1   **Responses of carnivore assemblages to decentralized conservation approaches**

2   **in a South African landscape**

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12   **Abstract**

13   1. Conservation efforts in South Africa play out across multi-use landscapes where formal

14   protected areas coexist with private wildlife business (ecotourism and/or hunting) in a

15   human-dominated matrix. Despite the persistence of highly diverse carnivore guilds,

16   management idiosyncrasies are often orientated towards charismatic large predators and

17   assemblage-level patterns remain largely unexplored.

18   2. We conducted an extensive camera-trap survey in a natural quasi-experimental setting in

19   KwaZulu-Natal, South Africa. We sampled across a protection gradient characterized by a

20   provincial protected area (highest and formal protection status), a private ecotourism

21   reserve, game ranches, and traditional communal areas (lowest protected status). We

22   evaluated assemblage-level and species-specific responses of free-ranging carnivores to the

23   varying management contexts and associated environmental gradients.

24   3. Despite similar assemblage composition between management contexts, site-scale

25   carnivore richness and occupancy rates were greater in the formal protected area than

26   adjacent private reserve and game ranches. Carnivore occupancy was more similar between

27   these private wildlife areas, although putative problem species were more common in the

28   private reserve, and contrasted with depauperate assemblages in least protected communal

29   lands. Variation in carnivore occupancy probabilities was largely driven by land use contexts,

30   i.e., the level and nature of protection, relative to underlying fine scale landscape attributes

31   (e.g., distance to conservation fences) or apex predator populations.

32   4. *Synthesis and applications.* Our findings provide convincing empirical support for the

33   added value of multi-tenure conservation estates augmenting and connecting South

34   Africa's protected areas. However, our emphasis on free-ranging carnivores exemplifies

35   the importance of maintaining areas under long-term formal protection and the risks

36   with viewing lucrative wildlife business as a conservation panacea. We suggest that

37   unmanaged carnivore species be formal components of carnivore reintroduction and

38   recovery programs to better gauge the complementary conservation role of South

39   Africa's private land.

40   *Keywords:* predator, conservation planning, protected areas, natural resource management,

41   camera-trap, community occupancy model, multi-species modelling, hierarchical Bayesian

42   models

43   **Introduction**

44   The expansion of human populations and extensive land conversion severely limit the space

45   and resources available for wildlife (Powers and Jetz 2019). Across southern Africa, the

46   restricted coverage and insular nature of the existing formally recognized protected area

47   network, coupled with socio-economic challenges and shortfalls in political commitments to its

48   enlargement (Watson et al. 2014), has prompted conservation action in multi-use landscapes

49   (Di Minin et al. 2013a). The establishment of national policies bestowing varying degrees of

50   custodial rights over wildlife to individual landowners motivated a shift towards the

51   decentralization of natural resource management, from state to private governance (Pitman et

52   al. 2016). Resulting innovation among the private sector gave rise to a rapid and widespread

53   conversion of rangelands from livestock farming and agriculture to areas dedicated to

54 commercial wildlife industry (i.e., ecotourism and hunting). Biodiversity-rich land informally

55 protected under private ownership is now perceived as an increasingly important, and

56 economically viable, complement to the conservation role of formal protected areas (IUCN

57 management categories I-IV; IUCN, 2018) (Clements et al. 2019). However, conflicts of interest

58 between wealth and wildlife conservation dominate local decisions, making the implementation

59 of evidence-based conservation practices challenging (Pitman et al. 2016).

60 In South Africa, the growth of ecotourism and commercial hunting industry is heralded as a

61 conservation success. Wildlife is largely perceived to benefit from the rise of the wildlife

62 business through the coverage, representativeness and connectivity of protected/restored

63 habitat (Clements et al. 2019), but outcomes for predator conservation are less clear (Lindsey et

64 al. 2008; Pitman et al. 2016). Outside protected areas, prospects for conserving predators are

65 conditioned by profit-based natural resource management and the underlying business models

66 and financial motives (Clements et al. 2016). Management interventions in private ecotourism

67 reserves are disproportionally motivated by flagship and charismatic megafauna with high

68 marketing value (Caro and Riggio 2013), particularly large carnivores, greatly contributing to

69 their recovery (Mossaz et al. 2015). In land set aside to commercial production of game

70 species, much focus is on harvestable species (mainly ungulates) and the conservation

71 potential of restored habitat is undermined by conflicts with free-ranging predators (Lindsey et

72 al. 2008; Thorn et al. 2013; Pitman et al. 2016). These contrasting management and

73 conservation regimes coincide across relatively small scales, imbedded in human dominated

74 landscapes (Di Minin et al. 2013a). As anthropogenic pressure increases and goals shift from

75 saving endangered species and habitats to sustaining biological diversity and ecosystem

76 function, evaluating emergent properties of biodiversity across alternative land-uses is critical

77 for developing evidence-based integrative conservation action (Caro 2015).

78 Mammalian carnivores are central to the assessment of the ecological consequences of

79 decentralized approaches to wildlife conservation in South Africa (Lindsey et al. 2008); due to

80 their role as fundamentally important drivers of ecosystem structure and functioning (Roemer et

81 al. 2009; Estes et al. 2011). Despite historically high disturbance levels (Boshoff et al. 2016),

82 South African ecosystems maintain functionally diverse carnivore guilds (Caro and Stoner

83   2003). However, "large-predator-oriented" conservation management (Winterbach et al. 2013)

84   and research (Brooke et al. 2014) commonly overlook most guild-members. Within areas

85   managed at least partly for biodiversity conservation, it is proposed that conservation of most

86   carnivores, usually smaller and elusive species, is achieved via umbrella effects of maintaining

87   large and charismatic predator populations (Caro 2003). Yet, previous research has challenged

88   the umbrella concept behind large-predator-centred conservation (Dalerum et al. 2009) and the

89   associated increase in top-down pressure remains largely unexplored. In contrast, large

90   carnivores have experienced widespread population declines and extinctions in non-protected

91   land, potentially triggering mesopredator releases that facilitate an increase in the abundance of

92   subordinate species (Ritchie and Johnson 2009) or more complex changes in intraguild

93   dynamics (e.g., intraguild cascades; Levi & Wilmers, 2012). This interplay of management

94   interventions directed at larger predators, with concurrent persecution and conservation at a

95   regional scale, may inadvertently precipitate cascading effects over the full carnivore

96   assemblage with unknown but potentially far reaching implications for ecosystem functioning

97   (Ritchie and Johnson 2009).

