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Zach J. Farris

Brian Gerber

Sarah Karpanty

Asia Murphy

Erin Wampole

See next page for additional authors

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Authors

Zach J. Farris, Brian Gerber, Sarah Karpanty, Asia Murphy, Erin Wampole, Felix Ratelolahy, and Marcella J. Kelly

1 **Exploring and interpreting spatiotemporal interactions between native and invasive**
2 **carnivores across a gradient of rainforest degradation**

3 Zach J. Farris^{1 Ψ}, Brian D. Gerber^{2 Ψ}, Sarah Karpanty³, Asia Murphy⁴, Erin Wampole², Felix
4 Ratelolahy⁵, and Marcella J. Kelly³

5 ¹ Department of Health & Exercise Science, Appalachian State University, Boone, NC, USA

6 ² Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island-
7 02881 USA

8 ³ Department of Fish & Wildlife Conservation, Virginia Tech, Blacksburg, VA, USA

9 ⁴ Department of Ecosystem Science and Management and Huck Institutes of the Life Sciences,
10 Pennsylvania State University, University, PA, USA

11 ⁵ Wildlife Conservation Society, Madagascar Program, Antananarivo, Madagascar

12 ^Ψ These authors contributed equally to this manuscript

13

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16 **Corresponding author:** Zach J. Farris, farriszj@appstate.edu, 828-262-6455

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34 **Abstract**

35 Studies of elusive carnivores often rely on passive sampling when investigating either spatial or
36 temporal interactions. However, inference on behavioral mechanisms are usually lacking. We
37 present an analysis that combines previously published spatial co-occurrence estimates and
38 temporal kernel density estimates to explore spatiotemporal interspecific interactions. We do so
39 by deriving a spatiotemporal value (STV) that is a relative measure of potential interaction in both
40 niche dimensions, across a gradient of degradation, for rainforest carnivore pairs in Madagascar.
41 We also use a conceptual framework to provide insight into the potential behavioral mechanisms
42 of habitat selection. Of the six native and three invasive carnivores, we estimate the spatiotemporal
43 interactions for twelve pairings, which range from no spatial/temporal relationship ($n = 5$) to
44 spatiotemporal aggregation or segregation ($n = 7$). We visualized these spatiotemporal interactions
45 along a fragmentation gradient and demonstrate that these interactions are not static, as STV
46 overlap increases with increasing anthropogenic disturbance. Of the three invasive carnivores
47 (free-ranging dogs *Canis familiaris*, cats *Felis species*, and small Indian civets *Viverricula indica*)
48 the latter had the highest number of spatial occurrence ($n = 4$) and spatiotemporal overlap ($n = 4$)
49 relationships with native carnivores. Our results highlight the potential for increasing direct and
50 indirect interactions between native and invasive species as forest degradation and invasive
51 predators increase. Our approach allows us to better understand adaptive behaviors, plasticity in
52 temporal activity, community assemblage, and to develop targeted conservation strategies to
53 manage ecological communities in rapidly changing ecosystems.

54 **Keywords**

55 Non-native species, Madagascar, niche dynamics, occupancy, spatial modelling, temporal
56 activity

57 **Introduction**

58 Interspecific interactions are important drivers of population and community dynamics
59 (Hardin 1960; Rosenzweig 1966). Studies of interspecific interactions investigate how species co-
60 occur or avoid each other spatially and/or temporally and, as a result, provide insight into behaviors
61 that contribute to species' survival and reproductive success (i.e., adaptive behavior). Including
62 extrinsic factors (e.g., habitat, landscape, anthropogenic disturbance) into these investigations
63 broadens our understanding of how realized niche dynamics might change across variable
64 environments and result in variable community assemblages. Improving our understanding of
65 interspecific interactions across both space and time is important if we are to develop effective
66 management strategies for wildlife populations and communities, especially as new challenges
67 emerge, resulting from altered landscapes and a changing climate (Rands et al. 2010).

68 For rare and elusive species, such as carnivores, investigations of interspecific interactions
69 can be challenging and are often lacking for many communities globally (Brooke et al. 2014;
70 Thompson 2013). As a result, attempts to investigate interactions among co-occurring carnivores
71 often include only a spatial or temporal component. Investigations of carnivore communities have
72 revealed that carnivores alter their spatial distribution (Durant 1998; Farris et al. 2015c;
73 Hersteinsson, Macdonald 1992; Linnell, Strand 2000; Mills, Gorman 1997; Mitchell, Banks 2005;
74 Rich et al. 2017; Vanak et al. 2013b) or their daily activity patterns (Farris et al. 2015a; Kitchen et
75 al. 1999; Major, Sherburne 1987; Palomares, Caro 1999; Wang et al. 2015; Wilson et al. 2010)
76 due to interspecific interactions. Investigations of interspecific interactions that combine spatial
77 and temporal analyses simultaneously, however, are exceedingly rare for elusive carnivores
78 (Karanth et al. 2017; Li et al. 2019; Moll et al. 2018; Niedballa et al. 2019; Smith et al. 2019). Yet,
79 such studies may provide heightened insight on the ultimate causes driving co-occurrence of
80 species' populations within communities, since investigations utilizing one dimension alone

81 (spatial or temporal) may fail to elucidate how species alter both spatial and temporal use
82 simultaneously to promote or discourage potential interactions. Additionally, studies combining
83 spatiotemporal components in a carnivore community consisting of native, co-occurring members
84 and non-native, invading species, are particularly important to our understanding of community
85 dynamics and for developing targeted action plans to manage biodiversity conservation.

