenging efficiency (i.e., carcass consumption rate) depends on
454 many factors besides the scavenger species present in the assemblage, such as carcass size
455 (Moleón et al. 2015, Turner et al. 2017), season (Selva and Fortuna 2007), habitat (Smith et al.
456 2017, Turner et al. 2017), and human impact (Sebastián-González et al. 2019). As previously
457 found for the structure of scavenger assemblages (Sebastián-González et al. 2020), carcass size
458 influenced the role of the species in scavenging networks. Nonetheless, human footprint, which
459 was relevant at assemblage level, did not have any effect for the species network values. Species
460 abundance may also affect the role of a species in a network, as happens in other mutualistic and
461 antagonistic assemblages (Vázquez et al. 2007). Abundant species may consume more carcasses
462 just by chance than rare species. However, the effect of this variable was not tested due to the lack
463 of data on species abundance for all study sites. Finally, the order of arrival of the species to the
464 carrion may also affect the final structure of the assemblage, as the presence of some species may
465 discourage or facilitate the use of the carrion by others (Jackson et al. 2020). Thus, future studies
466 should explicitly test the relationship between species traits, including abundance, and carrion
467 consumption efficiency on a global scale, accounting as well for the order of arrival to the carrion.

468 Our results are based on two widely used network metrics, while other metrics are available,
469 we did not use them because of several reasons. For example, Simmons et al. (2018) use motifs
470 (subgraphs representing patterns of interactions between a small number of species) to evaluate
471 the effect of indirect interactions of the species in a network mediated by their interaction with
472 other species. However, our bipartite network is formed by species and carcasses, not two sets of
473 interacting species. Carcasses are dead organic matter and cannot show behavioral or numeric
474 responses that drive most types of effects. Also, many studies evaluate the modularity of the
475 network and the network nodes (e.g., Schleuning et al. 2014). In a preliminary test, we found that
476 most of the networks did not show a significant modular pattern (results not shown), probably
477 because the carcasses are relatively homogeneous within a site, and thus modularity is not a
478 characteristic pattern of these networks. When present, modules mostly represented some
479 differences in the carcass settings, such as carcasses being in different microhabitats (for example,
480 in more open vs. closed vegetation). As the identification of these differences depended more on
481 the sampling design and they were out of the scope of the paper, we excluded the modularity
482 analyses from the study.

483 We have found that species-level network metrics can be used by managers to identify species
484 traits that affect network structure and, therefore, key species for the conservation of the
485 scavenging function (Coux et al. 2016). This approach has already been used in other systems,
486 such as seed-dispersal (Vidal et al. 2014) and plant-pollination interactions (Lázaro et al. 2019).
487 However, there is still a big gap between the identification of key species in ecological networks
488 and the implementation of these results in conservation programs; a gap that should be filled by
489 better communication between ecologists and managers. Besides, given the link between network
490 structure and ecosystem function (Peralta et al. 2014), which has also been found in scavenging
491 assemblages (Sebastián-González et al. 2020), our findings can give new insights to predict the
492 functional responses of scavenger assemblages to potential species extinctions in changing
493 environments. For example, vultures (i.e., obligate scavengers) in particular, and large and social
494 facultative scavengers, should be monitored and conserved to maintain efficient scavenging
495 function (e.g., Ordiz et al. 2013). Many of these key scavenger species have sharply declining
496 populations globally (Margalida and Ogada 2018, Ogada et al. 2012b), and thus integrating their
497 conservation policies into current and future development strategies of governments (Safford et al.
498 2019) and fostering social actors' positive perceptions of scavengers (Morales-Reyes et al. 2018)
499 is essential for maintaining the valuable ecosystem service provided by scavenger assemblages.

500

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533

534 **Supporting Information**

535 Additional supporting information may be found online at: [link to be added in production]

536

537 **Open Research**

538 All data (Sebastian-Gonzalez 2021) is available in Figshare:

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540

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Table 1. Description of the species biological and ecological traits used in this study and details on the different categories used for the classification and major hypotheses that support the use of each variable.

Trait	Description	Details (and examples)	Major hypothesis
Noisiness	Use of vocalizations	Noisy: Species vocalizes loudly while foraging (e.g., hyaenas) Quiet: Species forages quietly (e.g., reptiles)	Noisy species can be used as indicators of carcass presence
Vision	Visual acuity	High (e.g., vultures); Low (e.g., wild boars)	High visual and/or olfactory acuity can facilitate the rapid location of carrion and arrival of these species can be used by others as indicators of carcass presence
Olfaction	Olfactory acuity	High (e.g., foxes); Low (e.g., Old World vultures)	High visual and/or olfactory acuity can facilitate the rapid location of carrion and arrival of these species can be used by others as indicators of carcass presence
Mobility	Mobility capacity	Aerial: Flying species (i.e., birds) Terrestrial: Non-flying species (i.e. mammals and reptiles)	Aerial mobility and larger home ranges can enable a greater capacity to explore vast extents of territory and find carcasses. These species can be seen by others as indicators of carcass presence
Home range	Adult home range	Mean home range in km ² (continuous variable)	Aerial mobility and larger home ranges can enable a greater capacity to explore vast extents of territory and find carcasses. These species can be seen by others as indicators of carcass presence
Sociality	Foraging behavior	Social: Foraging in groups (e.g., <i>Gyps</i> vultures)	Facilitative behaviors are more common in social foraging strategies.