98   Across different lands uses, changes in intra-guild interactions work in tandem with human

99   disturbance and its influence on resource availability in determining carnivore assemblages'

100   structure (Schuette et al. 2013) and its ecological effects (Dorresteijn et al. 2015). Although

101   larger predators are more prone to human-carnivore conflict, smaller carnivores experience

102   retaliatory persecution (Blaum et al. 2009), poaching and use in traditional medicines (Doughty

103   et al. 2015), while also being impacted by domestic dogs (Vanak and Gompper 2009).

104   Moreover, human-induced changes in habitat structure related to variable management

105   paradigms can negatively affect African carnivores (Blaum et al. 2009). In contrast, the

106   maintenance of highly abundant small mammal populations in unprotected land (Caro 2003)

107   and the stocking of commercial ungulates (Pitman et al. 2016) may promote locally subsidised

108   carnivore populations (Mateo-Tomás et al. 2015). Importantly, African carnivores greatly differ in

109   their ecological requirements (Caro and Stoner 2003), and are therefore not uniformly

110   susceptible to change agents. Incorporating inter-specific heterogeneity is thus necessary to

111   fully understand guild-level responses under multi-tenure estates (Heim et al. 2019) .

112 In this study, we consider South Africa's unique socio-ecological context – where high-diverse

113 carnivore assemblages persist in intricate management mosaics – to explore the relative role of

114 formal protected areas and private wildlife businesses for carnivore conservation. We

115 investigate variation in the distribution and structure of free-ranging carnivore assemblages in a

116 natural quasi-experiment setting, spanning a spatial continuum consisting of a 108-year-old

117 provincial protected area ('conservation reference'), a private ecotourism reserve, commercial

118 game ranches, and communally managed Zulu tribal authority land ('disturbance reference').

119 Specifically, we evaluate how free-ranging carnivores respond to the varying management

120 contexts, and associated fine-scale changes in level of nature protection and human

121 disturbance (Rich et al. 2016) and apex predator populations (Ritchie and Johnson 2009). Using

122 a hierarchical community modelling framework, we quantify spatial variation in the composition,

123 richness and spatial structure of carnivore assemblages across this unique protection gradient.

124 We empirically test expectations that *i*) carnivore richness and occupancy are positively

125 influenced by the level of protection within conservation areas (protected area and private

126 reserve) and inversely related to human disturbance (Rich et al. 2016), and, *ii*) that reduced

127 large carnivore occurrence outside conservation areas will increase medium and small

128 carnivore richness and occupancy via complex intra-guild cascades (i.e., the mesopredator

129 release hypothesis, Ritchie and Johnson 2009).

130 **Materials and Methods**

131 *Study area*

132 Our study was carried out in the Maputaland-Pondoland-Albany Biodiversity Hotspot in northern

133 KwaZulu-Natal, South Africa. The area (27˚80'S 32˚34'E) represents a spatial gradient of human

134 intervention that includes two adjoining reserves (uMkhuze Game Reserve and Mun-ya-wana

135 Private Game Reserve) and surrounding un-protected land (Fig. 1). uMkhuze is a 440km^2

136 provincially managed protected area established in 1912, part of iSimangaliso Wetland Park, an

137 UNESCO World Heritage Site. The Mun-ya-wana, 270km^2, borders uMkhuze south-eastern limit

138 and is a private wildlife reserve managed primarily for ecotourism since 1991, composed of

139 multiple properties without internal fencing. These areas function as a single conservation

140 complex for free-ranging wildlife (i.e., specie able to cross reserve's perimiter fences; Balme et

141   al. 2010) but greatly differ in management objectives and legacy of human disturbance. Lions

142   *Panthera leo* are present in both uMkhuze and Mun-ya-wana but are maintained at higher

143   density in the private reserve: 0.03 and 0.13 individuals per km^2 at the time of our study,

144   respectively. Private land to the south comprises a mosaic of commercial game ranches for

145   production of wild ungulate species, occasionally mixed with domestic cattle, and represents

146   large expanses of natural habitat and low human densities. Here, larger carnivores (e.g.,

147   spotted hyaenas *Crocutta crocutta*, leopards *Panthera pardus*, side-striped jackals *Canis*

148   *adustus*) are currently and historically persecuted (Balme et al. 2009). Communally managed

149   land abutting the eastern boundary of Mun-ya-wana encompasses two distinct Zulu

150   communities, with interspersing households, pastures and semi-natural vegetation. Wildlife

151   fences separate each of the areas, however, with exception of lions, cheetahs *Acinonyx jubatus*

152   and wild dogs *Lycaon pictus*, unable to cross the fence or actively reallocated if escaping,

153   boundaries are permeable to carnivores (e.g., Balme et al. 2010). The entire study area has

154   been identified as a priority landscape for multi-objective planning, conservation of biological

155   diversity and development of wildlife businesses (Di Minin et al. 2013a). The prevailing

156   vegetation is similar throughout the region, dominated by savanna broad-leaf woodland

157   varieties, mostly *Vachellia* and *Terminalia* species, interspersed with open grasslands and semi-

158   open wooded- grassland.

159   *Carnivore surveys*

160   We deployed white-flash camera-traps (Cuddeback Professional model) at 294 sites across the

161   ~700km^2 study area in late dry season, between August and November (75 ± 15 average

162   effective trap-days per site) (Fig. 1, see Appendix S1 Table S1-1 in Supporting Information).

163   For logistic reasons, three areas were surveyed in 2017 and the protected area in 2018. We

164   used a regular 2.25 km^2 grid to guide camera placement. The average minimum distance

165   between nearest stations was 1312 m (SD = 140 m; range = 965 - 1833 m). We placed

166   unbaited cameras on game paths and gravel roads (Cusack et al. 2015), mounted on trees or

167   metal stakes, 30cm above ground, 2-3 m away from, and at an angle to, the target animal

168   passage zone, and programmed to photograph at minimum delay (1s for daytime and 30s for

169   night-time). We used the R package camtrapR (Niedballa et al. 2016) to process camera-

170   trapping images. Species-specific detection histories were generated using occasions of 24h

171   only for days where the cameras were operational.