86 Invasive species, particularly non-native carnivores, have had adverse effects on
87 biodiversity worldwide (Bonnaud et al. 2011; Loss et al. 2013; Nogales et al. 2013; Weston,
88 Stankowich 2013; Young et al. 2011). Research on interspecific interactions between native and
89 invasive carnivores are limited. However, studying spatial and temporal plasticity of native
90 carnivores in the face of new, unique competitors (i.e., non-native predators) is needed to
91 understand if/how coexistence occurs post invasion. Similarly, investigating adaptive behaviors of
92 native species during these invasion events will provide insight on how fitness may change as
93 resources diminish. Free-ranging dogs and cats are the most ubiquitous introduced, non-native
94 carnivores world-wide (Gompper 2013). Native carnivores are negatively affected by both free-
95 ranging dogs and cats as a result of competition (Vanak et al. 2013a; Vanak, Gompper 2009, 2010;
96 Young et al. 2011), direct aggression and intraguild predation (Hughes, Macdonald 2013; Ralls,
97 White 1995; Young et al. 2011), reduction of prey biomass (Frank et al. 2014; Loss et al. 2013;
98 Wierzbowska et al. 2016), altering of temporal activity and/or spatial distribution (Farris et al.
99 2015a; Farris et al. 2015c; Gerber et al. 2012a; Hernandez-Santin et al. 2016), and the introduction
100 of diseases and/or pathogens (Knobel et al. 2013; Rasambainarivo et al. 2017). As invasive
101 carnivore populations increase globally, their interactions with native carnivores must be assessed.
102 To better examine these interactions, we require a synthetic framework that incorporates both

103 spatial and temporal scales, and includes landscape and/or habitat variables that may mediate such
104 interspecific spatiotemporal interactions.

105 Considering patterns across only one niche axis between species', such as temporal use
106 independent of the spatial (or vice-versa), can potentially lead to erroneous conclusions of species
107 interactions. For example, one might conclude that a subordinate species has been temporally
108 displaced due to low temporal overlap, when in actuality the two species do not demonstrate any
109 spatial overlap because they use different local habitats. While there are numerous spatiotemporal
110 modelling approaches (see Cressie, Wikle 2015), few can accommodate typically sparse datasets
111 that are common in carnivore studies. Attempts to model and evaluate spatiotemporal interactions
112 between co-occurring carnivores and carnivore-prey pairings includes investigation via linear
113 models and frequentist statistics (Niedballa et al. 2019), analyses based on radio-tagged animals
114 and step selection functions (Vanak et al. 2013b), as well as analyses combining temporal activity
115 patterns and occupancy modelling (Karanth et al. 2017; Smith et al. 2019). While many of these
116 approaches were designed for non-invasive sampling of carnivore populations, few (if any)
117 provide a combined spatio-temporal interaction estimate that is also allowed to vary across
118 changing landscape and/or habitat variables. Including both spatial and temporal scales
119 simultaneously and investigating how these interactions vary across a landscape provides greater
120 insight into processes that drive competition between native species and between native and
121 invading exotics (Schliep et al. 2018). This is increasingly important as we consider anthropogenic
122 and invasive species effects on native carnivores' spatial habitat use and temporal activity patterns.
123 However, this approach could be applied to other data-poor taxa beyond carnivores.

124 We are specifically interested in understanding the patterns and drivers of spatiotemporal
125 occurrence and avoidance within a native-invasive carnivore community. We hypothesize that

126 native carnivores will demonstrate spatial segregation (avoidance) with invasive predators,
127 particularly when temporal overlap occurs and that spatiotemporal avoidance will be highest in
128 disturbed and/or anthropogenic landscapes.

129 **Methods**

130 *Study site*

131 From 2008 to 2013 we photographically surveyed, via remote cameras, the carnivore
132 community at seven study sites across the Masoala National Park (240,000 ha) and Makira Natural
133 Park (372,470 ha of protected area and 351,037 ha of community management zone) protected
134 area landscape of northern Madagascar. The seven sites varied in levels of degradation and
135 fragmentation, ranging from contiguous, primary rainforest to highly degraded forest patches
136 located approximately five km from the nearest contiguous forest. The Masoala-Makira landscape
137 supports six native species of carnivores, all members of family Eupleridae: fosa (*Cryptoprocta*
138 *ferox*), falanouc (*Eupleres goudotii*), spotted fanaloka (*Fossa fossana*), ring-tailed vontsira
139 (*Galidia elegans*), broad-striped vontsira (*Galidictis fasciata*), and brown-tailed vontsira (*Salanoia*
140 *concolor*) (Farris et al. 2015b). Additionally, three invasive carnivores have been documented
141 across the Masoala-Makira landscape: free-ranging dogs (*Canis familiaris*), cats (*Felis sp.*), and
142 small Indian civets (*Viverricula indica*) (Farris et al. 2015c). Not only is the behavioral ecology of
143 these species poorly known (Brooke et al. 2014; Goodman 2012), there is growing evidence from
144 previous work that invasive carnivores adversely affect native and endemic carnivores (Farris et
145 al. 2015a; Farris et al. 2017a; Farris et al. 2017b; Farris et al. 2015c; Gerber et al. 2012b;
146 Rasambainarivo et al. 2018; Rasambainarivo et al. 2017). For details on each native and local
147 carnivore body size, diet, IUCN classification, activity pattern, and habitat preference see Table 1

148 in Farris et al. (2015a). Local bushmeat hunting of all nine carnivore species exists across this
149 region and within the seven survey sites (Farris et al. 2015b; Golden 2009).

