

1 **Mesocarnivore community structuring in the presence of Africa's**  
2 **apex predator**

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21 **Abstract**

22 Apex predator reintroductions have proliferated across southern Africa, yet their ecological effects  
23 and proposed umbrella benefits of associated management lack empirical evaluations. Despite a  
24 rich theory on top-down ecosystem regulation via mesopredator suppression, a knowledge gap  
25 exists relating to the influence of lions (*Panthera leo*) over Africa's diverse mesocarnivore (<20kg)  
26 communities. We investigate how geographical variation in mesocarnivore community richness and  
27 occupancy across South African reserves is associated with the presence of lions. An interesting  
28 duality emerged: lion reserves held more mesocarnivore-rich communities, yet mesocarnivore  
29 occupancy rates and evenness-weighted diversity were lower in the presence of lions. Human  
30 population density in the reserve surroundings had a similarly ubiquitous negative effect on  
31 mesocarnivore occupancy. The positive association between species richness and lion presence  
32 corroborated the umbrella species concept but translated into small differences in community size.  
33 Distributional contractions of mesocarnivore species within lion reserves, and potentially  
34 corresponding numerical reductions, suggest within-community mesopredator suppression by  
35 lions, likely as a result of lethal encounters and responses to a landscape of fear. Our findings offer  
36 empirical support for theoretical understanding of processes underpinning carnivore community  
37 assembly and are of conservation relevance under current large-predator orientated management  
38 and conservation paradigms.

39

40 **Keywords:** *Lion, Panthera leo, mesopredator release, camera-trap, occupancy, hierarchical*  
41 *Bayesian models*

## 42 **1. Background**

43 Conservation management interventions in southern Africa's network of intensively managed and  
44 mostly fenced reserves are disproportionately motivated by maintaining populations of highly  
45 charismatic species that have high economic value, including large carnivores [1,2]. These  
46 behaviors can generally be attributed to the rise of ecotourism and the game viewing preferences  
47 of tourists. While large predator-centred management of southern Africa's reserves has generated  
48 positive conservation outcomes for large carnivores [3], the effects on broader biodiversity patterns  
49 are less well understood, particularly for less charismatic and overlooked, yet functionally important,  
50 taxa. Evaluating the alignment between commercially motivated carnivore management and  
51 biodiversity is therefore important for reconciling financial and conservation interests when the  
52 maintenance of ecosystem functioning is a conservation priority.

53 The African lion (*Panthera leo*) is a large carnivore that has received intensive conservation  
54 management in southern Africa. As apex predators, lions may play an important regulatory  
55 ecological role [4,5], are considered an indicator of ecosystem health [6], and are susceptible to  
56 many of the threats common across African wildlife (e.g., habitat loss, prey depletion, and human-  
57 wildlife conflict) [5,7]. There is growing consensus around the role of lions as flagship species [8],  
58 their economic and conservation value [2], and the need for increased investment in their  
59 conservation [6]. However, despite doubts of the usefulness of lion as umbrella species [9,10],  
60 there is a surprising lack of empirical studies evaluating the role of lions as conservation proxies.  
61 In South Africa, most lion populations are too small to be independently viable, intensively  
62 managed, constrained to small areas, and are reliant on assisted dispersal [11,12]. Lion  
63 populations in South Africa are therefore not reliable indicators of contiguous, less intensively  
64 managed ecosystems [10,13]. Nonetheless, the large capital investment in activities related to lion  
65 reintroductions and population maintenance (e.g. prey availability, population control, infrastructure  
66 development, anti-poaching efforts [12,14]) are likely to confer umbrella benefits to sympatric  
67 species [7,15].

68 There is, however, little understanding of the direct ecological effects of apex predator  
69 reintroductions on sympatric species in South Africa's numerous small, fenced reserves. Past  
70 research focus has been on lion-induced top down effects, specifically the regulation of ungulate  
71 species [e.g. 16], and the relatively few investigations of lion's influence over sympatric carnivores  
72 are mostly restricted to other large carnivore species [17–19]. Thus, an important knowledge gap  
73 exists relating to the influence lions have on the size, structure and composition of Africa's diverse  
74 carnivore assemblages [20], specifically communities of small and medium sized species (<20kg),  
75 here collectively called mesocarnivores [21]. Yet, mesocarnivore's functional role and susceptibility  
76 to suppression or facilitation by larger carnivore species [20,22–24] makes them central to  
77 evaluating the ecological outcomes of large-predator-centred conservation efforts and  
78 management paradigms [12].