172   *Community occupancy model*

173   We adopted the hierarchical formulation of the community occupancy model with data

174   augmentation to estimate species-specific occupancy probability while accounting for imperfect

175   detection (Dorazio and Royle 2005). In this framework, the occupancy of species i at a site j, z_{ij},

176   is a Bernoulli random variable governed by occupancy probability ψ_{ij}. Here, we defined

177   occupancy as the probability of a species using the area sampled by a camera-trap station (site)

178   during the survey period, since home-ranges for more vagile carnivores can encompass several

179   sites. Sites have k occasions (camera days) and observations y_{ijk} are assumed to be Bernoulli

180   distributed with detection probability p_{ijk}, conditional on the latent true occupancy state z_{ij}. Both

181   occupancy and detection parameters can be modelled as a logit-linear function of site-specific

182   covariates. Resulting species-specific models are linked by indexing parameters and latent

183   variables by species, assuming species-specific parameters are random effects derived from a

184   common underlying distribution governed by community hyperparameters. Hyperparameters

185   specify the mean community response and variation among species to a covariate. With this

186   formulation, we accommodate inter-specific heterogeneity underlying assemblage-level

187   responses. For our particular application, we estimated species–specific occupancy

188   probabilities as random effects with area-specific intercepts ($\beta_{0,i,area[j]}$). This allowed us to

189   specifically estimate differences in baseline occupancy across management contexts and

190   among species. For inferences about assemblage size, we augmented the observation data

191   with all-zero observations of hypothetical species (Dorazio and Royle 2005) up to a total of 22

192   wild and free-ranging carnivore species potentially occurring in the region (Rowe-Rowe 1992).

193   We implemented an area-specific species inclusion parameterisation that estimates a latent

194   binary indicator variable $w_{i,area}$ indicating whether or not each species is part of the community.

195   This formulation allows formal comparisons of assemblage composition across areas.

196   Besides relating assemblage size and structure to the management context (i.e., area), we were

197   interested in testing the influence of fine-scale environmental effects on species-level site

198   occupancy; namely, spatial variation in the level of protection and human disturbance,

199   occurrence of apex predator populations, and habitat structure. We modelled species-specific

200   site occupancy probability as a function of: 1) the distance of each station to the nearest

201   conservation fence (DIST_CF), where sites inside conservation areas (protected area and

202   private reserve) have positive values and sites outside are negative (Rich et al. 2016); 2) the

203   intensity of space use by lions in the vicinity of a camera (LION), using estimates from L.

204   Gigliotti (In press), based on sightings and radio-telemetry data from each reserve's monitoring

205   efforts, adjusted for our survey period; and 3) remote-sensed tree cover estimates (MODIS

206   vegetation continuous fields dataset, 250m resolution,

207   https://modis.gsfc.nasa.gov/data/dataprod/mod44.php) as a measure of the spectrum of

208   vegetation structure ranging from open grasslands to woodland savannas (TREE). Lion space

209   use intensity (scaled from 0 to 1) and tree cover were quantified as average values within a

210   500m radius buffer around each camera station (see Appendix S2).

211   We modelled variation in detection probability as a function of site-level (camera) covariates;

212   namely the average width of the trail structure targeted (TRAIL_W), measured directly in front of

213   the camera trap and 20m up and 20m down the road/path, and vegetation density (VEG_D) in

214   the immediate vicinity (30m) of each site using mean Enhanced vegetation index values

215   (infrared reflectance measure of vegetation productivity) for the survey period as a proxy. These

216   were derived from MODIS EVI datasets: https://lpdaac.usgs.gov/. We hypothesized higher

217   carnivore detection probability in wider trails, surrounded by dense vegetation (hence, higher

218   EVI) forcing individuals to move through the trail area. Prior to analysis, we ensured no strong

219   collinearity existed between covariates (correlation coefficients $|r|>0.7$) and standardized all

220   covariates to have a mean of 0 and standard deviation of 1, with exception of LION which was

221   re-scaled from 0-1 and involved setting all values to 0 for areas where lions do not occur.

222   Considering the strong *a priori* justification for all covariates, we fitted a single global model

223   (Zipkin et al. 2010) specified as:

224 $$w_{i,area} \sim Bernoulli(\Omega)$$

225 $$z_{ij} \sim Bernoulli\left(w_{i,area[j]}\psi_{ij}\right)$$

226
$$logit(\psi_{i,j}) = \beta_{0,i,area[j]} + \beta_{1,i}\text{DIST\_CF}_j + \beta_{2,i}\text{LION}_j + \beta_{3,i}\text{TREE\_C}_j$$

227
$$logit(p_{i,j,k}) = \gamma_{0,i} + \gamma_{1,i}\text{TRAIL\_W}_j + \gamma_{2,i}\text{VEG\_D}_j$$

228 The species-specific regression coefficients $\beta_{1:3,i}$ and $\gamma_{1:2,i}$ (say θ) are treated as species-

229 specific random effects from a community-level distribution:

230
$$\theta_i \sim Normal(\mu_\theta, \sigma_\theta)$$

231 We analysed the model using Markov chain Monte Carlo (MCMC) simulation in JAGS (version

232 3.4.0), called from R using R2Jags package (Plummer 2011). We generated three chains of 150

233 000 iterations each, discarding 30 000 as burn-in, and thinned by 10. We followed best practice

234 recommendations on prior choice (narrow normal priors for the μ's and Beta(0.001,1) for Ω,

235 Guillera-Arroita et al. 2019). To assess convergence, we visually inspected the trace plots and

236 used the Gelman-Rubin statistic (values <1.1 indicate convergence, Gelman et al. 2004). We

237 evaluated model fit by estimating the discrepancy between the deviance residuals of the

238 observed and simulated data from the fitted model (Broms et al. 2016). We obtained a Bayesian

239 P-value of 0.502, indicating that the model adequately fits the data. Below we report posterior

240 means and 95% Bayesian credible intervals (BCIs), i.e., 2.5% and 97.5% percentiles, unless

241 stated otherwise. The code for the community occupancy model is provided in Appendix S3.

242 **Results**

243 Across all management contexts, we detected 16 wild carnivores. We removed the three large

244 carnivores that were constrained by reserve fences (lions, cheetahs, wild dogs). For the

245 remaining 13 free-ranging carnivores, we recorded a total of 7224 detections over 23702

246 effective trap days (Appendix S1 Table S1-2). Grouping by body size, these included two large

247 (>25kg), three medium (5-25kg) and eight small (<5kg) species.