150 *Photographic sampling*

151 We established a camera grid at each of the seven sites, consisting of 20-25 camera stations
152 spaced at approximately 500 m between stations (based on the estimated home range of five of the
153 six native carnivore species, excluding the wide-ranging fosa). Each camera grid was operational
154 for an average of 63.4 days (± 2.4 SE) and we moved the 20-25 camera stations to a new grid. We
155 did not establish and survey at multiple camera grids simultaneously. Each camera station
156 consisted of two cameras placed on opposing sides of human (> 0.5 m in width) or animal (< 0.5
157 m in width) trails to capture both flanks of passing wildlife. We used both film (DeerCam DC300)
158 and digital (Reconyx PC85 & HC500, Wisconsin, USA, Moultrie D50 & D55, Alabama, USA,
159 Cuddeback IR, Wisconsin, USA) cameras that we set to high sensitivity, three photos per trigger
160 (when available, not all cameras had this option), 0 to 30 second time delay between triggers, and
161 placed 20-30 cm off the ground. We did not use bait or lure at any camera station and we checked
162 cameras every 5-10 days to change memory cards and ensure proper functioning. We
163 photographically sampled each site an average (\pm SD) of 67 ± 8 days (Farris 2014).

164 *Habitat sampling and landscape metrics*

165 We sampled habitat around each camera station at all seven sites across the landscape. At
166 each camera station we walked a 50 m transect in three directions (0, 120, and 240 degrees; Davis
167 et al. 2011) and sampled canopy height and percent cover at 10 m intervals along each transect
168 (totalling five samples per transect and 15 per camera station; Online Resource 1). We used the
169 point-quarter method (Pollard 1971) to estimate tree density and basal area at 25 m and 50 m
170 intervals along each transect. We estimated understory cover at 20 m and 40 m intervals along

171 each transect by establishing a 20 m transect running perpendicular to the 50 m transect. We
172 measured cover at three levels (0–0.50 m, 0.5–1.0 m, and 1.0–2.0 m) by holding a 2 m pole at 1 m
173 intervals along the transect and recording presence (1) or absence (0) of vegetation (Farris 2014).

174 We measured landscape features at each of the seven sites using Landsat satellite imagery
175 from 2004, 2006, and 2009 (WGS 84 datum, pixel size 29 m x 29 m) to classify land cover types
176 (rainforest, degraded forest, and matrix or non-forest) in Erdas Imagine (Intergraph Corporation,
177 Madison, AL, USA). For analysis in the program FragStats (McGarigal et al. 2012), we placed a
178 500 m buffer around individual camera stations (based on estimated home range of native
179 carnivores using ranging data and body size from camera traps) and clipped the classified imagery
180 for each of the resulting seven camera grid buffers (each providing an approximately 10–15 km²
181 area). We calculated the following landscape metrics from FragStats: 1) number of habitat patches:
182 total number of rainforest, degraded forest, and matrix patches (based on habitat classifications
183 from satellite imagery) within the buffer, where a patch is an area of habitat type separated from
184 similar habitat by ≥ 50 m, 2) largest patch index: the percentage of total buffered area comprised
185 by the largest rainforest patch, 3) landscape shape index (LSI) or the standardized measure of total
186 edge adjusted for the size of the buffered area (McGarigal et al. 2012), 4) percent rainforest within
187 the buffered area, 5) percent matrix or non-forest, cultivated area within the buffered area, 6) total
188 rainforest core area: the sum of the core areas (accounting for edge of depth of 500 m) of each
189 rainforest patch within the buffer, and 7) total edge (in m/ha) (McGarigal et al. 2012). Finally, we
190 calculated the distance of each camera station to the nearest forest edge (Dist. to Edge) and to the
191 nearest village (Dist to Village, Farris 2014). Previous research on Madagascar’s carnivores
192 (Gerber et al. 2010; Gerber 2011; Gerber et al. 2012b; Goodman 2012; Hawkins 1998; Hawkins,
193 Racey 2005) explored how landscape and habitat variables influence native carnivore spatial

194 distribution. However, we still lack an understanding of exactly which habitat and landscape
195 variables best explain space use for each individual carnivore species (both native and invasive),
196 including how anthropogenic changes to these landscapes affect native carnivore spatial
197 distribution. For spatiotemporal analyses, we included this wide range of variables to better
198 understand which factor(s) explains the space use of each individual carnivore and whether these
199 native-invasive interactions might be habitat- or behaviorally-mediated effects.

200 *Spatial co-occurrence analysis*

201 In a previous analysis (Farris et al. 2015c), we examined spatial co-occurrence between
202 native and invasive carnivores across the landscape with two-species, single-season occupancy
203 using the conditional probability parameterization (ψ_{iBa} parameterization, Richmond et al. 2010)
204 and included habitat and landscape covariates. We used the same data set described in the methods
205 here (sampled seven sites, each using 20-25 camera stations from 2008-2013). We used Akaike
206 Information Criterion [corrected for small sample sizes (AICc)] for model selection (Burnham,
207 Anderson 2002) and reported all top-ranking models ($\Delta AICc < 2.0$). This conditional modelling
208 approach accounts for imperfect detection (MacKenzie et al. 2004) and estimates the probability
209 of occurrence for the native (N) carnivore when the invasive (I) carnivore is present (ψ_{iNI}) and
210 when the invasive is absent (ψ_{iNi} , Farris et al. 2015c). This approach requires designation of a
211 dominant and subordinate species and in this study, we designated native carnivores to be the
212 subordinate to invasive species. While it is possible for a subordinate species to influence an
213 invasive species' spatial and temporal activity, thus influencing exploitative competition between
214 the two species, we used these designations as our goal was to explore the effects that invasive
215 species have on native species, given that all three invasive species are of larger body size than all
216 native species (excluding cat-fosa pairing, Farris et al. 2015a). We derived the species interaction

217 factor (SIF) to provide a measure of co-occurrence between target species. The SIF value is used
218 to determine if two species occur independently (SIF = 1.0), or have a higher (SIF > 1.0) or lower
219 (SIF < 1.0) probability of co-occurrence than random chance (MacKenzie 2006).

