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Title: Intraguild dynamics of understudied carnivores in a human-altered landscape

Running Head: Mesocarnivore interactions

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9 **Abstract**

10 Mesocarnivores constitute a diverse and often abundant group of species, which are increasingly

11 occupying higher trophic levels within multi-use landscapes. Yet, we know relatively little about

12 their interactions with each other, especially in human-altered areas. Using camera trap data

13 collected in a forestry concession in the Greater Gorongosa ecosystem of central Mozambique,

14 we examined the spatiotemporal relationships and potential for intraguild competition among

15 three understudied African carnivores: African civets (*Civettictis civetta*), bushy-tailed

16 mongooses (*Bdeogale crassicauda*), and large-spotted genets (*Genetta maculata*). After

17 accounting for habitat preferences and tolerance to anthropogenic factors, we found that African

18 civets and bushy-tailed mongooses avoid each other spatially and temporally. Additionally,

19 civets and mongooses were also both more likely to use sites farther away from human

20 settlements, possibly decreasing the total available habitat for each species if, competition is

21 driving this spatial partitioning. In contrast, we did not find evidence for spatial or temporal

22 partitioning between large-spotted genets and African civets, but bushy-tailed mongooses altered

23 their activity patterns where they co-occurred with genets. Our study contributes to scant

24 ecological knowledge of these mesocarnivores and adds to our understanding of community

25 dynamics in human-altered ecosystems.

26 **Keywords**

27 Competition, conservation, niche partitioning, species interactions

28 **Introduction**

29 Human population growth has caused rapid land use changes and the decline of apex carnivore

30 populations (Ripple et al. 2014). As a result, small to mid-sized carnivores (< 15 kg,

31 mesocarnivores hereafter, Roemer et al. 2009) are more frequently occupying higher trophic

32 levels than in the past, altering ecosystem dynamics (i.e., mesocarnivore release, Crooks & Soulé

33 1999; Ritchie & Johnson 2009). Spatial and temporal activity patterns of mesocarnivores are

34 typically shaped by habitat and food preferences and interactions with dominant species (e.g.,

35 Rich et al. 2017). In multi-use areas, mesocarnivores must also navigate human-altered

36 landscapes and human activities. People have had profound impacts on entire animal

37 communities through the exploitation of species, influencing landscapes of fear (Berger 2007),

38 changing the physical environment (Ellis 2011), and fundamentally changing how species

39 interact with each other (Oriol-Cotterill et al. 2015; Moll et al. 2018). Indeed, reducing risks of

40 encounters with humans likely plays a major role in where mesocarnivores and their prey

41 distribute themselves across the landscape (i.e., landscape of fear, Gaynor et al. 2019). This in

42 turn might cause sympatric mesocarnivore species to have fewer opportunities to partition in

43 space and time (Kiffner et al. 2015; Rota et al. 2016; Moll et al. 2018). Alternatively, species

44 more tolerant of anthropogenic landscapes and activity may use these areas as refuges from their

45 competitors (i.e., the "human shield" hypothesis, Berger 2007). Resource acquisition, competitor

46 avoidance, and human avoidance or tolerance collectively determine the activity patterns of

47 mesocarnivores, driving spatial and temporal niche partitioning and altering the ecosystem

48 services they provide (Schuette et al. 2013; Wang et al. 2015; Williams et al. 2017; Smith et al.

49 2018).

50 Dynamics among mesocarnivores and their resulting effects on community composition and

51 trophic cascades have been well studied in North America, Europe, and Australia (e.g., Johnson

52 & VanDerWal 2009; Levi & Wilmers 2012; Pasanen-Mortensen et al. 2013; Sivy et al. 2017)

53 and for larger carnivores in Africa (e.g., Creel & Creel 1996; Durant 1998; Rich et al. 2017). For

54 example, in the absence of wolves (*Canis lupus*) in much of the United States, coyotes (*Canis*

55 *latrans*) have become dominant carnivores, suppressing or changing the activity patterns of

56 smaller carnivores such as foxes (*Urocyon cinereoargenteus*, *Vulpes velox*, and *Vulpes vulpes*)

57 and increasing bird diversity (Harrison et al. 1989; Fedriani et al. 2000; Thompson & Gese 2007;

58 Levi & Wilmers 2012). In urban environments, these dynamics change such that foxes, which

59 are more tolerant of human infrastructure, more frequently use urban areas as a refuge from

60 coyotes while still avoiding people spatially and temporally (Moll et al. 2018).

61 Despite the abundance and diversity of mesocarnivores in sub-Saharan Africa, however, little is

62 known about their intraguild dynamics. African civets (*Civettictis civetta*) and large-spotted

63 genets (*Genetta maculata*), for example, are widespread, and their diet and habitat preferences

64 overlap with several other carnivores (Caro & Stoner 2003). This theoretically makes them

65 vulnerable to interspecific competition (Caro & Stoner 2003), yet little is known about their

66 spatial or temporal activity patterns or how they interact with each other (Admasu et al. 2004; Do

67 Linh San et al. 2013; Ramesh & Downs 2014). Of the studies that have investigated

68 mesocarnivore interactions (e.g., Waser 1980; Maddock & Perrin 1993; Schuette et al. 2013; de

69 Satgé et al. 2017; Ramesh et al. 2017; Rich et al. 2017), few have occurred outside of protected

70 areas or have incorporated human activities into their models. How mesocarnivores partition

71 spatially and temporally to avoid each other may shift in human-modified landscapes, depending

72 on their tolerance for human presence and activities. Furthermore, some of these studies only

73 investigate co-occurrence among potentially competing mesocarnivores without incorporating

74 habitat preferences (de Satgé et al. 2017; Ramesh et al. 2017) or anthropogenic factors (Rich et

75 al. 2017), which may be stronger drivers of spatial or temporal activity patterns than the potential

76   competitor. The paucity of ecological data on the mesocarnivores of sub-Saharan Africa, the

77   high potential for competitive interactions between them, and their shifting ecological roles in

78   multi-use landscapes highlight important knowledge gaps. To help fill these knowledge gaps, we

79   used camera trap data to better understand the spatiotemporal dynamics of mesocarnivore site

80   use in a forestry concession in the Greater Gorongosa ecosystem of central Mozambique. The

81   Gorongosa ecosystem could provide an interesting case study on how mesocarnivores interact

82   with each other in human-modified landscapes, due to the low densities of large carnivores (e.g.,

83   lions (*Panthera leo*), leopards (*Panthera pardus*), hyenas (*Crocuta, Hyaena brunnea*), and wild

84   dogs (*Lycaon pictus*)) following decades of civil unrest in the region, and growing human

85   populations and infrastructure development (Bouley et al. 2018; Easter et al. 2019). Here,

86   mesocarnivores face relatively few top-down pressures aside from potentially competing among

87   each other and avoiding people. This allows us to test theories about interspecific competition

88   among species with shared ranges, habitats, diets, and body sizes (Maddock & Perrin 1993; de

89   Satgé et al. 2017). For example, temporal overlap among activity patterns of competing

90   carnivores could facilitate spatial partitioning among them (Carter et al. 2015). Alternatively,

91   subordinate species may have a higher temporal overlap with people if dominant competitors

92   displace them from more preferred time periods (Schuette et al. 2013).