79 Mesocarnivores, are a numerous and diverse, yet understudied [25], group of mammals, and an  
80 important component of ecosystem function, structure, and dynamics [26,27]. A rich body of theory  
81 predicts profound ecosystem-level cascading effects resulting from apex predator mediated top-  
82 down processes, such as mesopredator suppression and release [5,23]. While research on intra-  
83 guild carnivore interactions have traditionally focused on highly competing species, recent evidence  
84 has exposed the potential for overlooked suppression pathways by large carnivores over a broader  
85 range of sympatric mesopredators [24,28]. Lion-induced suppression of mesocarnivore  
86 communities may thus be an important unheeded aspect of 'lionscapes' along with proposed  
87 umbrella benefits. Such reasoning motivates practical and theoretical interest in relating  
88 geographical variation in mesocarnivore diversity to the presence of lions; but this requires linking  
89 the scales at which variation in diversity is observed to the ecological levels at which the processes  
90 hypothesized to affect diversity operate [29]. Killing, harassment and other kinds of competitive  
91 interference by lions on subordinate mesocarnivores [20,30] can theoretically induce local  
92 numerical (e.g., population declines) and behavioural (e.g., altering the exploitation of space)  
93 responses [23] (but see [17]). Both processes manifest at the population level by the abundance  
94 and distribution of a species at the landscape (or reserve) scale. Multiple species responses to

95 apex predators, lion-focused management, or associated changes to within community dynamics  
96 [31], shape higher level community patterns and can drive spatial variation in composition and  
97 diversity of mesocarnivore assemblages. In concert, these patterns are difficult to evaluate as it  
98 requires spatially replicated sampling of mesocarnivore communities over large geographical  
99 extents which include variation in apex predator populations and environmental contexts  
100 [22,32,33]. Fenced reserves operating under a variety of management objectives, including  
101 decisions to reintroduce lion populations, provide a unique setting to test multiple hypotheses  
102 related to drivers of mesopredator community structure under a natural experimental framework.

103 Here, we leverage an extensive camera trapping dataset collected across South African reserves  
104 (Fig. 1), to investigate correlates of geographical variation in mesocarnivore communities' structure  
105 at two distinct community organization levels: we quantify among reserves variation in *i*) species  
106 richness and *ii*) species-specific occupancy rates (i.e proportion of occupied/used area within a  
107 reserve), a proxy for local relative abundances [34]. Primarily, we are interested in the extent to  
108 which geographic variation in mesocarnivore richness and occupancy is linked to the presence or  
109 absence of lions; specifically, whether species richness and occupancy are positively associated  
110 with lions as would be expected if lion management conferred benefits to sympatric species (a  
111 variant of the umbrella-concept) [7,23], or are negatively associated with lion presence as predicted  
112 with mesopredator suppression [23,24]. In addition to the association with lion presence, we  
113 simultaneously account for inherent anthropogenic and ecological variation among reserves  
114 (reserve size, surrounding human population density, structural habitat diversity and baseline top-  
115 predator pressure in the absence of lions [leopard density]). Finally, we compared mesocarnivore  
116 community evenness-weighted diversity across reserves [35]), specifically contrasting communities  
117 with and without lions present. Importantly, including lion presence as a multi-level predictor of  
118 geographic variation in mesocarnivore richness and reserve-specific occupancy patterns provides  
119 a novel and integrated approach to explore two concepts widely used to advocate the conservation  
120 surrogacy of lions – umbrella and keystone species – and how these may act in tandem [9].

121

## 122 **2. Materials and Methods**

123 **(a) Study area.** We targeted  $R = 17$  reserves across two South African provinces, Limpopo and  
124 KwaZulu-Natal (Fig. 1; *SI Appendix* Table S1). These were a combination of provincial parks ( $n=9$ )  
125 and privately managed ( $n=8$ ) conservation areas, all providing varying levels of protection to wildlife  
126 (IUCN categories II–VI) and ranging in size from  $150\text{km}^2$  to  $907\text{km}^2$ . Approximately half of these  
127 held lion populations during the surveys ( $n=9$ ). Reserves were predominantly mixed savanna  
128 habitat, but included semi-arid savanna, thicket, forest, montane grassland, and coastal belt  
129 vegetation. Climate typically varies along a North-South gradient from arid in the north to warm  
130 temperate climates at the more southern sites [36].