220 Using results from Farris et al. (2015c) we had 12 native-invasive carnivore pairings with
221 sufficient captures to provide spatial co-occurrence estimates (Table 1). In this previous research,
222 one carnivore pairing demonstrated spatial aggregation (SIF > 1.0) and six demonstrated spatial
223 segregation (SIF < 1.0) relationships. The remaining five pairings demonstrated no spatial
224 relationship (SIF = 1.0; spatial distribution is independent of the other species). The six spatial
225 segregation relationships (SIF < 1.0) indicated that six native carnivores have lower probability of
226 occupancy when an invasive carnivore is present (ψ_{iNI}) compared to when the invasive is absent
227 (ψ_{iNi}). Small Indian civets had the highest number of spatial interactions for invasive carnivores.
228 The number of habitat patches (#Patches, $n = 5$) and distance to the nearest village (Village, $n =$
229 3) were the most common variables to explain relationships of co-occurrence (Online Resource
230 2).

231 *Temporal analysis*

232 In a previous analysis of each carnivore (Farris et al. 2015a), we modelled captures (capture
233 events/available hours), where a capture event is all photos of distinct individuals of a given species
234 within a 30 min period (to ensure independence in photo captures) using a nonparametric kernel
235 density analysis to estimate the probability density of temporal activity distribution for each
236 species (Ridout, Linkie 2009). We conducted model selection, making inference from the most
237 simple, parsimonious model. Finally, for each native- invasive carnivore pairing, we estimated the
238 coefficient of overlap of the probability densities throughout the entire diel period using an
239 estimator supported for small sample size [denoted Δ_1] (Ridout, Linkie 2009). This coefficient is

240 bounded by 0 and 1 such that $\Delta_1 = 0$ indicates no overlap and $\Delta_1 = 1.0$ indicates complete overlap
241 in daily activity pattern. High temporal overlap does not mean the carnivores occur together during
242 the same 24 h period, but indicates they overlap in their use of diel cycle periods (i.e., dawn, dusk,
243 day, night).

244 Using results from Farris et al. (2015a), we estimated temporal overlap for 16 of the 18
245 potential native- invasive carnivore pairings (Table 1). In this previous research, the estimates of
246 temporal overlap ranged from a low of 0.23 (nocturnal small Indian civet and diurnal ring-tailed
247 vontsira) to a high of 0.88 (diurnal dog and diurnal brown-tailed vontsira). The coefficient of
248 overlap (proportional overlap, 0 – 1.0) across the entire diel cycle from this previously published
249 kernel density analysis (Farris et al. 2015a) revealed a high degree of overlap (e.g. temporal
250 aggregation) among temporal activity patterns for native and invasive carnivore pairings (average
251 $\Delta_1 = 0.59 \pm \text{SD } 0.23$, Table 1).

252 *Relative species interaction*

253 Here, we focus on providing a theoretical framework to investigate carnivore interactions
254 from passive spatial sampling (e.g., camera-traps) and we derive a measure of spatiotemporal
255 overlap that incorporates landscape and/or micro-habitat variables. We do so by combining results
256 of the two-species, spatial co-occurrence model (Farris et al. 2015c) and the temporal, non-
257 parametric circular kernel density estimator (Farris et al. 2015a). We combine these two
258 approaches because 1) the co-occurrence models can account for a major source of bias: that sites
259 may be used by one or both species, yet species can go undetected (MacKenzie 2006) and 2) the
260 circular density estimator is a flexible approach to estimate highly variable diel activity patterns
261 that are common for many species (Gerber et al. 2012a).

262 This approach, combining the two-species interaction factor (SIF, spatial) and the kernel
263 density analysis (Δ_1 , temporal), allowed us to calculate a spatiotemporal value (STV), or measure
264 of spatiotemporal overlap, for each native- invasive carnivore pairing across important landscape
265 features. Specifically, we calculated the STV by multiplying the SIF value, which varied across
266 the landscape or habitat covariate included in each co-occurrence model, by the normalized
267 interaction of the two species' temporal activity density, Δ_1 , within 30 minute periods across the
268 diel cycle from our kernel density analysis (i.e., $STV = SIF * \Delta_1$). The STV value provides a
269 measure of overlap for each carnivore pairing such that a value of 0 indicates no overlap and as
270 the STV value increases this indicates increasing spatial *and* temporal overlap, and thus increasing
271 potential for direct interaction. Because the temporal activity analyses do not distinguish between
272 sites where both species occurred or otherwise, we estimate a population-level (across all sites)
273 temporal profile. This was a necessity for sparse data reasons that are typical of carnivore data.