93   We investigated the potential for competitive interactions among three common but understudied

94   mesocarnivores: African civets, large-spotted genets, and bushy-tailed mongooses (*Bdeogale*

95   *crassicauda*; Table 1). We tested two hypotheses (Figure 1). Our first hypothesis is that these

96   species will segregate in space based largely on habitat preferences and tolerance of people.

97   Several studies have shown that genets are more tolerant of areas with people than other

98   carnivores (Fuller et al. 1990; Pettorelli et al. 2010; Schuette et al. 2013; Ramesh & Downs

99   2014), and bushy-tailed mongooses prefer forested areas (Caro & Stoner 2003; Pettorelli et al.

100   2010; Kingdon 2015). Our second hypothesis is that the smaller mesocarnivores (genets and

101   mongooses) will avoid the larger mesocarnivore (civets) in space and/or time due to being at a

102   competitive disadvantage for resources. Body size can influence competitive interactions among

103   species, with larger species able to outcompete or directly harm smaller species (Palomares &

104   Caro 1999; Donadio & Buskirk 2006). For example, de Satgé et al. (2017) found that striped

105   polecats (*Ictonyx striatus*) and small-spotted genets (*Genetta genetta*) avoided their larger

106   competitor, the African wildcat (*Felis silvestris lybica*), but these relationships have not been

107   examined for our study species. Species interactions shape community structure, abundance, and

108   distributions, and may have important cascading effects on ecosystem services and function

109   (Crooks and Soulé 1999; Schuette et al. 2013; Williams et al. 2017). Understanding intraguild

110   interactions among species in varying environmental conditions (e.g., low competition risk from

111   large carnivores, varying degrees of anthropogenic disturbance) allows conservation managers to

112   better predict the species of mesocarnivores that are most vulnerable to anthropogenic changes,

113   assess the indirect effects on other species in the community, and weigh the risks to wildlife

114   populations while managing landscapes for human and wildlife coexistence (Cardillo et al. 2005;

115   Pettorelli et al. 2010).

116   **Materials and Methods**

117   **Study Area**

118   Our study site was in central Mozambique, east of Gorongosa National Park's buffer zone. This

119   area has a sub-tropical climate with a wet season from November to April and dry season from

120   May to October. We conducted our surveys in a Forest-Stewardship Council (FSC) certified

121   forestry concession (460 km^2, Figure 2) composed mostly of miombo woodlands (*Brachystegia*

122   spp.) with a range of tree cover from patches of dry miombo woodlands and open grasslands to

123   moist, closed-canopy riverine forests (Stalmans & Beilfuss 2008). Elevation decreases gradually

124   from approximately 350 to 150 m from the Cheringoma Plateau in the west to the confluence of

125   the Chiteme and Chimiziua Rivers to the east. There are two small settlements (< 500

126   households) within the concession: Condue to the southwest and the forestry's sawmill and

127   living headquarters in the southeast. All roads in the concession are single-track, dirt roads,

128   created mainly for timber harvest, and a larger road and parallel railway bisects the concession

129   and the park's buffer zone. Roads that were not being used for concession activities were mostly

130   inactive and grown-over. Our team only conclusively documented two individual leopards and

131   no other large carnivores (e.g. hyena, wild dog, lion) at the time of this study. This allowed for

132   studying how mesocarnivores interact with minimal influence of larger, dominant carnivores in

133   the area.

134   **Carnivore Detection Data**

135   To measure carnivore site use, we deployed infrared camera traps (Bushnell Trophy Cam 24MP

136   and 14MP no-glow Aggressors) at 77 sites within the forestry concession. We used a four km^2

137   hexagonal grid with approximately two km separating each site to guide our camera trap

138   placement, but we prioritized roads and animal trails where possible, following protocols from

139   other studies that quantified carnivore space use (Carter et al. 2012; Rosenblatt et al. 2016). Due

140   to a limited number of cameras and time for deployment, traps consisted of either pairs or single

141   cameras to protect against possible failures while covering greater areas, and we rotated traps in

142   four successive blocks from June to October 2017 (Sollmann et al. 2012; Ahumada et al. 2013;

143   Rovero et al. 2016). Each camera trap was active for an average of 28 days (Wegge et al. 2009;

144   Athreya et al. 2013). We mounted each camera on a tree at about 45 to 60 cm above the area or

145   trail of interest. Identifying individuals with these cameras, especially at traps with only one

146   camera, is challenging. To reduce detection bias, we only considered detections of the same

147   species independent if they occurred at least 30 minutes after the last time that species was

148   detected at that trap, regardless of if another species passed within those 30 minutes (Wang et al.

149   2015; O'Connor et al. 2017).

150   **Temporal Overlap**

151   To investigate the interactions between mesocarnivores, we first examined their daily activity

152   patterns for temporal overlap. Each species is considered nocturnal (Pettorelli et al. 2010; Estes

153   2012), but fine scale avoidance between species could lead to temporal niche partitioning

154   (Schuette et al. 2013; Carter et al. 2015). We extracted the timestamps from each independent

155   photo of bushy-tailed mongooses, civet, and genet to create kernel density estimates of daily

156   activity patterns of each species. We compared the activity patterns of each species from camera

157   traps it was detected without a potential competitor to activity patterns of that species at camera

158   traps where it and its potential competitor were detection. These density distributions were used

159   to calculate the coefficient of overlapping, $\hat{D}$, which ranges from 0 to 1, with 1 representing

160   complete temporal overlap between the estimated activity times of a species pair, and 0

161   representing no temporal overlap between a species pair. We report $\hat{D_1}$ due to smaller sample

162   sizes in some comparisons (fewer than 75 observations) and consider $\hat{D_1} > 0.80$ (approximately)

163   to be a strong overlap (Allen et al. 2018). We performed all analyses in R (R Core Team 2013),

164   using the package 'overlap' (Meredith & Ridout 2017).