131 **(b) Carnivore surveys.** We used ancillary camera-trap data on small- and medium-sized  
132 carnivores collected while documenting leopard densities in target reserves between 2013-2016  
133 [37]. From the original data set, we considered only surveys conducted between April and  
134 September, correspondent to the dry season in the region, to avoid confounding aspects  
135 associated with seasonality and to increase comparability across surveys. The number of surveys  
136 in each reserve varied from one to three. The final dataset comprised  $S = 33$  reserve-by-year  
137 surveys. On average in each survey (mean  $\pm$  sd),  $40\pm 5$  camera-trap stations were deployed,  
138 spaced  $1935\pm 275$  m apart, for  $46\pm 4$  days; totaling 1318 stations and 61019 effective trap days (see  
139 *SI Appendix* Table S1 for survey details). Camera locations were selected to target intersections  
140 between features commonly used by leopards (i.e., roads, drainage lines, and game trails). At each  
141 location, two Pantheracam V4, V5, or V6 xenon flash cameras with infrared motion sensors were  
142 set at opposite sides of the target feature, at a height of 30–40 cm above the ground and angled  
143 parallel to the slope. Cameras were programmed to record a single photograph per trigger. See *SI*  
144 *Appendix* for additional description of camera-trapping protocols.

145 Although designed explicitly for the estimation of leopard density, the survey design was adequate  
146 for our inference objective. This is achieved by the surveys' wide spatial coverage, thus allowing

147 for reserve-scale comparisons, with average per-survey number of sites and duration within the  
148 recommended guidelines to obtain precise estimates of species richness, occupancy and detection  
149 rates with camera trap arrays [38], and using a trail-based camera placement suggested to increase  
150 the detection probability of a wide range of carnivore species [39].

151 **(c) Multi-region community occupancy model.** We use a multi-region community model to jointly  
152 define geographical variation in community- and species-level attributes, while formally accounting  
153 for imperfect detection, heterogeneity in detectability and heterogeneity in occurrence probabilities  
154 [40]. The model expands the species-by-site (here, camera-trap stations) data structure typical of  
155 multispecies occupancy models [41] to data collected across distinct regions (here, reserve-by-  
156 year surveys). This allows for formal testing of hypotheses about drivers of variation in species  
157 richness and occupancy across multiple regions and the derivation of biodiversity metrics with full  
158 error propagation [40]. Note that the ecological definition of site occupancy and the nature of the  
159 occupancy-abundance relationship is species-specific and our interest was in relative differences  
160 in species-specific occupancy rates among regions [34].

161 We summarized mesocarnivore daily encounter frequency data from  $S = 33$  regions, with reserve  
162 specific observed species richness ranging from 8 to 16 (median 12). Since we were interested in  
163 geographical variation at the reserve-scale, we included covariates as a linear combination of  
164 effects with a logit-link transformation on two state variables: reserve-specific species richness ( $\Omega_r$ )  
165 and species-by-survey occupancy rates ( $\psi_{is}$ ). We modelled occupancy probability using species-  
166 by-survey random intercepts with species-specific hyper-parameters. Hyperparameters specify the  
167 mean community response and variation among species to a covariate. With only 17 reserves and  
168 33 surveys, besides the effect of lion presence, we limited the model's fixed effects on richness  
169 and occupancy parameters to three additional parameter-specific broad proxy variables, allowing  
170 us to evaluate a global model of community response [42]. Model formulation details are reported  
171 in *SII Appendix* and the JAGS model code is given in *SIII Appendix*.