248 Richness parameters had right-skewed posterior distributions, so we report results as estimate's

249 mode. Of the potential 22 free-ranging carnivores that potentially occur in the region, 14 (13-22)

250 species were predicted to be present in our study area. Within the different management areas,

251 carnivore richness was similar in the protected area (PA), private reserve (PR), and the game

252   ranch (GR): 10 (10-18), 9 (9-17), and 10 (10-20), respectively; but lower in communal land (CL):

253   7 (7-16), (Fig. 2A, Appendix S4 Fig. S4-1). Four species were recorded in only one

254   management area: serval *Leptailurus serval* in the PA, marsh mongoose *Atilax paludinosus* in

255   GR and African wildcat *Felis silvestris lybica* and selous's mongoose *Paracynictis selousi* in CL.

256   The remaining nine species, including the two large carnivores (spotted hyaena and leopard),

257   were present in all but CL. Five species occurred in all areas. See Appendix S1 Fig. S1-1 for a

258   visual representation of assemblage composition among management areas.

259   Species richness at camera sites varied more markedly across management areas: average

260   site-scale species richness was highest in the PA (6.03, 3–8), similar in the PR (4.24, 1–8) and

261   GR (3.97, 1–8), and lowest in CL (1.54, 0–5) where only six sites had more than two co-

262   occurring carnivores (Fig. 2B, Appendix S4 Table S4-1).

263   The average species-specific occupancy among areas followed a similar pattern (Fig 2C):

264   average occupancy was highest in the PA (0.55, 0.06–0.92), lower in the PR and GR (0.42,

265   0.16–0.80 and 0.35, 0.08–0.74, respectively), and lowest in CL (0.17, 0.09–0.25). Comparing

266   species-specific occupancy among management contexts, occupancy probability tended to be

267   highest in the PA (Fig. 3, Appendix S4 Table S4-2). Specifically, 23 out of 33 species-area pairs

268   had occupancy rates that were higher in the PA (i.e., >0.95 probability that the difference is

269   greater than 0, Fig. 4, Appendix S4 Table S4-3). Considering species occurring in both the PA

270   and its area pair, in only three instances did a species have higher occupancy outside the PA:

271   side-stripped jackal in PR and the stripped polecat *Ictonyx striatus* in both GR and CL. Species-

272   specific mean occupancy was similar between the PR and GR, except for the spotted hyaena

273   and the side-striped jackal, which were more widespread in PR, and the banded mongoose

274   *Mungus mungus,* which more common in GR. Occupancy probability was lowest in CL for 9 out

275   of 10 carnivores that occurred in multiple areas (Fig. 3).

276   Few carnivores exhibited strong associations with the site-scale variables hypothesized to

277   influence occupancy probability, with observed responses (i.e., BCIs not overlapping zero)

278   greatly varying among species in direction and strength (Table 1, Appendix S4 Fig. S4-2). No

279   consistent assemblage-level effects were detected as can be noted from the diffuse hyper-

280   parameter posterior distributions. For those species that did show responses to site-level

281   variables, spotted hyaena occupancy was positively related to distance to conservation fences

282   (β = 0.42, 0.02–1.03), while tree cover had a positive effect on the occupancy of leopard (β =

283   0.55, 0.20–0.92) and banded mongoose (β = 0.60, 0.13–1.18), and a negative effect on jackal

284   (β = -1.21, -1.91–-0.60) and white-tailed mongoose *Ichneumia albicauda* (β = -0.38, -0.67–-

285   0.10). Overall, species had higher detection probabilities in sites with high vegetation density

286   while larger carnivores' detectability was also higher in wider trails (Table 1, Appendix S4 Fig.

287   S4-2).

288   **Discussion**

289   Our research highlights a key role of formally recognized protected areas for free-ranging

290   carnivore conservation in South Africa's intricate multi-tenure landscapes. We found that

291   carnivore site richness and occupancy are higher in the protected area than in adjacent private

292   reserve and game ranches, and, especially in communal land. Our findings are consistent with

293   the hypothesized importance of increasing levels of protection, although we did not detect

294   accentuated differences between the ecotourism focussed private reserve and the commercial

295   game ranches. Using a quasi-natural experiment, we provide empirical evidence of the value of

296   multi-tenure conservation estates in augmenting and connecting South Africa's state-mandated

297   protected area network. However, we also highlight the importance of considering the specific

298   management paradigms employed to achieve such aims. Wildlife-oriented management can

299   result in the maintenance of similar level of carnivore richness but striking differences in finer

300   scale patterns such as distribution (local occupancy) and co-occurrence (local richness)

301   patterns, particularly for free-ranging and unmanaged taxa.

302   *Variation in free-ranging carnivore assemblages across management contexts*

303   Carnivore assemblage size and composition was similar across management contexts, with

304   exception of the highly disturbed communal land where none of the large and conflict-prone

305   carnivores occurred. This is consistent with previous research reporting similar mammal

306   richness, particularly carnivores, between areas dedicated to wildlife protection, albeit under

307   different conservation status, and extensive wildlife use areas (Kinnaird and O'brien 2012; Rich

308   et al. 2016). The permeability of perimeter fences to carnivore movement may act, however, to

309   homogenize adjacent carnivore assemblage composition. While the depauperate assemblage

310   observed in the communal lands is telling, precisely due to potentially high dispersal, species

311   richness in this context is likely a poor descriptor of the effects of relative differences across

312   other management contexts and respective conservation value. Across areas maintaining larger

313   expanses of natural habitat and enforcing some level of protection, species responses are likely

314   to differ in more subtle ways and at different scales, such as intraspecific variation in occupancy

315   rates.

316   Assuming occupancy rates as proxy for local abundance (Steenweg et al. 2018), our results

317   suggest that free-ranging carnivores are generally more common inside the provincial protected

318   area, the only area under formal protection and long-term conservation management (Fig. 2C).