165 **Co-Abundance**

166 *Analysis*

167 We used two-species, N-mixture models to estimate the abundance of mesocarnivores relative to
168 each other while accounting for differential environmental effects and imperfect detection (Royle
169 2004; Brodie et al. 2018). Because we did not identify individuals, a site where 20 mongooses,
170 for example, were detected could be 20 detections of the same individual repeatedly using that
171 site in front of the camera. Therefore, we refer to the predicted abundances produced by these
172 models as a metric for how often a species used a given site. N-mixture models use repeated
173 counts of a population over time to estimate local abundance for a species i at location j ($N_{i,j}$) by
174 assuming $N_{i,j} \sim \text{Poisson}(\lambda_{i,j})$. The number of independent detections of a species in one day
175 counted as one count. Thus, if a camera trap was active for 20 days, there were 20 counts. We
176 modeled the expected count of a species i at each location j ($\lambda_{i,j}$) given environmental and
177 anthropogenic covariates using a log-link function (Royle 2004). To include the effect of one
178 species' abundance on another, δ estimates the coefficient, or effect, of a species' abundance (N_1)
179 on the other species in a pair: $\log(\lambda_{2,j}) = \alpha_2 + \alpha_2 (\text{Covariate})_j \ldots + \delta * N_{1,j}$.

180 An estimated negative value of δ would therefore indicate a negative correlation between the
181 abundances of species 1 and species 2, suggesting the potential of competitive exclusion (Brodie
182 et al. 2018). A positive estimate indicates that abundances of the two species increase together,
183 which could indicate a lack of competitive effects (Brodie et al. 2018), optimal habitat and
184 sufficient resources for both species (Rich et al. 2017), or, in some cases, mutualistic
185 relationships. We considered δ estimates significant if the 95% credibility interval did not
186 overlap zero. Similar to other occupancy models (MacKenzie et al. 2002; Mackenzie & Royle
187 2005), N-mixture models assume population closure.

188 The strength of this modelling approach lies also within its ability to account for imperfect
189 detection and mitigate biases that may alter estimations of $N_{i,j}$, as true abundance cannot be
190 observed. To do this, the species' level detection probability (p) is modeled as $p_{i,j,k}$: $n_{i,j,k} \sim$
191 $\text{Bin}(N_{i,j,k}, p_{i,j,k})$, where n represents the number of detections of a species (i) at a location (j) for
192 each replicate count (k) and follows a binomial distribution. We modeled the detection

193   probability of each species in a pair based on a different set of variables expected to affect the

194   observation process, which is detailed below.

195   *Covariates*

196   We hypothesized that these species would vary in their habitat preferences and tolerance to

197   human disturbance, so we incorporated natural and anthropogenic covariates into our co-

198   abundance models. We predicted that habitat type and cover, distance to water (m), distance to

199   the nearest human settlement (m), and human activity would influence species abundance

200   (Schuette et al. 2013; Ramesh et al. 2017; Rich et al. 2017).

201   We used the Normalized Difference Vegetation Index (NDVI) calculated from a cloud free,

202   Landsat 8 image (Path 67, Row 73) acquired July 2017 and downloaded from USGS Earth

203   Explorer (https://earthexplorer.usgs.gov/) to represent habitat type, cover, and forage availability

204   (DeFries & Townshend 1994; Pettorelli et al. 2005; Ladle et al. 2018). We created a land cover

205   map using a random forest classification model, our field notes, and Google Earth imagery, but

206   based on the results of an ANOVA test and visual assessments of the two maps, we determined

207   that NDVI values provided the same information as our land cover map. We therefore used

208   NDVI instead of the categorical land cover map because it is a continuous variable frequently

209   used in occupancy analyses (Burton et al. 2012; Rich et al. 2017). We calculated the mean NDVI

210   within a 500 m buffer surrounding each camera trap to determine how much each carnivore

211   would likely use that location based on the general vegetation attributes of the nearby area

212   (Carter et al. 2013; Ladle et al. 2018). We chose 500 m because it is the approximate size of a

213   genet's home range, which is the smallest known home range of our three species (Estes 2012;

214   Williams et al. 2017).

215   To measure how water availability affects species abundance, we combined the GPS points we

216   took from the ground where we followed creeks and rivers with spatial river data from the

217   HydroSHEDS dataset (Lehner et al. 2006) to determine the location of permanent water sources

218   in our study area. We then calculated the distance from each camera trap to the nearest water

219   source in ArcGIS 10.5.1.

220   For our anthropogenic variables, we estimated human activity levels as the proportion of days

221   people or vehicles were detected at each camera trap, for the number of days each trap was

222   active. We did not believe that human activity would impact detection because these species are

223   nocturnal (Estes 2012), but we predicted that areas with greater human activity, such as those

224   where logging was occurring (Brodie et al. 2018) or near an active road (Smith et al. 2018), may

225   affect the abundance of carnivores using that area. We also included the distance of each trap to

226   the nearest settlement in kilometers, calculated in ArcGIS 10.5.1. The abundance model is

227   therefore specified as:

228    $\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i(\text{NDVI})_j + \alpha 2_i(\text{water})_j + \alpha 3_i(\text{settle})_j + \alpha 4_i(\text{human})_j + \delta_i(N_{1,j})$

229   We included a different set of site-level covariates for the detection model that we expected may

230   affect the localized detection process or space use of an animal. Carnivores often utilize trails

231   and roads when traveling (Cusack et al. 2015; Kolowski & Forrester 2017), so we included a

232   binary variable for whether a trap was located on (1) or off (0) a trail. We also included a binary

233   variable for if a trap consisted of two cameras (1) or one (0) which may affect the detectability of

234   smaller species (Pease et al. 2016). We used the Julian date for each sampling day of each

235   individual camera trap site to help account for changing detection rates over the study period and

236   possible bias associated with pseudoreplication. This covariate measures the changes in detection

237   rates that may have to do with seasonality or the progression of our sampling, with only one

238   block of cameras active at a time and each block successively following the previous one.

239   Finally, we calculated the slope at each camera trap using a Digital Elevation Model in ArcGIS

240   10.5.1 (Ahumada et al. 2013; Rovero et al. 2014; Brodie et al. 2018). We therefore specified the

241   detection model as:

242    $\text{logit}(p_{i,j,k}) = \beta 0_i + \beta 1_i(\text{trail})_j + \beta 2_i(\text{paired})_j + \beta 3_i(\text{slope})_j + \beta 4_i(\text{survey days})_j$

243   We checked all continuous covariates for collinearity with the Pearson's correlation coefficient.

244   We initially considered including elevation in our models, but it was significantly correlated with

245   distance from water (Pearson r = 0.71), so we discarded this covariate. Additionally, variation in

246   detection probabilities may partially depend on which of our sampling blocks the camera traps

247   were located in. To account for this, we developed models that incorporated a random effect for

248   our blocks, using several combinations of the variables listed above. However, models did not

249 converge when these random effects were included. Therefore, instead of using models with

250 unreliable coefficient estimates, we dropped blocks as a random effect and used fixed-effect

251 models in subsequent analysis in order to make stronger inferences on the effects of ecologically

252 meaningful, camera trap-level covariates (i.e., distance of each camera trap from water, distance

253 from human settlements, human activity levels at each camera trap, average NDVI within 500 m

254 of each camera trap).