274 *Conceptual framework for interpreting spatiotemporal overlap*

275 There are four potential states when considering spatiotemporal overlap between species
276 (Figure. 1). High spatial or temporal overlap by itself does not indicate costly species interactions,
277 nor does low spatial or temporal overlap by itself indicate the displacement of the subordinate
278 species. Inferring the consequences of low or high overlap depends on understanding the
279 mechanisms that led to the observed pattern (Figure 2), which necessitates knowledge of each
280 species' ecology. Or alternatively, a study design that allows inference to compare the spatial and
281 temporal activity of the subordinate species in areas with and without the potential competitor. The
282 ecological mechanisms and likely costs that could cause low spatial and/or temporal overlap
283 between species are: i) a separation in niche, which could be an evolutionary outcome of reduced
284 competition between native species (no fitness costs), ii) a separation in niche, due to the

285 subordinate species switching their preferred habitat, resource(s), or temporal activity (likely
286 inducing fitness consequences due to using fewer or lower quality resources or marginal habitat
287 that could increase mortality risks or reduce reproductive success), iii) no interactions because two
288 species do not occupy the same space (no fitness costs), iv) no interactions because the species do
289 not overlap along any niche axes despite sharing the same space (no fitness costs), or v) species
290 overlap in space and have high indirect interactions through interference or exploitative
291 competition of shared resources that are temporally available to both species (likely inducing
292 fitness costs due to competition). To identify the likely process that led to the observed pattern of
293 low temporal overlap, and thus the consequence and importance of low overlap, several additional
294 pieces of evidence are needed: i) degree of spatial overlap, ii) potential for direct or indirect
295 competition, and iii) whether the subordinate species is altering its temporal activity pattern due to
296 the potential for direct or indirect interactions with the dominant species.

297 We outline the possible types of interactions (i.e., direct, indirect, no interaction) for each
298 combination of spatial and temporal overlap in Figure 3. Direct interactions between carnivore
299 species include aggression/harassment, intraguild predation, kleptoparasitism, and disease
300 transmission. High spatial overlap (i.e., SIF) indicates that two carnivores are using the same space
301 more than expected at random, while high temporal overlap indicates the chance of interacting at
302 the same place and time is high, it does not necessarily mean the two carnivores are active during
303 the same 24 hr period. Rather, it indicates the two overlap in their use of the diel cycle. As a result,
304 if there is high overlap in both space and time, any combination of direct, indirect, and no
305 interactions may occur. Otherwise, when there is either low spatial or temporal overlap (but not
306 both), it is more likely that indirect or no interactions occur, and when there is both low spatial and
307 temporal overlap, no interactions are most likely (Figure 3). Interpreting the lack of interaction is

308 perhaps the most challenging. To do so requires one to consider the fundamental and realized niche
309 of both species. The lack of interaction may result from two species simply coexisting in
310 fundamentally separate niche spaces, or that one species may have altered its spatiotemporal
311 activity in response to the dominant species (Figure 2).

312

313 **Results**

314 Over this six year period, we conducted 13 photographic surveys across seven sites
315 surveying for a total of 824 days, providing 15,253 trap nights (defined as a 24 hr period that an
316 individual camera station surveyed with no malfunctions occurring). We collected approximately
317 120,000 photographic captures. Of these photographic captures, 2,991 were of a carnivore species
318 with 1,639 captures of the six native carnivores and 1,352 captures of the three invasive carnivores.

319 *Spatiotemporal interactions*

320 Using estimates from our spatial co-occurrence modelling and temporal overlap, we were
321 able to estimate spatiotemporal values for eight native-invasive carnivore pairings. Small Indian
322 civets had the highest number of spatiotemporal overlap relationships ($n = 4$), followed by dogs (n
323 $= 3$), and cats ($n = 1$, Figure 4). The highest likelihood of spatiotemporal overlap occurred between
324 small Indian civets and broad-striped vontsiras (STV = 23.20, Figure 4 h) occurring between the
325 hours of 23:00-24:00 in habitat primarily made up of patchy, non-forest matrix. Dogs had a high
326 likelihood of spatiotemporal overlap with fosa and falanouc between the hours of 06:00 – 08:00,
327 particularly in patchy degraded habitat (Figure 4 a-b). Feral cats had a high likelihood of
328 spatiotemporal overlap with falanouc, which increased moving away from villages, during the
329 hours of 05:00 – 07:00 (Figure 4 d). The small Indian civet had a high likelihood of spatiotemporal
330 overlap with three native, nocturnal carnivores (falanouc, fanaloka, and broad-striped vontsira)

331 occurring between the hours of 20:00 – 06:00 (Figure 4 e-h). Two native-invasive carnivore
332 pairings showed highly variable spatiotemporal overlap across the diel cycle: the diurnal dog and
333 nocturnal broad-striped vongsira (Figure 4 c), and the nocturnal small Indian civet and diurnal ring-
334 tailed vongsira (Figure 4 g). Six of the eight spatiotemporal relationships revealed increasing
335 overlap as anthropogenic disturbance (measured in distance to village, percent rainforest/matrix,
336 and patchiness) increased (Figure 4).

337 Our conceptual framework (Figure 1) provided four potential scenarios: 1) spatial and
338 temporal segregation (Figure 1, Top-left), 2) spatial segregation and temporal aggregation (Figure
339 1, Top-right), 3) spatial aggregation and temporal segregation (Figure 1, Bottom-left), and 4)
340 spatial aggregation and temporal aggregation (Figure 1, Bottom-right). Three of the native-
341 invasive carnivore pairings (dog-falanouc, dog-broad-striped vongsira, and Indian civet-ring-tailed
342 vongsira) fall under scenario one above, by demonstrating low spatial overlap/segregation (spatial
343 segregation, $SIF < 1.0$) and low temporal overlap (temporal segregation). Three of the native-
344 invasive carnivore pairings (Indian civet with fanaloka, with falanouc, and with broad-stripe
345 vongsira) fall under scenario two above by demonstrating low spatial overlap (spatial segregation),
346 but high temporal overlap (temporal aggregation, Figure 1 Top-right). We did not observe any
347 scenario three examples (spatial aggregation, temporal segregation, Figure 1, Bottom-left).
348 Finally, the cat and falanouc was the only native-invasive carnivore pairing to fall under scenario
349 four (spatial aggregation, temporal aggregation, Figure 1, Bottom-left) given the high spatial and
350 temporal overlap.