319   Species occupancy decreased with decreasing protection status, from formal protected areas,

320   to private reserves and game ranches, and to communal lands, a pattern that spanned the full

321   body mass range, although larger free-ranging predators benefited more from increased

322   protection (Fig. 4). Interestingly, this result is contrary to expectations under the mesopredator

323   release hypothesis, which predicts increases in the occurrence of medium- and small-sized

324   species where suppression by dominant large carnivores is alleviated (Ritchie and Johnson

325   2009). We suggest disturbance agents outside the protected area may prevail over changes in

326   intra-guild dynamics. In fact, higher carnivore occupancy inside conservation areas relative to

327   unprotected areas has been shown in Kenya (Kinnaird and O'brien 2012; Schuette et al. 2013)

328   and Botswana (Rich et al. 2016), and attributed to human disturbance and associated threats,

329   such as retaliatory killing (Thorn et al. 2013) or livestock husbandry and vegetation

330   encroachment (Blaum et al. 2007; Blaum et al. 2009). The transversal importance of the formal

331   protected areas relative to game ranches and communal lands is consistent with this general

332   pattern; however, carnivore occupancy was also lower in the private reserve, where species

333   currently occur with seemingly minimal human interference.

334   Proactive management practices have been shown to positively influence carnivore

335   communities (Farr et al. 2019; Oberosler et al. 2019), yet this is unlikely to be the explanation

336   for observed differences in carnivore occupancy between the protected area and private

337   reserve (Fig. 2-4) since anti-poaching efforts and management capacity are similar. Spatial

338 variation in lion encounter risk also did not influence carnivore occupancy as we might have

339 expected based on evidence of top-down suppression of sympatric carnivores by lions (Vanak

340 et al. 2013). While we failed to detect site-scale patterns of lion avoidance, differences in

341 occupancy can reflect intensified numerical control by lions at the population-level within the

342 private reserve (Jiménez et al. 2019).

343 A non-exclusive, potential explanation for the observed differences is the historical differences

344 in disturbance trajectories between the protected area and private landscapes. Prior to the

345 growth of South Africa's commercial wildlife industry, most landscapes had been severely

346 disturbed and wildlife populations greatly depleted (Boshoff et al. 2016). At over 100 years old,

347 uMkhuze is one of the oldest protected areas in South Africa; a long-term 'conservation island'.

348 In contrast, the ecotourism reserves and game ranches in the region are former livestock and

349 agricultural farms that were restored less than four decades ago. While large carnivore

350 populations originate from human-led reintroductions, the unmanaged free-ranging carnivores

351 echo a more natural restoration process of depleted populations. Little is known about

352 population demography of medium and small African carnivores; particularly how management

353 idiosyncrasies, such as large predator reintroductions and their maintenance at oftentimes

354 unnaturally high-densities in ecotourism reserves, or targeted persecution in ranchland (Lindsey

355 et al. 2008), influences the recolonization and recovery of free ranging predators. We suggest

356 wild populations recovery trajectories following habitat transformation may thus be a

357 fundamental but often unheeded aspect underlying conservation assessments in southern

358 Africa private lands.

359 Nevertheless, the conservation value of private wildlife areas was reinforced by the contrast to

360 the depauperate carnivore assemblage found in communal lands. Prospects for predator

361 conservation in South Africa's private lands have been attributed to habitat protection and large

362 carnivores' reintroductions (Mossaz et al. 2015) but suggested to be undermined by increased

363 human-carnivore conflict on game ranches (Lindsey et al. 2008; Pitman et al. 2016). While we

364 observed distributional contractions in game ranches relative to the private reserve for larger

365 and putative problem species (hyaena and jackal), most other free-ranging carnivores were

366 similarly or more common in game ranches. For species less susceptible to conflict, game

367 ranchland under extensive management and low cattle stocking rates (Blaum et al. 2009), like

368 in our study area, may provide similar suitable habitat to private reserves, with analogous

369 vegetation structure, abundant resources and low human encroachment. Smaller species may

370 also benefit from a decrease in top down pressure with restricted distribution of dominant

371 carnivores outside the private reserve. Hence, our results support the potential of game

372 ranching as a compatible land-use option for carnivore conservation but also the need for

373 holistic conflict mitigation strategies, such as the formation of conservancies (Lindsey et al.

374 2009) or the implementation of guild-level revised control and trophy hunting statutory systems

375 and coexistence programmes, as done for leopards in the region (the only conflict-prone large

376 carnivore widespread in game ranchland) (Balme et al. 2009).

377 Carnivore species exhibited stronger responses to the varying management contexts, rather

378 than associated site-scale landscape attributes. This is perhaps expected as covariates

379 measured at a finer-scale are correlated with management practices and are thus more variable

380 between, rather than within, areas, leading to context dependent processes we did not consider.

381 The occupancy patterns that emerge may also reflect an important role of wildlife fences, not as

382 barriers to wildlife movement, but as effective physical barriers to external disturbances such as

383 poaching and human-wildlife conflict (Packer et al. 2013). This is evidenced by the positive

384 influence of distance to conservation fences on the distribution of larger and wider-ranging

385 species, more susceptible to edge effects (Balme et al. 2010). However, observed meaningful

386 associations between occupancy and arboreal cover (Table 1) suggest variable species

387 associations with dry-woodland savannas structure that are transposable across contexts.

388 *Implications for carnivore conservation in multi-tenure landscapes*

389 Our assessment of structural differences in free-ranging carnivore assemblages suggests that

390 formal protected areas are of highest conservation value compared to private wildlife

391 businesses and communal lands, which is significant given the strong carnivore research and

392 conservation history of private wildlife areas in the region (Balme et al. 2009). This supports the

393 need for often disregarded guild-level considerations in predator management plans and

394 regional carnivore conservation efforts. The success of such endeavours depends on the

395 development of mechanistic links between guild-level carnivore responses and applied

396   conservation management, as attempted for large African predators (Winterbach et al. 2013).

397   Fortunately, an increasing understanding of South African private landowner's strong

398   conservation motivations, rather than singly economical driven options, creates scope for

399   realigning ecotourism, hunting activities, and biodiversity conservation, under more holistic

400   initiatives (Cousins et al. 2008; Di Minin et al. 2013b; Clements et al. 2016).

401   Importantly, our work provokes hypothesis on ecosystem wide cascading effects with several

402   socioecological ramifications. Much theory on predator ecosystem function concerns the role of

403   apex species where they have been retained or restored. For subordinate carnivores,

404   abundance increases are expected in the absence of apex predators (Roemer et al. 2009;

405   Ritchie et al. 2012), while the implications of standing variation in mesopredator abundance and

406   distribution, irrespective of apex predator effects, remain generally unknown or

407   underappreciated. Non-apex, often free-ranging, African carnivores likely play major roles as

408   scavengers and regulators of small-vertebrate communities, with valued consequences for pest

409   control, seed consumption and dispersal, or waste removal and disease control (Roemer et al.