		Family: Foraging in family groups (e.g., lions) Solitary: Foraging alone or in pairs (e.g. lynx)	Individuals may use other more conspicuous species to detect food.
Scavenging	Scavenging specialization	Facultative: Facultative scavenger (e.g. birds excluding vultures, mammals and reptiles) Obligate: Obligate scavenger (i.e. vultures)	Trophic strategies showing a high degree of specialization in carrion consumption such as obligate scavengers, carnivorous diets or top predators are present in species more adapted to carrion consumption and thus able to access and facilitate access to the carrion to other more generalist species
Predation	Predatory behavior	Top: Top predator (e.g. brown bears <i>Ursus arctos</i>) Meso: Mesopredator (e.g. raccoons <i>Procyon lotor</i>) Non_pred: Non predator (e.g. vultures)	Trophic strategies showing a high degree of specialization in carrion consumption such as obligate scavengers, carnivorous diets or top predators are present in species more adapted to carrion consumption and thus able to access and facilitate access to the carrion to other more generalist species
Diet	Main diet	Carnivorous (e.g. ocelots <i>Leopardus pardalis</i>); Omnivorous (e.g. mongooses)	Trophic strategies showing a high degree of specialization in carrion consumption such as obligate scavengers, carnivorous diets or top predators are present in species more adapted to carrion consumption and thus able to access and facilitate access to the carrion to other more generalist species
Body mass	Mean adult weight	Mean adult (female and male) weight in kg (continuous variable)	Larger-sized individuals are more conspicuous and more easily detectable. They are also stronger and have more abilities to open through the carcass skin, facilitating access to other species

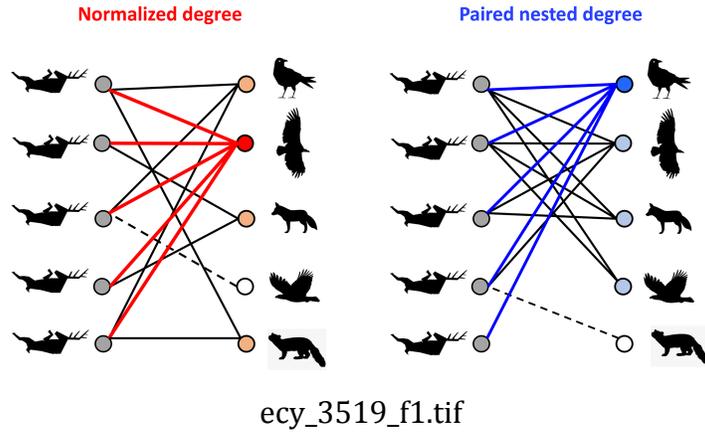
Table 2. Model averaged coefficients from Generalized Linear Mixed Models relating the network metrics (normalized degree and paired nested degree) of the species with the significant functional traits (i.e., those with CI not overlapping with zero) from Appendix S1: Tables S4 and S5. Species and network ID are included in all models as random factors. We present the model coefficients and the 97.5% upper and 2.5% lower level confidence intervals. Models with statistical support (i.e., intervals non-overlapping with zero) are highlighted in bold. We also show the sample size of each model (N).