351 **Discussion**

352 We demonstrate the effectiveness of a spatiotemporal model that combines methods in co-
353 occurrence modelling (spatial) and kernel density analysis (temporal) to explore interactions

354 between native and invasive carnivores. We demonstrate how anthropogenic disturbance
355 influences these spatiotemporal interactions between native and invasive carnivores by showing
356 that species interaction factors (SIF) and spatiotemporal values (STV) are not static, but change
357 across a variable landscape. We found evidence of spatiotemporal interspecific interactions
358 between multiple native and invasive carnivore pairings, we provide interpretation of each
359 carnivore pairing, and we highlight the effectiveness of this modelling approach for informing
360 managers of wild carnivore community ecology or other elusive or data-poor species.

361 For scenario one relationships (low spatial overlap/segregation), we observed three native-
362 invasive pairings (dog-falanouc, dog-broad-striped vontsira, and Indian civet-ring-tailed vontsira).
363 Free-ranging dogs in Madagascar are widespread and their diets diverse (Farris et al. 2015b;
364 Goodman 2012); however, their diet has not been shown to overlap with the falanouc, which feeds
365 primarily on earthworms and invertebrates (Goodman 2012). However, we did demonstrate a
366 strong potential increase in interaction in this pairing as habitat becomes more patchy and
367 degraded. As forest degradation and fragmentation increases throughout Madagascar, the potential
368 interactions between dogs and falanoucs, particularly during crepuscular periods, should be
369 monitored. The diurnal activity of dogs and their extensive use of degraded, forest edge (Farris et
370 al. 2017a), contrasts with the nocturnal activity and preference for contiguous forest of the broad-
371 striped vontsira (Farris et al. 2015b; Goodman 2012), which likely contributes to the high
372 variability in Figure 4 c and adds further support to our interpretation of little to no interaction.
373 Small Indian civets diverge greatly with ring-tail vontsira in temporal activity (Farris et al. 2015a;
374 Gerber et al. 2012a) and Indian civets are found almost exclusively in edge, open, and matrix
375 habitat (Gerber et al. 2012b; Goodman 2012), adding support to our interpretation of little to no
376 interaction between small Indian civet and ring-tailed vontsira.

377 For scenario two relationships (low spatial overlap, high temporal overlap), we observed
378 three native-invasive carnivore pairings (Indian civet with fanaloka, with falanouc, and with broad-
379 stripe vontsira). The small Indian civet is known to consume a wide-range of resources, including
380 prey items with wide spatial distributions that are used by all three of these native carnivores (i.e.
381 rodents, small vertebrates, and invertebrates, Goodman 2012). We suggest the potential for indirect
382 interactions with Indian civets is highest for the fanaloka and the broad-stripe vontsira as the
383 overlap in shared resources is greatest, given the apparent specialization in diet by the falanouc.
384 Our STVs demonstrate that these potential interspecific interactions with Indian civets are likely
385 to increase for fanaloka (Figure 4 e) and broad-striped vontsira (Figure 4 h) as degradation and
386 fragmentation increase.

387 We observed no scenario three relationships (high spatial overlap, low temporal overlap).
388 Spatial aggregation between invasive and native carnivores was rare, as would be expected for
389 most habitats where non-native predators invade. This scenario of spatial aggregation presents a
390 serious risk to native species as it would threaten any potential shared resources (e.g. indirect
391 interaction) and possibly result in disease transmission to native carnivores (e.g. potential for direct
392 interaction; Rasambainarivo et al. 2018; Rasambainarivo et al. 2017).

393 For scenario four (high spatial and temporal overlap), we observed only one native-
394 invasive relationship (cat and falanouc). The type of interaction between cats and falanoucs is
395 likely to vary depending on habitat. Occupancy estimates (Farris et al. 2015b) revealed that the
396 falanouc had similar occupancy across the entire landscape (from non-degraded to degraded), but
397 cats show considerably higher occupancy in degraded forest. In degraded forest, these two
398 carnivores had very high spatial overlap ($SIF = 2.0$) and that was explained by distance to village
399 ($\psi_{iNI} \neq \psi_{iNi}[\text{Village}]$, Farris et al. 2015c). This reveals that within non-degraded forests, where

400 cats are more rare, direct and indirect interactions are unlikely to occur. However, as degradation
401 increases these two carnivores are highly likely to come into direct contact (Figure 4 d). We
402 suggest this presents a serious threat to falanoucs potentially in the form of aggression, harassment,
403 and disease transmission from cats, which are of similar body size (Goodman 2012).

404 Five carnivore pairings resulted in no spatial relationship (SIF = 1.0) and, as a result, failed
405 to fit into the four interaction scenarios above. We interpret these relationships as two carnivores
406 occurring together within a study area but with no spatial interaction (Figure 1). However, we
407 highlight the relationship occurring between dogs and brown-tailed vontsirras, and cats and fosas,
408 as both reveal no spatial overlap, but high temporal overlap. Despite the finding of no spatial
409 overlap, we suggest there is strong potential for these invasive species to negatively affect these
410 natives as the result of the rapid changes in rainforest habitat, the plasticity in habitat selection and
411 resource use for these two invasive species, and the expansive ranges of dogs, cats, and fosas.