410   2009; O'Bryan et al. 2018). Even with the minimal changes in assemblage structure observed in

411   this study, important differences in functional diversity can occur (Fig 2; Bruno and Cardinale

412   2008). These are central points to the hidden intricacies of food webs that underlie predator

413   management plans (Ritchie et al. 2012) and broader ecosystem-wide effects of domestication

414   and commodification of wildlife, identified as a pressing issue for biodiversity conservation in a

415   recent horizon scan for South Africa as the government aims to further unlock financial income

416   from wildlife (Seymour et al. 2019).

417   Multi-tenure conservation estates have emerged as the conservation model for southern Africa

418   (Di Minin et al. 2013a). Our work with free-ranging carnivores corroborates the complementary

419   value of private land for carnivore conservation (Lindsey et al. 2008; Clements et al. 2019) but

420   also exemplifies the risks of viewing wildlife business as a conservation panacea (Caro 2015;

421   Pitman et al. 2016). We encourage future similar work that evaluates the transferability of our

422   findings to other southern African multi-use landscapes. Nevertheless, rather than generalizing

423   the singular conservation value of land under formal and strict protection, we believe the higher

424   free-ranging carnivore occupancy in the protected area illustrates well the need for adequate

425   conservation benchmarks guiding management and conservation models (Hayward 2009). 'Old'

426   protected areas such as uMkhuze are the closest references to pristine nature in highly

427   transformed landscapes of South Africa (with exception of few larger systems like Kruger

428   National Park). On the other hand, the widespread implementation of private wildlife areas,

429   whether or not legally gazetted, is a relatively recent process (ca. five decades, Lindsey et al.

430   2008). This historical contrast implies fundamental differences between preservation and

431   restoration norms in conservation practice across land tenure types (Hobbs et al. 2009).

432   Ensuring the long-term maintenance of formal protected areas is thus of paramount importance

433   as parallel efforts to unravel patterns and processes involving overlooked but functionally key

434   taxa become part of coordinated systematic conservation planning across multi-tenure estates

435   (Clements et al. 2019).

436   **Authors' contributions**

437   GCS and LHS conceived the ideas and designed the study; GCS collected the data; GCS and

438   CS analysed and interpreted the data with contributions of LHS and MSR; GCS led the writing

439   of the manuscript. All authors contributed critically to the drafts and gave final approval for

440   publication.

450   **Data availability statement**

451 Data available via the figshare repository https://doi.org/10.6084/m9.figshare.12287555

452 (Curveira-Santos & Swanepoel, 2020).

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614 **Table 1.** Coefficient estimates of hyper-parameters for site covariates hypothesized to influence

615 occupancy and detection probability, from the community occupancy model. Species responses

616 are the count of species with coefficient's 95% Bayesian credible intervals (BCIs) not

617 overlapping zero, summarized by the direction of the response.

Community-level hyper-parameter	β	SD	95% BCI	Species responses	
				+	-
Occupancy probability ($\beta_{1:3}$)					
Distance to conservation fence (DIST_CF), m	0.20	0.14	-0.08–0.47	1	0
Lion encounter risk (LION), 0-1	0.58	0.51	-0.45–1.56	0	0
Tree cover (TREE_C), %	-0.02	0.23	-0.47–0.42	2	2
Detection probability ($\gamma_{1:2}$)					
Trail width (TRAIL_W), m	0.09	0.13	-0.18–0.34	3	0
Vegetation density (VEG_D), n.a.	0.24	0.13	-0.00–0.50	7	1

618

619
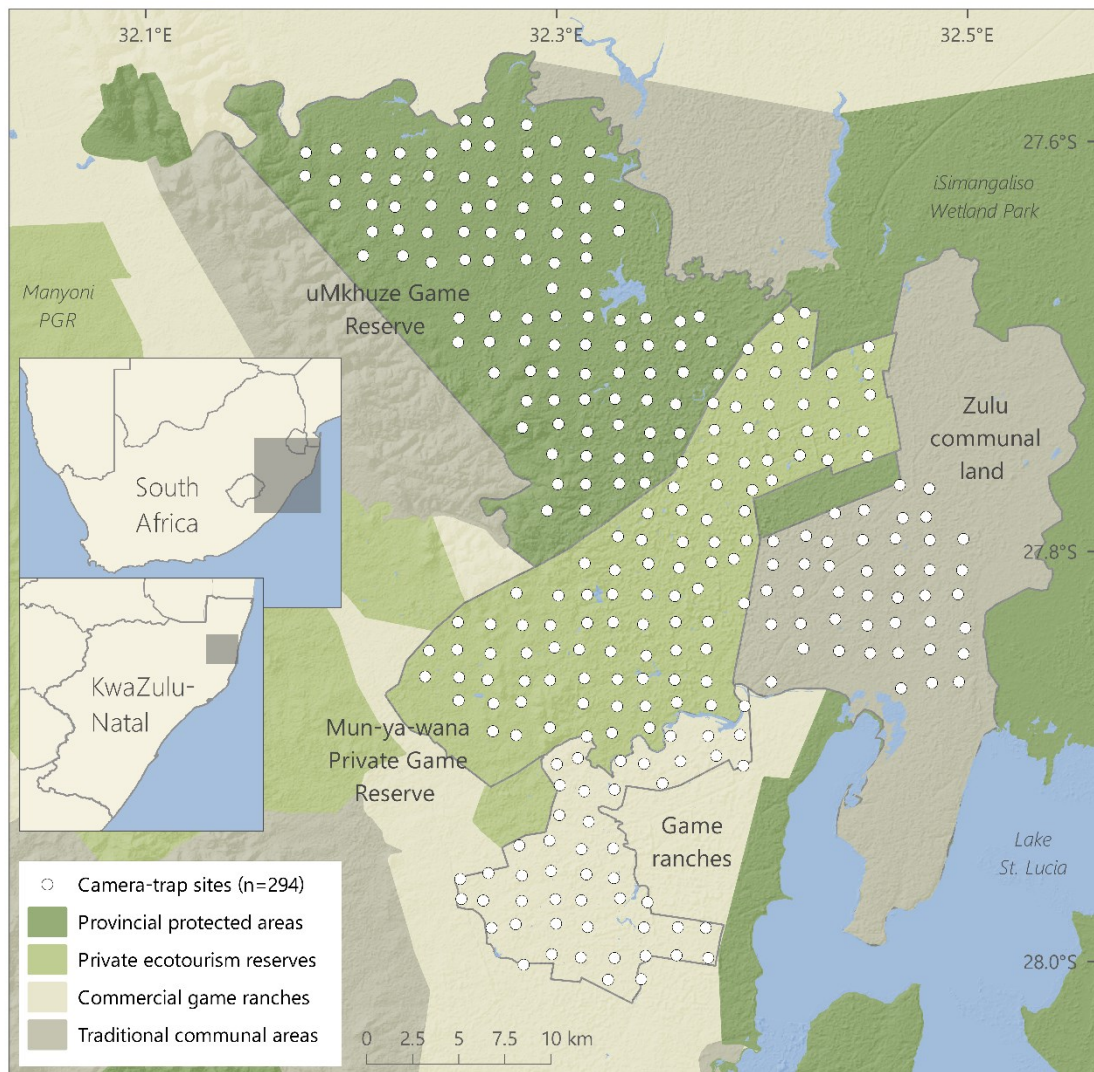
Fig. 1. Camera-trapping surveys conducted across a landscape gradient of human intervention
in the Maputaland region of northern KwaZulu-Natal, South Africa.