255 We used a Bayesian approach with minimally informative priors (McElreath 2015) to estimate

256 model parameters. This approach provides two advantages. First, Bayesian analysis allows for

257 the explicit estimates of latent N_{1j} values which are used to estimate N_{2j} values (Brodie et al.

258 2018). Second, by assigning regularizing priors to all the parameter coefficients, we reduce

259 overfitting while creating a "skeptical" model, which interprets values above or below zero to be

260 less plausible. Therefore, we are more confident in the significance of a parameter estimate if the

261 95% credibility intervals (CIs) do not overlap zero (McElreath 2015). We implemented our

262 models with R (R Core Team 2013) using the package R2jags (Plummer 2011). We ran three

263 chains of 100,000 iterations and discarded the first 50,000 as a burn-in for each species pair and

264 thinned the remaining 50,000 iterations by 20. We assessed model convergence by visually

265 examining trace plots and with the Gelman-Rubin diagnostic, where Rhat values > 1.1 indicate

266 poor convergence (Gelman et al. 2014).

267 **Results**

268 **Carnivore Detection Data**

269 Cameras were active for 2,090 trap days. Two of the sites had malfunctioning cameras, leaving

270 75 sites to analyze. We obtained 168 independent detections of bushy-tailed mongooses at 36 of

271 our camera traps, 152 detections of African civets at 29 traps, and 120 detections of large-spotted

272 genets at 25 traps. Five other carnivore species were detected at much lower frequencies: marsh

273 mongooses (*Atilax paludinosus*) were detected 40 times; servals (*Leptailurus serval*) were

274 detected 12 times; leopards were detected 8 times; white-tailed mongooses (*Ichneumia*

275 *albicauda*) were detected 6 times; and honey badgers (*Mellivora capensis*) were detected 5

276 times.

Temporal Partitioning

Each of our three mesocarnivores were active between the hours of 6 pm and 6 am and each species' activity patterns strongly overlapped with those of their potential competitors across the study site ($\hat{D}_1 > 0.8$; Figure 3). However, bushy-tailed mongooses appear to shift to being more crepuscular when using the same site as a potential competitor (Figure 4). Mongoose activity patterns remained strongly overlapping with civet activity patterns, ($\hat{D}_1 = 0.83$), but was not strongly overlapped with genet activity ($\hat{D}_1 = 0.75$). Further, civets and mongooses appear to have inverse activity patterns when in the presence of the other (Figure 4). There was very little difference in the activity times of genets when in the presence of a competitor, however, and their activity patterns hardly changed at all when in the presence of civets ($\hat{D}_1 = 0.94$; Figure 4).

Spatial Partitioning

Our models estimated a negative correlation between African civet (largest of the mesocarnivores) and bushy-tailed mongoose site use, a positive correlation between large-spotted genet and bushy-tailed mongoose site use (about the same size), and African civet and large-spotted genet site use were not correlated (Figure 5). Civet and mongoose site use was strongly correlated with settlement proximity, and mongooses were more likely to use more forested sites (areas with high NDVI, Figure 6). Genet site use did not have a strong relationship with any of the habitat variables in the abundance models (Figure 6). The slope at each camera trap, the dates traps were active, and whether a camera trap was placed on a trail were significant predictors for these species' detection probabilities, detailed below, but whether a camera trap consisted of a single camera or pair of cameras was not strongly correlated with any of their detection probabilities (Table 2). The estimated effect of each coefficient in the detection and abundance models and their 95% CIs shifted slightly for each species depending on which other species they were paired with, which is detailed below.

Civet-Genet

Civet abundance did not have a significant relationship with genet abundance (mean: -0.06, 95 % CI: -0.36 – 0.22; Figure 5). In the civet-genet model, civet abundance was strongly related to distance from the nearest settlement, with abundance increasing as distance from settlements

305   increased (mean: 0.82, 95% CI: 0.40 – 1.28). In contrast, there was not a strong relationship

306   between genet abundance and settlement distance (mean: 0.07, 95% CI: -0.43 – 0.60; Figure 6).

307   The other covariates in the abundance model (distance to rivers, NDVI, and human activity) did

308   not have strong effects on either genet or civet abundance (Figure 6).

309   The detection probability of both species significantly increased for camera traps that were

310   located on a trail. Civet detection probability also decreased further into the dry season. The

311   slope and number of cameras at each trap did not significantly change either species' detection

312   probabilities (Table 2).

Civet-Mongoose

314   Our models estimated a negative relationship between civet and bushy-tailed mongoose

315   abundance (mean: 0.26, 95% CI: -0.55 – -0.03; Figure 5). Both species' abundances were

316   positively related to increasing distance from settlements (civet mean: 0.82, 95% CI: 0.39 – 1.29;

317   mongoose mean: 0.61, 95% CI: 0.22 – 1.12). Bushy-tailed mongoose abundance was also

318   positively correlated with NDVI (mean: 0.38, 95% CI: 0.04 – 0.74) and negatively correlated

319   with distance to water (mean: -0.40, 95% CI: -0.76 – -0.08) with higher abundances predicted in

320   forested areas near water. In contrast, civet abundance had a weaker, but negative relationship

321   with NDVI (mean: -0.26, 95% CI: -0.62 – 0.10; Figure 6).

322   Civet detection probabilities were higher later in the season and when cameras were placed on

323   trails but were not strongly related to the number of cameras or the slope at each site. Bushy-

324   tailed mongoose detection probabilities decreased for traps located near steeper slopes and was

325   not strongly correlated with any of the other detection covariates (paired cameras, on/off trails,

326   and date; Table 2).

Genet-Mongoose

328   Genet and bushy-tailed mongoose abundances were positively correlated (mean: 0.24, 95% CI:

329   0.11 – 0.38; Figure 5). None of the parameter coefficient estimates significantly differed between

330   the two species, despite mongoose abundance being more strongly related to NDVI (mean: 0.50,

331   95% CI: 0.14 – 0.88), and distance from settlement (mean: 0.38, 95% CI: 0.04 – 0.74; Figure 6).

332 Bushy-tailed mongooses, again, were less likely to be detected at sites with steeper slopes, but

333 neither species had significant relationships with any of the other covariates (Table 2).