412 The ultimate goal of spatial, temporal, and/or spatiotemporal analyses is to accurately
413 interpret behavior, spatial distribution, and/or activity patterns of co-occurring species with the
414 aim of deciphering between habitat and behaviorally mediated effects. While this is a fundamental
415 goal for behavioral and community ecologists alike, interpretation remains challenging despite the
416 development of a diverse set of novel sampling and modelling approaches in recent years. Our 3-
417 dimensional figures visually demonstrate the challenge in interpretation. For example, Figure 2
418 demonstrates how a species may alter or change spatial or temporal (or both) states depending on
419 the presence and amount of overlap with a dominant species. However, to understand if this
420 alteration in spatial/temporal state results from the presence of the dominant requires a study
421 design in which the target species is studied in both the presence and absence of the dominant.
422 Figure 3, however, demonstrates that each possible spatiotemporal overlap scenario could include

423 a no interaction scenario between the co-occurring species. To interpret these scenarios and infer
424 interaction, we require detailed natural history, movement (home range), and behavioral
425 information on both co-occurring species. Given that we have not studied these native carnivores
426 in both the presence and absence of invasive carnivores, and the fact that much natural history and
427 behavioral information is lacking for each of the native carnivores, we are currently unable to
428 differentiate between behavioral and habitat mediated effects.

429 Detailed information on resource and habitat use for both native and invasive species
430 would improve our ability to make more accurate predictions of species interactions. Karanth et
431 al. (2017) used similar sampling and modelling approaches to explore carnivore spatiotemporal
432 interactions and compared these interspecific interactions across sites with varying resource
433 availability. This approach allowed researchers to demonstrate carnivore plasticity in spatial and
434 temporal activity as resource and co-occurring carnivore density varied across the landscape,
435 highlighting mechanisms contributing to carnivore sympatry. Carnivores in our study may
436 demonstrate similar variability in spatial and temporal activity across the landscape. However, the
437 Karanth et al. (2017) study investigated three native, sympatric carnivore species. The same
438 variation in spatial and temporal patterns that permitted sympatry in that carnivore community,
439 may not alleviate negative interactions for Madagascar's native-invasive community as invasive
440 predators present a novel threat and native carnivores may not yet have developed behavioral
441 adaptations to avoid conflict with invasive species. Vanak et al. (2013b) conducted a similar
442 investigation of intraguild interactions and found similar plasticity in carnivore spatial and
443 temporal activity in response to variation in season, resource availability, and potential threats.
444 Their investigation was conducted in a closed system (85 km² fenced conservation area), allowing
445 researchers to examine fine-scale, avoidance behaviors with variations in resource availability.

446 Using our spatiotemporal model in this type of closed system where resource availability is well
447 known, would provide more detailed insight and allow researchers to identify which type of
448 interspecific interaction is occurring. Few systems, however, allow for the type of investigation
449 carried out by Karanth et al. (2017) and Vanak et al. (2013b). Our survey and modelling
450 approaches can provide researchers a useful approach to investigate and interpret potential
451 interspecific interactions or possible outcomes for co-occurring species in open systems where
452 important data on resource availability may not be available.

453 Our modelling approach is useful for identifying precise locations in space and time where
454 species are likely to co-occur. For example, we demonstrate that dogs and fosas are most likely to
455 co-occur between the hours of 05:00 and 09:00 with potential interactions increasing as the habitat
456 becomes more patchy. Similarly, in multi-year carnivore surveys across Ranomafana National
457 Park (RNP), Madagascar (Farris et al. 2017a) we found dogs and fosas had high probabilities of
458 spatial co-occurrence ($SIF > 1.0$), resulting in strong potential for indirect and direct interactions.
459 These results could provide valuable insight for managers working across RNP to address this
460 burgeoning conservation issue. For example, these findings could be used to develop targeted
461 education programs that inform people living near forest habitat or traveling with their dogs to
462 forested areas of the negative impacts their dogs may have on fosas and co-occurring wildlife.
463 Policies that instruct, or encourage, people to leave their dogs at home when traveling into the
464 forest during this time period, or change the time of day they take dogs to the forest, could greatly
465 decrease the probability of direct and indirect interactions between these two carnivores and result
466 in increased spatial habitat and resource use of fosa across these forested areas. Additionally, the
467 results of this study highlight potential interactions between multiple native carnivores and free-
468 ranging cats and dogs. These findings on where interactions are likely to occur on the landscape

469 are being used to inform veterinarian clinics and disease ecology research currently on going
470 throughout Madagascar's eastern rainforest region. These potential interspecific interactions
471 between native and invasive carnivores also are being used to inform managers and researchers on
472 where to establish vet clinics and where disease transmission may be occurring. Additional studies
473 of native and invasive carnivores across Madagascar's rainforest ecosystem are needed to better
474 understand these interspecific interactions. In particular, we need information on resource use by
475 Madagascar's native carnivores to determine if they have the same plasticity in resource use and
476 activity, as has been observed in other studies (Karanth et al. 2017; Kronfeld-Schor, Dayan 2003;
477 Vanak et al. 2013b). Investigations of fine scale behaviors will allow us to understand the severity
478 of threat posed to native carnivores by invading invasive carnivores.