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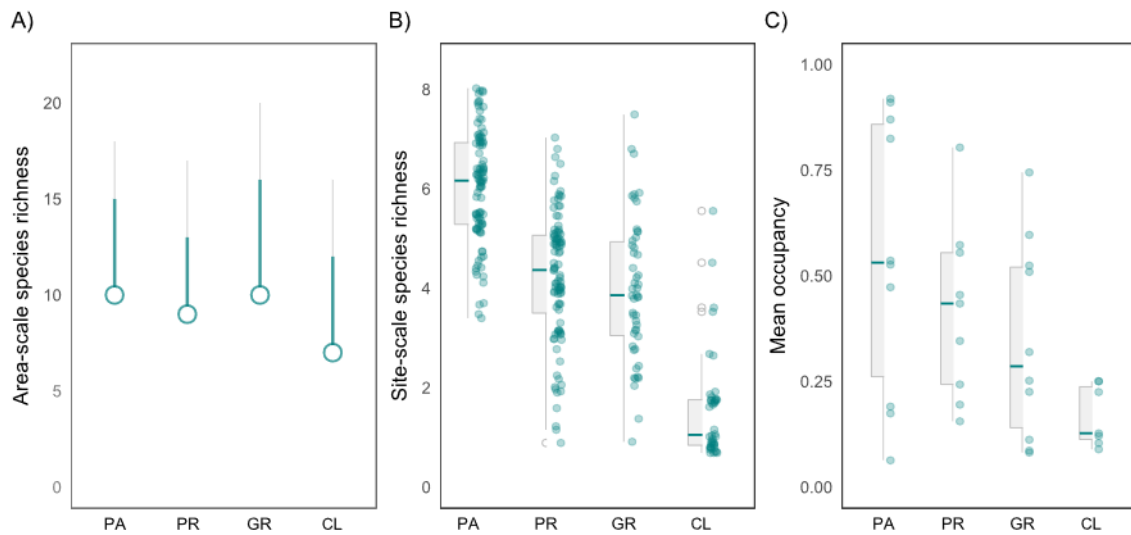
Fig. 2. Area-specific summaries of: A) total assemblage species richness (central estimates are modes and 66% Bayesian credible intervals are highlighted as estimates had right-skewed posterior distributions); B) species richness estimates per camera-trapping site; and C) average species-specific occupancy. Points for site richness and species occupancy estimates are posterior distribution means and error bars were omitted for visual clarity. PA - provincial protected area, PR - private game reserve, GR - commercial game ranches, CL - Zulu communal land.