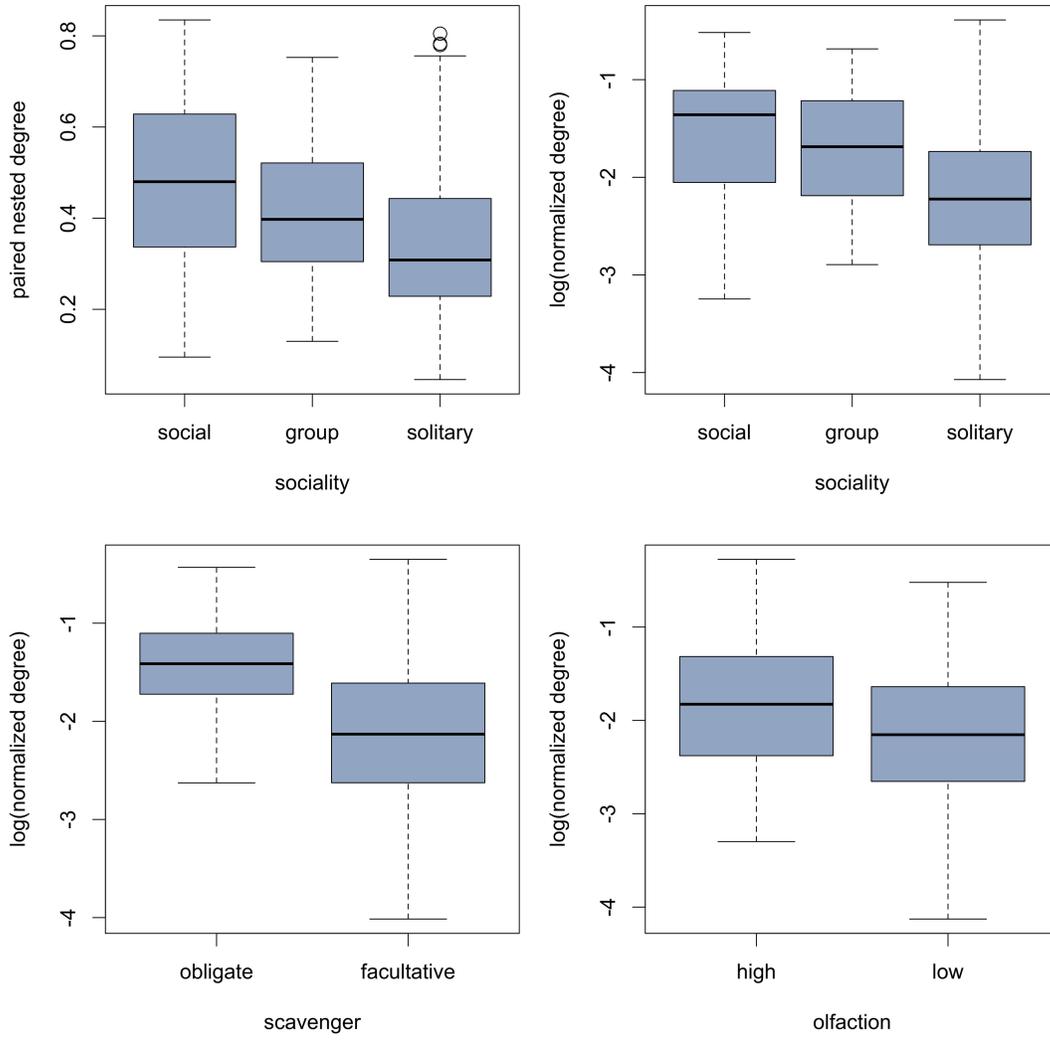
Network metric	Variable	Class	Coefficient	Lower	Upper
Normalized degree (N=364)	Sociality	Social	0.194	-0.506	0.895
		Family	0.625	0.156	1.094
	Scavenging	Obligate	1.451	0.882	2.080
	Olfaction	Low	-1.110	-1.641	-0.578
	Diet	Omnivorous	0.358	-0.064	0.780
Paired nested degree (N=359)	Sociality	Family	0.381	0.082	0.681
		Social	0.833	0.399	1.267
	Log (Home range)		0.099	-0.027	0.224
	Carcass weight		0.293	0.053	0.533

Figures captions

Figure 1. Conceptual figure representing the two network metrics used: normalized degree (i.e., scavenging breadth) and paired nested degree. The normalized degree is the proportion of realized interactions calculated, while the species' paired nested degree is the average *paired overlap* of the species. For every pair of species, the paired overlap is the percentage of times a species appears in the same carrion than the other species. Each panel represents a scavenger assemblage where left nodes (i.e., circles) characterize individual monitored carcasses and each right node identifies a scavenger species. Lines link scavenger species consuming a specific carcass. In the left panel, the vulture has the highest degree (red node and lines) and the eagle has the lowest degree (white node and dashed line). Species with a high degree appear in the largest number of carcasses. In the right panel, the raven (blue node and lines) has the highest paired nested degree of the assemblage whereas the genet (white node and dashed line) has the lowest. Species with a high paired nested degree may establish facilitation interactions with the other species, such as signaling carcass availability or opening carcasses to allow others to feed. Silhouettes from The Noun Project <https://thenounproject.com>, authors: m. turan ercan, bmijnlieff, Matt Dean, Imogen Oh and Ricardo Moreira.

Figure 2. Relationship between the contribution to network structure and the significant species traits from Table 2. These representations show the relationship among the predictor and response variables predicted by one-predictor models and it does not account for the effect of the other variables, as in the multivariate model in Table 2. These models include the species and network ID as random factors.





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