172 **(d) Model Covariates.** We modeled species richness as a linear function of reserve-by-year-  
173 specific covariates reflecting: i) lion presence (LION); ii) reserve size (AREA), based on species-  
174 area relationship predictions [43] and potential of larger reserves to buffer edge effects [44]; iii)  
175 surrounding human population density (HUM) [45], as proxy for human-wildlife conflicts [46–50];  
176 and iv) structural habitat diversity (HDIV), under expectations that habitat heterogeneity promotes  
177 species richness [43] (Eq. 1 in *SII Appendix*). We simultaneously modelled occupancy probability  
178 in relation to lion presence and as a linear function of reserve-scale measures of anthropogenic  
179 pressure (human density, as above), assuming human-induced disturbance hampers population  
180 densities and/or constrains species distributions, and of local leopard densities (LEOP), to account  
181 for the main role of leopards on intraguild dynamics [20], particularly as the apex predator in the  
182 absence of lions, and known influence over mesocarnivore species [51] (Eqs. 2-4 in *SII Appendix*).

183 We used lion camera-trapping images from our surveys to code lion presence as a binary variable  
184 (LION). This information was checked against knowledge on lion population of each reserve to  
185 account for the unlikely event that our surveys fail to obtain a single lion record despite the presence  
186 of the species. We extracted reserve size (AREA) from area summaries of official property limits in  
187 GIS software (Quantum GIS 2.18) and calculated average human population density (HUM) within  
188 a 10 km buffer area surrounding each reserve from the 2015 WorldPop estimate for number of  
189 people per 100m grid square ([https://africaopendata.org/dataset/south-africa-population-density-  
190 2015](https://africaopendata.org/dataset/south-africa-population-density-2015)). As a proxy for habitat diversity (HDIV), we calculated the Simpson's Landscape Diversity  
191 Index for each reserve based on 2013-14 national remote-sensed land cover data for South Africa  
192 ([https://egis.environment.gov.za/national\\_land\\_cover\\_data\\_sa](https://egis.environment.gov.za/national_land_cover_data_sa)). We used survey-specific leopard  
193 density estimates (LEOP) from spatial capture–recapture models applied to leopard data from the  
194 same camera-trap surveys [37,52]. We checked for multicollinearity by evaluating pairwise  
195 correlations between covariates and ensuring no highly correlated pairs ( $r > 0.6$ ) were included in  
196 the analysis. All covariates were normalized between zero and one.

197 **Diversity metrics.** Since species richness estimates do not account for evenness among species,  
198 we used survey-specific occupancy-based Hill number estimators [35] to calculate the effective  
199 number of species and further elucidate the potential influence of lion presence on mesocarnivore  
200 diversity. Hill numbers are a mathematical family of diversity indices that differ among themselves  
201 only by an exponent  $q$ . Hill numbers for  $q>0$  summarize two commonly-used biodiversity metrics (i)  
202 Shannon diversity ( $q=1$ , the Shannon entropy exponentiated), and (ii) Simpson diversity ( $q=2$ ,  
203 inverse of the complement of the Gini–Simpson index). Both indices translate the degree of  
204 dissimilarity across species in each community but differ in relative importance given to rare  
205 species. Species richness is a Hill number of order  $q=0$ . Hill numbers were computed as derived  
206 quantities within the Bayesian hierarchical model, allowing for error propagation and derivation for  
207 these metrics. We compared Hill numbers measures by deriving the difference in the average index  
208 for reserves with and without lions; doing that in a Bayesian framework allowed us to derive the  
209 posterior distribution, and therefore summary statistics, of the difference in the effective number of  
210 species in relation to lion presence. Since Hill numbers of order  $q=1$  and  $q=2$  were highly correlated  
211 ( $r=0.97$ ), we present results only for the former in the main text.

### 212 **3. Results**

213 Camera trapping effort included 1,318 camera-trapping stations (sites), 61,360 trap days, and  
214 resulted in a total of 13,667 records of 22 mesocarnivore species (*SI Appendix* Table S2). There  
215 was considerable variation in estimated median species richness among reserves (Fig. 2; *SI*  
216 *Appendix* Table S3), ranging from 12 to 19 (95% Bayesian credible interval (BCI): 10-21). Species  
217 richness showed a positive relationship with lion presence at the reserve scale ( $\beta_{\Omega,LION} = 0.51$ , BCI:  
218  $-0.16 - 1.21$ , 0.93 probability of a greater than zero effect; Fig. 2B). Mesocarnivore richness was  
219 also positively associated with human population density surrounding the reserves ( $\beta_{\Omega,HUM} = 0.88$ ,  
220 BCI:  $-0.33 - 2.16$ , 0.92 probability of a greater than zero effect). Reserve size ( $\beta_{\Omega,AREA} = -0.20$ , BCI:  
221  $-1.94 - 1.70$ ) and habitat diversity ( $\beta_{\Omega,HDIV} = 0.21$ , BCI:  $-0.62 - 1.06$ ) did not have clear effects as

222 predictors of relative change in community richness, i.e. low probability of effects estimates being  
223 different than zero (SII Appendix Table S4).