334 **Discussion**

335 Although important to ecosystem functioning, little is known about mesocarnivore ecology in

336 human-modified landscapes. We have provided evidence for fine-scale spatial and temporal

337 partitioning among sympatric carnivores in a forestry area of Mozambique. Our results indicate

338 that, after accounting for differences in habitat preferences and sensitivities to anthropogenic

339 factors, bushy-tailed mongooses and African civets partition in space and time. Further, while

340 large-spotted genet site use and activity patterns were not affected by either of the other two

341 species, bushy-tailed mongooses seemed to adjust their activity patterns to avoid genets. While

342 our findings did not lend support to either of our hypotheses, the spatiotemporal patterns of these

343 species warrant further exploration.

344 Differences in foraging strategies, dietary preferences, and the relative abundance of food may

345 explain how genets can occupy the same spatial and temporal niches of these other two

346 mesocarnivores (Waser 1980; Ray & Sunquist 2001; Caro & Stoner 2003; Angelici & Luiselli

347 2005; Estes 2012). Genets are more arboreal than civets and mongooses, which may allow for an

348 even finer scale spatial partition between these species (Maddock & Perrin 1993). However, the

349 high spatial overlap of mongoose and genet site use is likely further facilitated by mongooses

350 avoiding genets in time (Figure 4). Little is known about the foraging behaviors of bushy-tailed

351 mongooses, but genets are more carnivorous than civets; they often stalk and hunt prey whereas

352 civets are ambush carnivores and more opportunistic omnivores (Ray & Sunquist 2001; Estes

353 2012). Such differences have been shown to mediate competitive exclusion in other systems,

354 such as the avoidance of Iberian lynx (*Lynx pardinus*) by red foxes but not by Eurasian badgers

355 (*Meles meles*), which have a more distinctive foraging strategy (Fedriani et al. 1999). Finally,

356 shared resources tracked by all these species, such as prey species (i.e. rats, *Cricetomys*

357 *gambianus*, *Thryonomys gregorianus*) may be abundant, as suggested by our camera trapping

358 detections but not explicitly quantified. If abundant resources can support a higher number of

359 these mesocarnivores, competitive interactions or resource partitioning would not be necessary

360 (Brodie et al. 2018). Our study did not quantify forage or prey availability since our study

361   species consume such a variety of animal and plant species (Caro & Stoner 2003; Williams et al.

362   2017), but Rich et al. (2017) found that, generally, carnivore occupancy in Botswana depended

363   more on resource availability than the presence of competing species. Indeed, civet occupancy

364   was negatively related to the detection rates of similarly sized carnivores in Botswana during the

365   dry season, but positively related to them in the wet season, possibly due to greater resource

366   availability (Rich et al. 2017).

367   Civets and mongooses appeared to avoid each other in space and time at fine scales at our site

368   (Figures 4, 5). In contrast to genets and mongooses, though, civets and mongooses appear to both

369   adjust their activity patterns when using the same sites, exhibiting inverse activity patterns with

370   and without the other present, rather than one more strongly avoiding the other. However, civets

371   and mongooses may be seeking different resources that were not represented in our models,

372   indicating that the negative relationship between mongoose and civet site use more accurately

373   represents different preferences rather than competition or avoidance. For example, civets are

374   more frugivorous than others in their guild and have been considered hypo-carnivorous (less than

375   30% of its diet consists of meat, Waser 1980; Ray & Sunquist 2001; Amiard et al. 2015). Civets

376   are also typically seen in more open habitats, whereas bushy-tailed mongooses have exhibited

377   strong avoidance of open habitats (Pettorelli et al. 2010). However, this variance should be

378   captured in the NDVI variable of our models, which does show positive correlations between

379   mongoose site use and forested areas and the opposite (though weaker) relationship with civet

380   site use.

381   It is important to understand intraguild interactions among mesocarnivores in multi-use

382   landscapes, where the presence of people may drive different patterns than what would be

383   expected in protected areas (Waser 1980; Schuette et al. 2013; Massara et al. 2016). Civets and

384   mongooses were both more likely to occur in higher numbers farther away from human

385   settlements. Other studies have documented similar patterns, where carnivore occupancy is

386   reduced near permanent settlements (Burton et al. 2012; Carter et al. 2013; Schuette et al. 2013;

387   Williams et al. 2017). This result is disconcerting because mesocarnivores provide ecosystem

388   services, from which people could benefit. For example, these species likely play a large part in

389   limiting rodent and other pest populations in cropland areas, and, by extension, limiting the

390   spread of zoonotic diseases (Ostfeld & Holt 2004; Williams et al. 2017). Additionally, civets

391 (e.g., *Paguma larvata*, *Paradoxurus hermaphroditus*, *Viverra zibetha*) in particular are

392 considered important seed dispersers (Nakashima et al. 2010; Caughlin et al. 2014). However,

393 these services are reliant on both the abundance and diversity of mesocarnivores, which, as

394 supported by our results as well as other studies, can be limited in human-altered areas (Burton et

395 al. 2012; Schuette et al. 2013; Williams et al. 2017). The selection of habitats farther from

396 settlements by both mongooses and civets likely further limits resource availability and

397 opportunities for niche partitioning (Massara et al. 2016; Moll et al. 2018). Human populations

398 are projected to rapidly grow in Mozambique, including in the Gorongosa region (United

399 Nations 2017). The expansion of settlements may exacerbate the negative interactions between

400 civets and mongooses by pushing them out of viable habitats and facilitating more interactions

401 between these and other potentially competing species whose interactions and basic ecologies

402 remain unknown (Do Linh San et al. 2013).

403 Competitive interactions are also important to consider for conservation planning, specifically

404 the restoration of large carnivore populations. Mesocarnivores often spatially or temporally avoid

405 large carnivores to reduce the potential for competition or even predation (Johnson &

406 VanDerWal 2009). Leopards are the only known large carnivore to occur at our site, and they

407 were rarely detected, likely due to low population sizes following Mozambique's civil war

408 (Bouley et al. 2018; Easter et al. 2019). The recovery of leopards and other large carnivores to

409 pre-war densities and facilitation of their movement between protected areas in the region,

410 including through our study site, is a priority for Gorongosa National Park managers. We were

411 unable to test how leopards affected mesocarnivore abundance due to low sample sizes, but their

412 presence and recovery could alter intraguild dynamics. For example, in one of the few studies

413 that examined the effect of leopards on mesocarnivore occupancy, Ramesh et al. (2017) found

414 that honey badgers (*Mellivora capensis*), slender mongooses (*Galerella sanguinea*), and striped

415 polecats (*Ictonyx striatus*) were detected less often at sites where leopards were detected.

416 Additionally, leopards have been known to kill and eat civets (Palomares & Caro 1999).

417 Leopards may therefore reduce the amount of available habitat for subordinate carnivores.

418 Alternatively, they may suppress medium-sized carnivores such as civets, releasing mongooses,

419 other competitors, and their prey from interference and predatory pressures. These carnivore

420 cascades have been noted in North America, Australia, Europe, and East Africa (e.g., Creel &

421 Creel 1996; Johnson & VanDerWal 2009; Levi & Wilmers 2012; Pasanen-Mortensen et al.

422 2013; Sivy et al. 2017).