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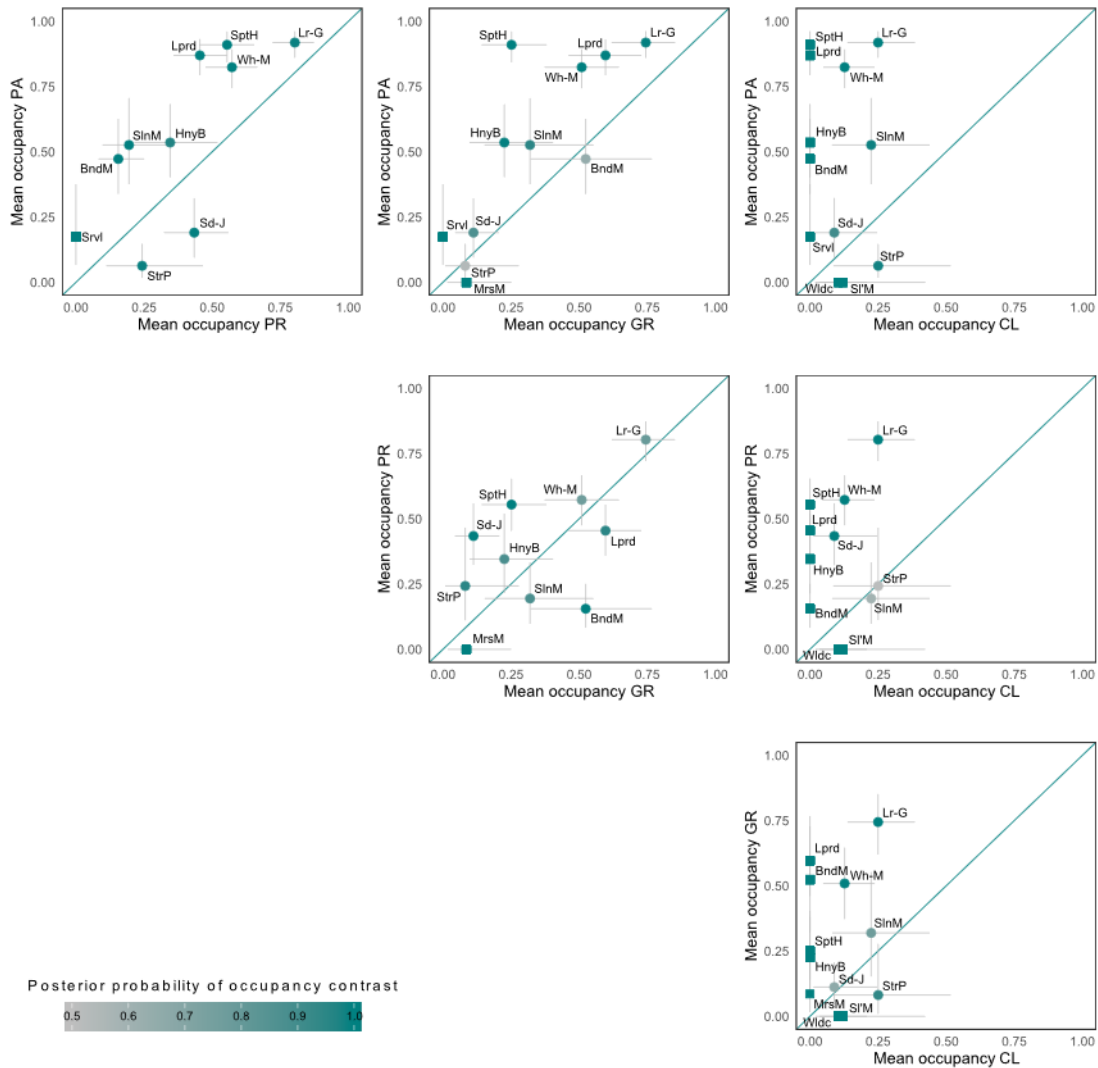
Fig. 3. Species-specific mean realized occupancy estimates between management contexts (PA - provincial protected area, PR - private game reserve, GR - commercial game ranches, CL - Zulu communal land). Points above the diagonal bar indicate higher species occupancy in the area displayed on the y-axis, whereas points below the diagonal bar reflect higher species occupancy in the x-axis area. Squares indicate species present in a single area and error bars represent 95% Bayesian credible intervals. The colour of the points represents the proportion of the posterior difference (i.e., the occupancy contrast) with the same sign as the mean (Appendix S4 Table S4-3). SptH – Spotted hyaena, Lprd – Leopard, Srvl – Serval, Sd-J – Side-striped jackal, HnyB – Honey badger, Wldc – African wild cat, Wh-M – White-tailed mongoose, MrsM – Marsh mongoose, Lr-G – Large-spotted Genet, Sl'M – Selous's mongoose, BndM – Banded mongoose, StrP – Striped polecat, SlnM – Slender mongoose.

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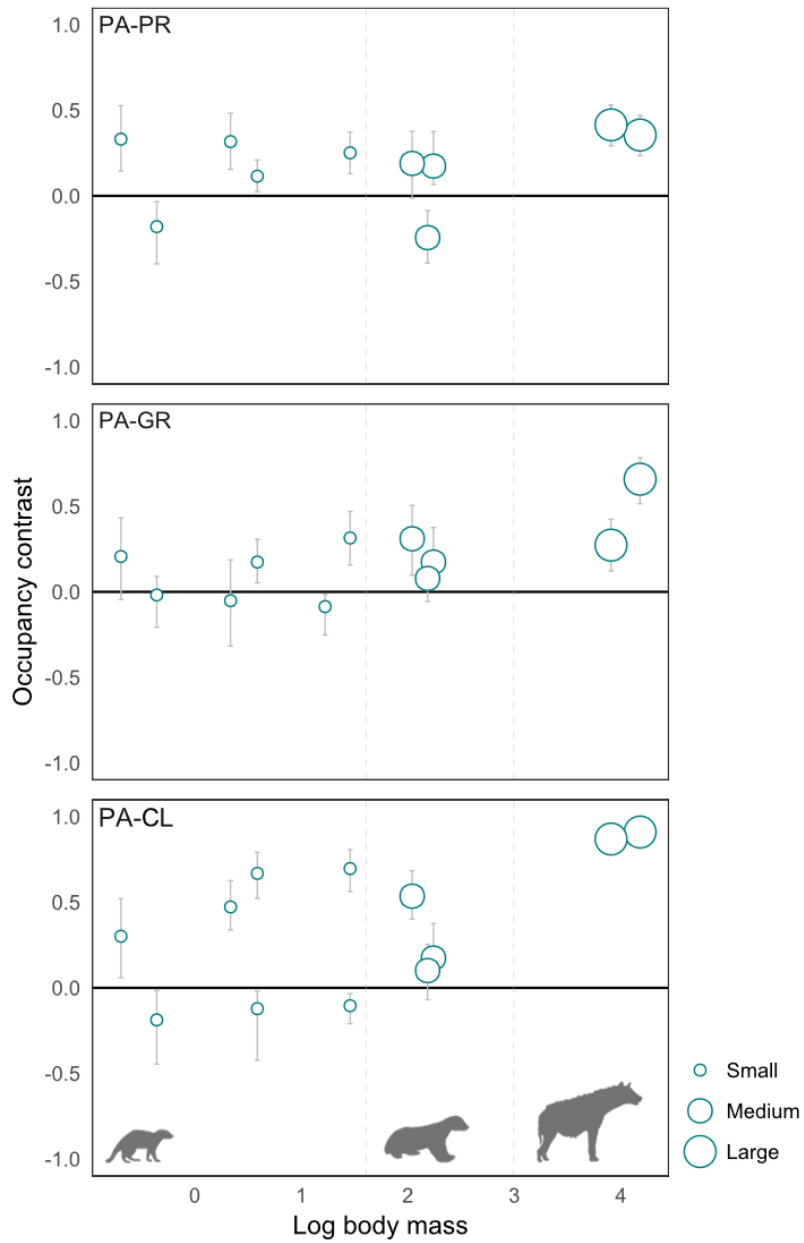
Fig. 4. Species-specific occupancy contrasts between the provincial protected area (PA) and adjacent land uses (PR - private game reserve, GR - commercial game ranches, CL - Zulu communal land) plotted by carnivore body mass. Occupancy contrasts were derived by pairwise subtracting area- and species-specific mean realized occupancy estimates. Vertical dashed lines and symbol size group carnivore species according to body mass classes: small (<5kg), medium (5-15kg) and large (>15kg).