224 Species-by-survey estimates of average occupancy rates ( $\psi$ ) showed a high degree of inter- and  
225 intra-specific heterogeneity (Fig. 3A). Across surveys, the community mean occupancy probability  
226 was moderately low ( $0.29 \pm 0.29$ ; mean  $\pm$  SD), with species-specific means ranging from  $0.02 \pm$   
227  $0.10$  for the Selous's mongoose (*Paracynictis selousi*) to  $0.82 \pm 0.15$  for the African civet (*Civettictis*  
228 *civetta*). Lion presence negatively influenced mesocarnivore species occupancy, with a mean  
229 community-level response of  $\mu\beta_{\psi,LION} = -0.98$  (BCI:  $-1.61 - -0.39$ ; Fig. 3B). Unlike richness, average  
230 mesocarnivore occupancy was higher when lions were absent compare to when they are present  
231 ( $0.35 \pm 0.29$  and  $0.25 \pm 0.28$ , respectively; Fig. 3). Species-specific responses to lion presence were  
232 bimodal, with 16 out of 22 species exhibiting a clear negative response (i.e. probability of a negative  
233 effect  $>0.9$ ), while for other species the probability of a positive or negative signal for this effect was  
234 close to chance. Only the occupancy of side-striped jackals (*Canis adustus*) was positively  
235 associated with the presence of lions. Similarly ubiquitous among species, human population  
236 density had a negative effect on mesocarnivore occupancy ( $\mu\beta_{\psi,HUM} = -1.66$ ; BCI:  $-2.65 - -0.74$ ;  
237 probability of a negative effect  $>0.9$  for 13 species; Fig. 3B). Leopard density had a less clear  
238 community-level effect ( $\mu\beta_{\psi,LEOP} = -0.69$ ; BCI:  $-1.83 - 0.39$ ; Fig. 3B), with a mix of negative and  
239 positive responses (4 species each). Full summaries of posterior distributions for community- and  
240 species-level covariate coefficients, and species-by-survey occupancy estimates are provided in  
241 SII Appendix, Tables S5-9.

242 On average, mesocarnivore communities had higher effective number of species in the absence of  
243 lions (Fig. 4; SII Appendix Table S10) as expressed by reserve-by-year-specific occupancy-based  
244 Shannon diversity Hill number estimates.

245

#### 246 4. Discussion

247 We jointly describe geographic variation in mesocarnivore community size and patterns of species-  
248 specific occupancy across a network of reserves in South Africa. We provide empirical support for  
249 the potential role of the African lion and lion-focused management as structuring agents of these  
250 communities, a matter of theoretical importance for understanding mechanisms underpinning  
251 carnivore community assembly, and of conservation relevance in the context of large-predator  
252 orientated management paradigms [2,6,49].

253 **(a) Multi-level mesocarnivore community structure.** Our findings suggest that lion presence  
254 may have a profound influence on the structure of mesocarnivore communities. Namely, an  
255 interesting duality emerged: lion presence was associated with slightly more mesocarnivore-rich  
256 communities, yet mesocarnivore occupancy rates, a proxy for local abundances [34], were lower  
257 in the presence of lions.