423 These multi-faceted interactions between carnivores, people and their environment are critical to

424 understanding the spatiotemporal dynamics of sympatric carnivores. Our study demonstrates the

425 importance of considering each of these elements to better understand the ecology of these

426 mesocarnivores, which few studies have addressed. However, the following limitations of our

427 study in addition to the other possible drivers of spatiotemporal partitioning discussed above

428 (e.g., prey and forage availability) should be carefully considered. First, as discussed in the

429 methods, we experienced issues with overparameterization which limited our ability to fully

430 account for the possible effects of pseudoreplication between our camera trap blocks or

431 individual sites. Second, African civets have larger home ranges (See Table 1) than the distance

432 between our camera traps (~1.5 km), and their detections may be autocorrelated. Lastly, some

433 basic ecological information is still lacking for these species, such as the foraging strategies,

434 home range sizes, and habitat preferences of bushy-tailed mongooses, which would help

435 untangle their relationships with sympatric species. Such studies are much needed in

436 anthropogenic landscapes, which are ubiquitous worldwide.

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638

Figure 1: Conceptual diagram of hypothesized spatial relationships between African civets, large-spotted genets, and bushy-tailed mongooses, accounting for the influences of top-down (Predation/Fear) and bottom-up (Resources) factors. In hypothesis one, these three species have little relative influence on each other (dashed arrows) and are spatially distributed based on habitat preferences. In hypothesis two, spatial distributions are largely determined by competitive interactions based on body size (solid arrows).

Figure 2: Map of our study site within a sustainable forestry concession adjacent to Gorongosa National Park and its buffer zone in central Mozambique.

Figure 3: Overlap of daily activity patterns for each species pair across all detections. The estimate of overlap (Δ, with 0 indicating no overlap and 1 indicating complete overlap) is indicated by the grey area. Blue and black ticks indicate the raw time stamps used to create the density curves, and 95% confidence intervals are given in parentheses. Activity patterns of each species pair strongly overlapped ($\Delta > 0.8$).

Figure 4: Daily activity pattern overlap for each species for when they were detected at the same camera traps as their competitors (blue dashed lines) and for when they were detected at camera traps where their competitors were not (black lines). The estimate of overlap (Δ, with 0 indicating no overlap and 1 indicating complete overlap) is indicated by the grey area. Blue and black ticks indicate the raw time stamps used to create the density curves, and 95% confidence intervals are given in parentheses. Activity patterns between genets and civets changed the least when the other was present, while mongoose activity patterns varied more greatly if civets or genets used the same area.

Figure 5: Estimated correlations between species abundances. The black lines represent the mean correlation estimate for each pair: -0.26 for bushy-tailed mongooses and African civets, 0.24 for bushy-tailed mongooses and large-spotted genets, and -0.01 for large-spotted genets and African civets (on the logit scale). Dashed lines indicate 95% confidence intervals.

Figure 6: Violin plots of the coefficient estimates for each variable in the abundance models of each species pair (African civets shown in purple, bushy-tailed mongooses shown in blue, and large-spotted genets shown in orange). Black lines through the violins indicate estimates at the 2.5%, 50%, and 97.5% intervals. Mongooses were more likely to use sites farther away from

668   settlements, close to rivers, and in greener, or more forested, areas. In contrast, civets' site use

669   was not significantly correlated with rivers or NDVI but were also more likely to use sites farther

670   away from settlements. Genet site use was not significantly correlated with any of the covariates.

671

672   **Table 1:** Ecological characteristics of our three study species observed in central Mozambique:

673   African civets, bushy-tailed mongooses, and large-spotted genets. All species are nocturnal and

674   opportunistic generalists. However, these species consume varying amounts of small vertebrates,

675   invertebrates, fruits, and plants which may affect spatial and temporal partitioning.

Common Name	Species Name	Size	Range	Home Range Size	Habitat Preferences	References
African civet	*Civettictis civetta*	7-20 kg	Widely distributed in Sub-Saharan Africa	5-11 km²	Anywhere with adequate cover and food, usually near water.	Caro & Stoner 2003 (size, habitat); Estes 2012 (range, home range, habitat)
Bushy-tailed mongoose	*Bdeogale crassicauda*	2 kg	Common within portions of Tanzania, Mozambique, Zimbabwe, Zambia, Malawai	Unknown	Woodland/scrub and forested areas.	Caro & Stoner 2003 (size, habitat); Pettorelli et al. 2010 (range); Rovero et al. 2017 (habitat)
Large-spotted genet	*Genetta maculata*	2 kg	Widely distributed in	0.5-1 km²	Anywhere with adequate cover	Caro & Stoner

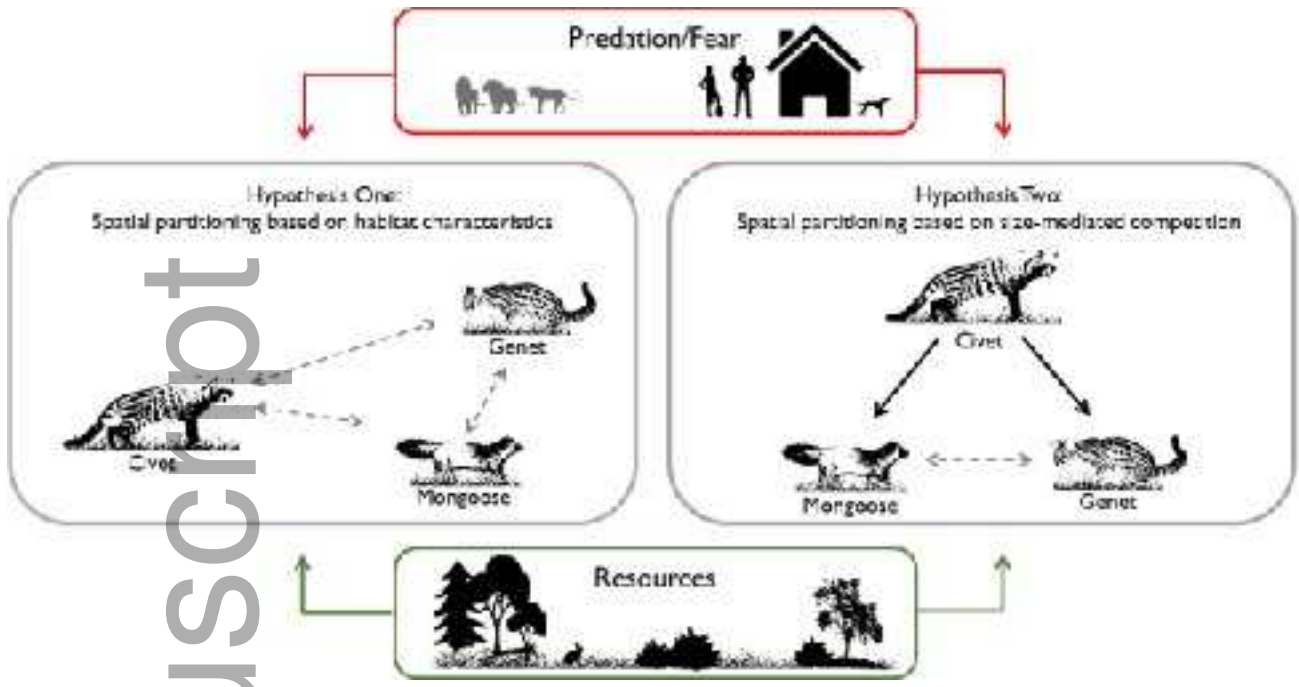|	Sub-Saharan Africa	and food. Tolerant of human-modified areas.	2003 (size, habitat); Estes 2012 (range, home range); Schuette et al. 2013 (habitat)

676

677

678

679 **Table 2:** Detection parameter estimates (on the logit scale) for African civets, bushy-tailed

680 mongooses, and large spotted genets detected in a forestry concession in central Mozambique.

681 'On trail' was a binary variable for if a camera trap was placed on a road or trail. 'Paired

682 cameras' is also a binary variable for if a camera trap had one (0) or two (1) cameras. 'Survey

683 days' refers to the Julian date of each survey day, and the slope is the slope measured at each

684 camera trap at 30 m resolution. Asterisks indicate estimates with 95% credibility intervals that do

685 not overlap zero. Civets and genets were more likely to be detected on trails. Civets were less

686 likely to be detected later in the dry season, and mongoose were less likely to be detected on
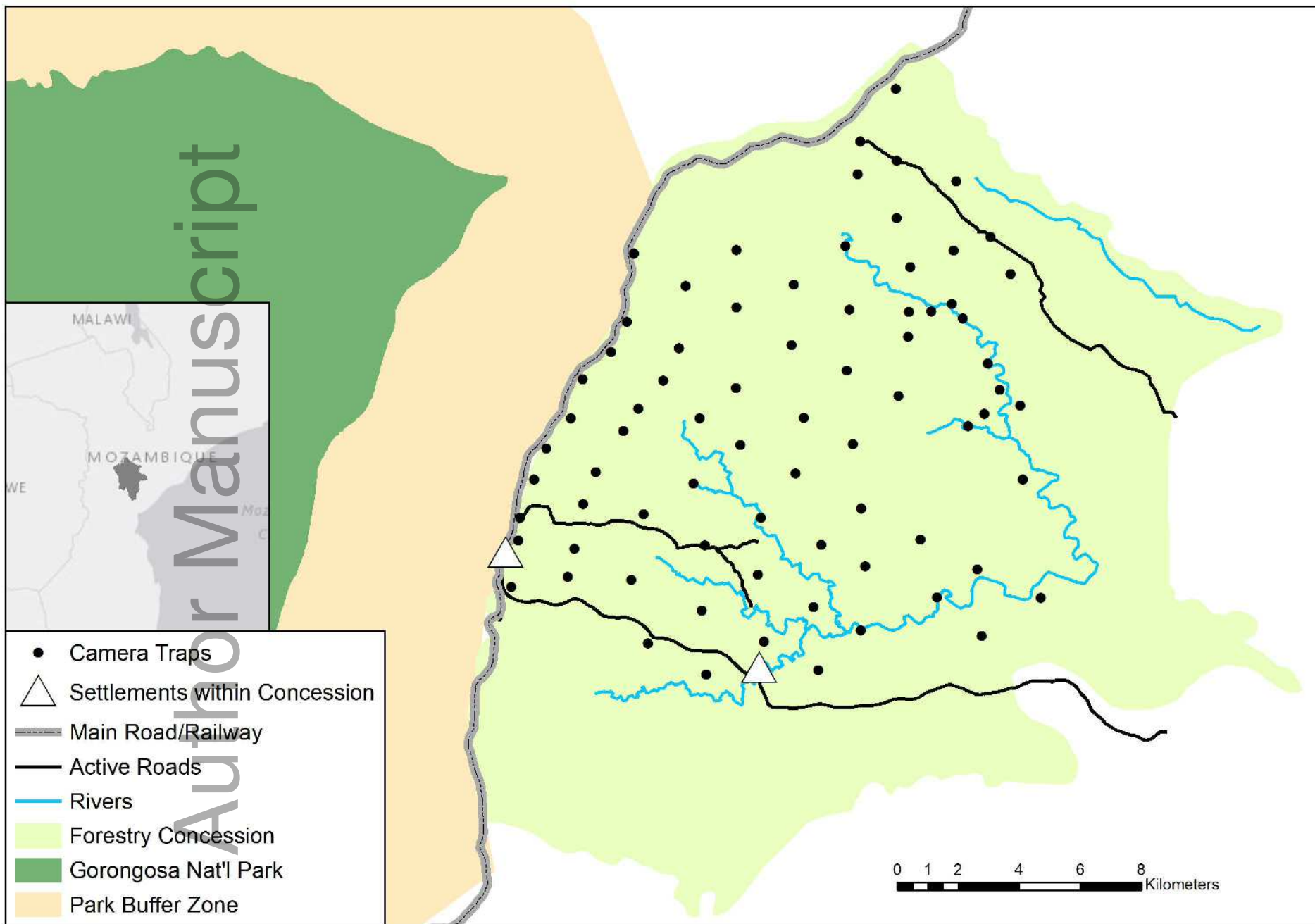
687 steeper slopes.

Species	On Trail	Paired Cameras	Survey Days	Slope
Civet	1.82*	0.04	-0.51*	-0.11
Genet	2.87*	-0.04	0.22	-0.18
Civet	1.76*	0.04	-0.51*	-0.09
Mongoose	0.03	-0.06	-0.13	-0.44*
Genet	2.95*	-0.14	0.22	-0.18
Mongoose	-0.04	-0.20	-0.11	-0.47*

688

ece3_6290_f1.tif

Legend:
- Camera Traps
- Settlements within Concession
- Main Road/Railway
- Active Roads
- Rivers
- Forestry Concession
- Gorongosa Nat'l Park
- Park Buffer Zone