258 Associations of apex predators with high biodiversity have been attributed to common suitable  
259 biotic and abiotic conditions, mediated by large predator's sensitivity to disturbance or dependence  
260 on productive and heterogeneous ecosystems [9]. Even if decisions to introduce lions in South  
261 Africa were largely motivated by economics of ecotourism rather than biodiversity conservation  
262 priorities [14], the sizeable budgets and management capacity necessary to successfully introduce  
263 and sustain lion populations [12,14] may favor the species richness of sympatric mesocarnivore  
264 communities by mitigating common threats [53,54]. Complementarily, resource facilitation and  
265 apex predator induced cascades are two additional pathways by which lion presence can  
266 causatively favor more species rich mesocarnivore communities. Lions are the single predator of  
267 very large ungulates (e.g. giraffe [*Giraffa camelopardalis*], buffalo [*Syncerus caffer*]) which  
268 subsequently provide carrion for scavengers [55]. By constraining other large, albeit subordinate,  
269 carnivores [18,19], lions can also create enemy-free spaces for sympatric mesocarnivores, thereby  
270 promoting species persistence. However, such effects may not be unequivocally present [17].  
271 Increased mesocarnivore richness associated with lion presence corroborates claims for broader  
272 biodiversity benefits of maintaining lions [7]. However, in absolute terms, lion presence translated

273 into, on average, just one additional species in the mesocarnivore community. While such small  
274 difference may be intrinsically valuable and ecologically relevant for relatively species poor taxa,  
275 depending on species identity and functional redundancy [56], this pattern suggests that direct and  
276 indirect effects of lion presence are more likely to manifest at the population level rather than  
277 modulate extreme extinction events.

278 In contrast to the positive association of lions with mesocarnivore richness, but in accordance with  
279 theoretical expectations [23,27,57], we provide rare empirical support for repeated community-wide  
280 mesopredator suppression by lions. Lions are predicted to suppress sympatric large carnivores  
281 through combinations of direct, i.e., lethal, encounters, and indirect, i.e., fear and loathing,  
282 responses [18,19] [but see 17]. Here we propose the same mechanisms may apply across almost  
283 the entire South African mesocarnivore assemblage. While lions are among the most frequent  
284 intraguild killer species [30], the body-mass ratio between lions and the species that were  
285 negatively influenced by lions was outside the range where this behavior is deemed to be most  
286 prevalent and ecologically beneficial ( $>2$  and  $<5.4$  [30]). However, these predictions are largely  
287 untested empirically, potentially undervaluing alternative competition pathways (e.g.  
288 kleptoparasitism) and the role of predatory and incidental killing by hyperpredatory felids [28].  
289 Recent evidence suggests carrion provisioning by large carnivores may potentiate largely  
290 asymmetric lethal interactions due to the scavenging behavior of mesocarnivore species (i.e., the  
291 “fatal attraction hypothesis”), therefore enhancing rather than ameliorating suppression at wider  
292 spatial scales [24]. Thus, instead of benefiting from cascading effects of antagonistic interactions  
293 between lions and sympatric large carnivores [58], African mesocarnivores may experience  
294 superadditive suppressive effects [24]. Further research is needed to elucidate net suppressive  
295 effects of the complete large carnivore guild over mesocarnivores and how these propagate across  
296 guild levels as potentially modulated by lion presence [51]. The risk of killing or harassment by lions  
297 may also induce behavioral changes to avoid direct encounters. The “landscape of fear” associated  
298 with apex predators [59] can be particularly strong for mesocarnivores as they are poorly adapted  
299 to escape [23], especially in fenced environments with artificially high apex predator densities [12].

300 The resulting numerical reductions and corresponding distributional contractions within reserves  
301 are likely mechanisms by which community-wide occupancy reductions in the presence of lion  
302 presence may emerge and outweigh the presumable benefits associated with increased  
303 management capacity of lion reserves.

304 The apparent dichotomy between the positive and negative effects of lions on species richness and  
305 occupancy, respectively, suggest that net suppressive effects by lions may not impact  
306 mesocarnivore species to the point of local extinction. The lack of a common negative response in  
307 species richness in the presence of lions can also result from synergisms and feedbacks between  
308 regulatory processes due to the smaller carnivore's strong predisposition to intraguild competition  
309 [20,31]. Cascading effects of restricted species-specific occupancy may reduce lateral competition  
310 among mesocarnivores, thus facilitating coexistence and promoting mesocarnivore persistence by  
311 controlling dominant species with potential to outcompete others [60]. Conversely, competitive  
312 processes within the mesocarnivore communities, unaccounted for here but warranting further  
313 investigation, can also modulate the observed species-specific associations with lion presence.  
314 The net facilitative versus suppressive effect of an apex predator should also depend on changes  
315 in such competitive interactions [24], which may ultimately favor some mesocarnivore species, for  
316 example the observed positive response of the side-striped jackal to the presence of lions.

317 The effective number of mesocarnivore species (i.e., evenness-weighted diversity) was also lower  
318 in reserves where lions were present. While descriptive, evenness is regarded as an important  
319 component of biodiversity [61], and our result raises further questions about the surrogacy potential  
320 of lions in fenced and intensely management reserves. At the same time, we provide support to an  
321 additional community-wide intraguild regulation dimension to the usually invoked keystone role of  
322 lions. While these results reflect emergent patterns in accordance with standing theoretical  
323 expectations, we cannot, however, infer causation. We argue that, despite lacking specific  
324 mechanisms, our observational approach provides an informed starting point [62] for detailed  
325 investigations of the specific processes that play across complex multi-trophic interaction networks.

326 Future lion reintroductions and translocations create scope for stronger evidence under before-  
327 and-after comparisons or, ideally, cross-over designs. Additionally, we did not incorporate  
328 information about lion demography and distribution. The adaptive management of lion populations  
329 [63], makes it difficult to link fluid population states to emergent ecological effects. Hence, we opted  
330 for a conservative presence/absence approach that refers to differences in respect to baseline apex  
331 predator states and management intentions. The heterogeneity we observe in mesocarnivore  
332 diversity among reserves where lions were present concurs, nonetheless, with growing consensus  
333 around context dependency of large predator effects [64]. The extent to which ecological responses  
334 of mesocarnivore communities depend on the structure of the local lion population (e.g. density,  
335 sex ratios, age classes) and subjacent management idiosyncrasies [11,12] warrants further  
336 research.

337 There was little support for the effects of habitat diversity or reserve size on mesocarnivore species  
338 richness. This is perhaps expected as most of the species we encountered are widely distributed  
339 in the region, and as versatile and habitat generalist species [20], possess broader bioclimatic  
340 niches Moreover, reserves are not discrete units within a completely hostile landscape matrix and  
341 fences are permeable to most carnivore species [65]. Even land now protected in each reserve  
342 was, in many cases, highly disturbed prior to growth of South Africa's wildlife industry, potentially  
343 inducing unaccounted historical 'extinction filters' [66]. Indeed, contrary to our initial hypothesis, we  
344 found a positive relationship between mesocarnivore richness and human population density in the  
345 reserve's surroundings. This result is likely the outcome of human-dominated areas serving as  
346 source populations of individuals traversing into the reserve boundaries, particularly the two  
347 domestic carnivores included in our study. Nevertheless, anthropogenic pressure did have a  
348 pervasive negative influence over species-specific occupancy rates. It is likely that proximity to  
349 reserve boundaries or the extent to which external anthropogenic stressors bleed into reserves,  
350 i.e., edge effects [53], may result in negative species-specific responses that manifest as variation  
351 among species within reserve occupancy rates. Although we did not account for interaction among  
352 predictors, the umbrella benefits of more effective protection in lion reserves may counteract

353 potential suppressive effects, particularly for most conflict prone mesocarnivores. For instance, the  
354 caracal did not exhibit a strong negative response to lion presence but was highly impacted by  
355 human pressure. Leopards in South Africa are also known to be affected by edge effects [53],  
356 hence increased protection in lion reserves may similarly mask leopard's influence over sympatric  
357 mesocarnivores [51]. Alternatively, leopard effects may not scale proportional to density [67], with  
358 observed mesocarnivore occupancies already referring to baseline states under the ubiquitous  
359 presence of leopards, as opposed to local lion reintroductions.

360 **(b) Theoretical and applied implications.** We provide empirical evidence for geographical  
361 variation in mesocarnivore communities structure that is associated with the presence of lions. This  
362 is of particular conservation relevance considering the disproportional attention given to lions as  
363 flagship and umbrella species [6,7], and the potential for lions to modulate the important ecological  
364 role of mesocarnivores [27]. Our results highlight the difficulty in disentangling the benefits of the  
365 umbrella species concept based on species richness [9] from the ecological effects of highly  
366 interactive apex predators. Increasing species richness remains a goal of many conservation  
367 practitioners. However, species richness is one, arguably simplistic, biodiversity measure [68] that  
368 fails to capture underlying nuances that our multi-level approach has highlighted. More subtle  
369 changes in the distribution and abundance of key functional groups, such as mesocarnivore  
370 occupancy and evenness, are often unheeded aspects of biodiversity change with far reaching  
371 implications for ecosystem functioning. This presents a fundamental challenge for applied  
372 conservation management, where management objectives need to balance ecological responses  
373 at multiple level of spatial and biological organization.