MALAWI

MOZAMBIQUE

0 1 2 4 6 8 Kilometers
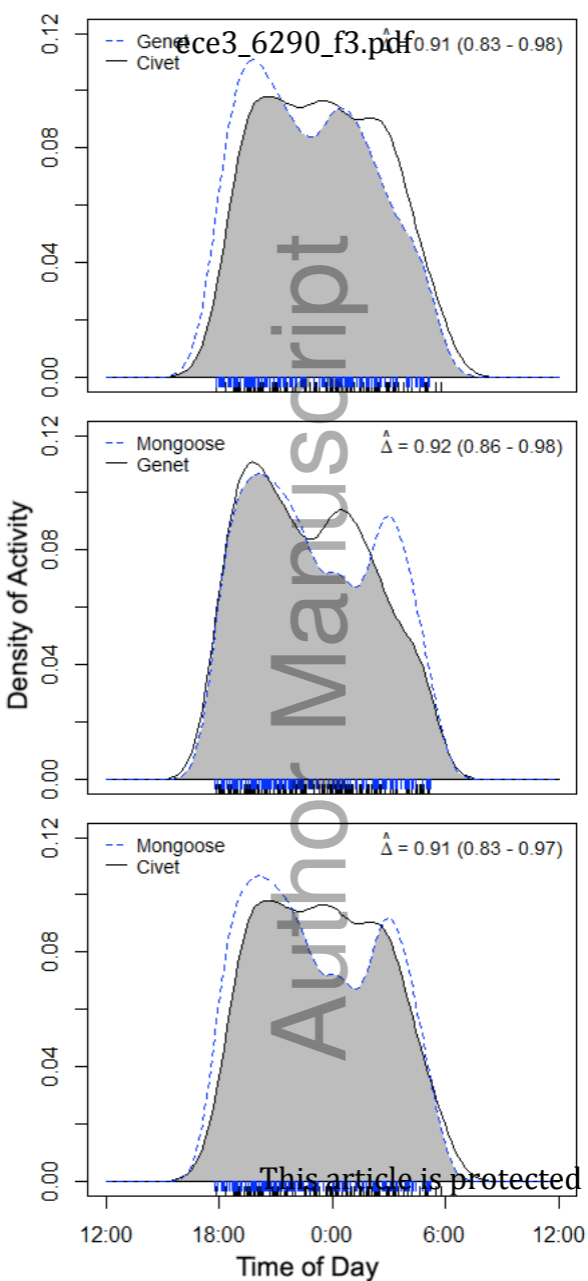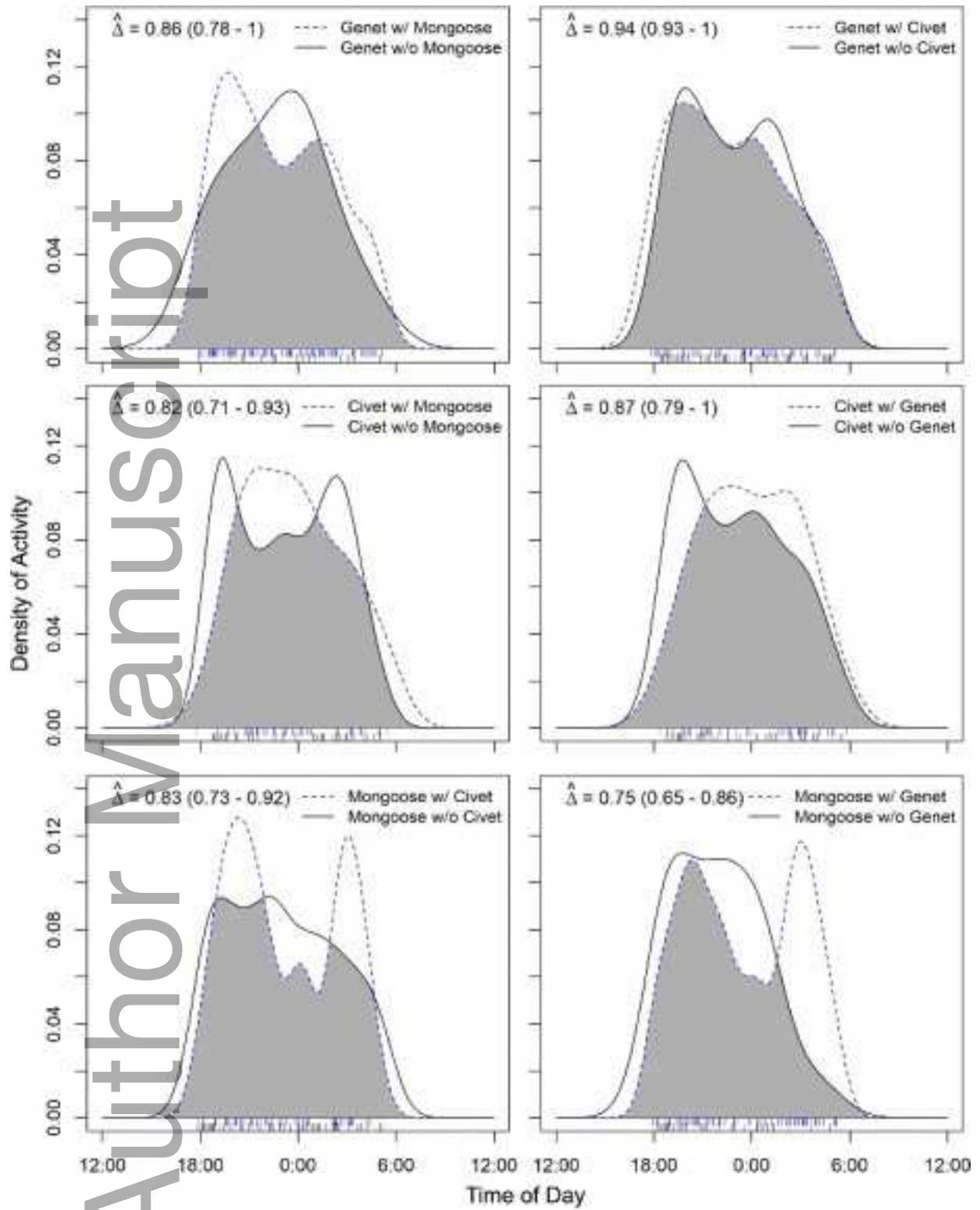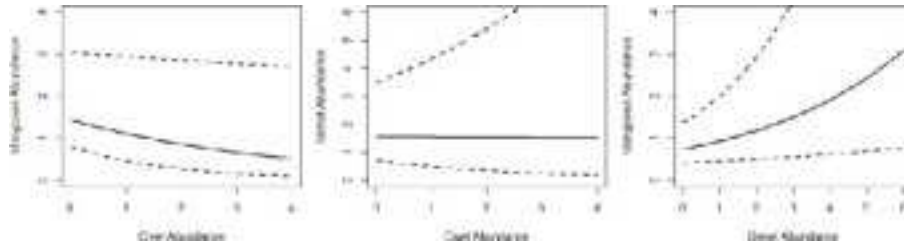
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