374 African mesocarnivores are important predators of small vertebrates (e.g. rodents, lagomorphs and  
375 birds [20], including pest species [69]). Many are also facultative scavengers significant to waste  
376 removal [70]. Moreover, they consume and disperse seeds and prey on a vast array of herbivores  
377 and detritivores, thus are important also to vegetation communities [71]. Without adequate  
378 conservation benchmarks or baselines [72], it is impossible to ascertain whether apparent

379 mesocarnivore occupancy declines due to lion presence in small reserves impairs the delivery of  
380 such ecosystem functions or if mesopredator release in the absence of lions increases pressure  
381 over vulnerable lower trophic levels, with detrimental cascading effects [23]. In this context, the  
382 comparison of our results with similar studies carried out in large and unfenced protected areas,  
383 home to remaining free-ranging lion populations, could produce valuable insights. Our results make  
384 a case for top-down control via mesopredator suppression in small South African reserves with  
385 vast applications in conservation of biodiversity and habitat restoration [9,73]; but the degree of  
386 mesocarnivore effects and apex predator dominance are likely to be highly context-dependent and  
387 dynamic [64], marked by rapid and variable growth rates of reintroduced lion populations [63].  
388 Although there is intrinsic value of reintroducing lions as a restored ecosystem-component itself [6]  
389 and as integrative part of metapopulation conservation efforts [74], we call for a more holistic view  
390 of African carnivore assemblages and ecosystem-wide implications of management and  
391 conservation interventions [75].

392

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399

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404

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- 604

605 **Figure captions**

606 **Figure 1.** Reserves target of the 33 camera-trapping surveys implemented across Limpopo and  
607 KwaZulu-Natal provinces, South Africa. 1- Venetia-Limpopo GR, 2- Zingela NR, 3- Lajuma RC, 4-  
608 Wonderkop NR, 5- Makalali GR, 6- Welgevonden GR, 7- Timbavati PGNR, 8- Atherstone GR, 9-  
609 Tembe EP, 10 – Ithala GR, 11 – Somkhanda GR, 12 – uMkhuze GR, 13 - Manyoni PGR, 14 –  
610 Munyawana PGR, 15 – iWP E. Shores, 16 - Hluhluwe-iMfolozi P, 17 - Ophate GR. See *SI Appendix*  
611 Table S1 for survey details.

612 **Figure 2.** Across reserve variation in mesocarnivore species richness. Points are posterior medians  
613 and error bars represent 66% and 95% Bayesian credible intervals. Vertical lines represent species  
614 richness means across reserves. A) Reserve-specific species richness estimates; filled and open  
615 symbols represent estimates in the presence and absence of Lions, respectively. B) Coefficient of  
616 lion presence (LION) covariate effect on mesocarnivore species richness.

617 **Figure 3.** Patterns and drivers of mesocarnivore species occupancy. A) Species- and survey-  
618 specific occupancy estimates. Filled blue symbols represent survey-specific estimates in the  
619 presence of lions. Squares represent species-specific mean occupancy across surveys. Error bars  
620 were omitted for visual clarity. B) Effect size of relationship between species occupancy and lion  
621 presence (LION), Human population density in reserve's surroundings (HUM) and leopard density  
622 (LEOP). Points are posterior distribution means and error bars represent 95% Bayesian credible  
623 intervals, colored by the probability of an effect, calculated as the proportion of the posterior with  
624 the same sign as the mean. Vertical blue lines mark community mean effects.

625 **Figure 4.** Reserve-by-year-specific mesocarnivore diversity expressed as occupancy-based  
626 Shannon diversity Hill number ( $q=1$ , the Shannon entropy exponentiated). Horizontal bars  
627 represent Hill number's means across surveys. Points are posterior distribution means and error

628 bars represent 95% Bayesian credible intervals. Filled and open symbols represent estimates in  
629 the presence and absence of lions, respectively.