479 The theoretical and statistical modelling approach discussed herein provides a synthetic
480 framework to explore the potential for interspecific interactions between invading, non-native
481 carnivores and rare, elusive native carnivores. Also, this approach allows researchers to collect
482 data non-invasively while exploring potential interactions across multiple dimensions, which is
483 ideal for investigations of wild carnivores. We encourage future carnivore spatiotemporal activity
484 studies to frame questions in terms of theoretical considerations (i.e., Table 1) and appropriate
485 study designs to identify potential behavioral mechanisms driving carnivore species interactions.

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637 **Figure Legends**

638 **Fig. 1** Conceptual framework for types of potential spatial and temporal overlap between a
 639 dominant (e.g., *C. familiaris*) and subdominant carnivore (e.g., *C. ferox*). Top left, species
 640 significantly differ in space use and temporal activity; top right species share temporal patterns
 641 but do not significantly overlap in space use; bottom left, species overlap in space use but differ
 642 significantly in temporal activity; bottom right, species significantly overlap in space use and
 643 temporal activity.

644 **Fig. 2** Conceptual framework for potential spatiotemporal shifts by a subdominant species (e.g.,
 645 *C. ferox*) in response to an invading dominant species (e.g., *C. familiaris*) with varying levels of
 646 spatiotemporal overlap. The subdominant can respond by, 1) staying in the current state (no
 647 response), 2) transitioning states and thus shifting their spatial and/or temporal activity (altering
 648 interaction strength), or 3) transitioning states independent of the dominant species' invasion.
 649 Arrows represent directional shifts with associated potential change in interaction consequence at
 650 the new state (e.g., Green → Orange = moving from a neutral state to intermediate negative
 651 state). The subdominant species should stay at the current state if the consequences of the
 652 interaction (Figure 3) are neutral or less negative than moving to an alternative state (e.g., *C.*
 653 *ferox* would not transition from a green state if all alternative states lead to orange or red).
 654 Conversely the subdominant should transition if the current state had a higher negative
 655 interaction potential than an alternative state. For example, if *C. ferox* initially had low temporal
 656 and spatial overlap with *C. familiaris* (upper left), however, due to reduction in habitat
 657 availability was forced to respond by increasing spatial overlap with *C. familiaris* (lower left),
 658 where in the new state *C. ferox* may experience fitness costs via indirect interactions with *C.*
 659 *familiaris*, or none if fundamental niches are divergent (Figure 3)

660 **Fig. 3** Conceptual framework for potential interactions given four possible interspecific
661 spatiotemporal patterns of a subdominant (e.g., *C. ferox*) and dominant carnivore (*C. familiaris*).
662 Each state has 1-3 possible interaction categories (no interaction, indirect interaction or direct
663 interaction) that give rise to probable interaction outcomes between species with either no
664 (green), possible (blue), or direct (orange) fitness cost for the subdominant

665 **Fig. 4** Likelihood of spatiotemporal interactions for native and invasive carnivore pairings
666 occupying the Masoala-Makira landscape, NE Madagascar. Each pairing reveals the estimated
667 spatiotemporal value (STV, Y-axis), which varies based on time of day (X-axis) and landscape
668 or habitat variable (Z-axis). Increases in height and color gradient reveal higher likelihoods of
669 potential interspecific interaction for each carnivore pairing. Carnivore pairings include, a) dog
670 *Canis familiaris* and fosa *Cryptoprocta ferox*, b) dog and falanouc *Eupleres goudotii*, c) dog and
671 broad-striped vontsira *Galidictis fasciata*, d) cat *Felis species* and falanouc, e) small Indian civet
672 *Viverricula indica* and spotted fanaloka *Fossa fossana*, f) small Indian civet and falanouc, g)
673 small Indian civet and ring-tailed vontsira *Galidia elegans*, h) small Indian civet and broad-
674 striped vontsira.

675

676 Table 1. Summarized estimates (SE) from Farris et al. (2015c) for spatial co-occurrence among
677 native- invasive species pairings, including occupancy of native (N) when invasive (I) is present
678 (ψ_{NI}) and when absent (ψ_{Ni}), species interaction factor (SIF), coefficient of temporal overlap
679 (Δ^1) estimates from Farris et al. (2015a), and average spatiotemporal value (STV). SIF estimates
680 in bold indicate value with error do not overlap zero.

681 Farris ZJ, Kelly MJ, Karpanty SM, Ratelolahy F (2015c) Patterns of spatial co-occurrence
682 among native and invasive carnivores in NE Madagascar. *Animal Conservation* 19:189-198.

683 Farris ZJ, Gerber B, Karpanty SM, Murphy A, Ratelolahy F, Kelly MJ (2015a) When carnivores
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685 *Journal of Zoology (London)* 296:45-57.

686

Species	psiNE (SE)	psi Ne (SE)	SIF	Δ^1	Avg. STV
<i>C.familiaris</i> & <i>C.ferox</i>	0.51 (0.06)	0.51 (0.06)	0.95 (0.09)	0.44	1.84
<i>C.familiaris</i> & <i>F.fossana</i>	0.43 (0.05)	0.43 (0.05)	1	-	-
<i>C.familiaris</i> & <i>E.goudotii</i>	0.23 (0.05)	0.69 (0.11)	0.51 (0.11)	0.39	0.99
<i>C.familiaris</i> & <i>G.elegans</i>	-	-	-	0.87	-
<i>C.familiaris</i> & <i>G.fasciata</i>	0.24 (0.06)	0.90 (0.15)	0.59 (0.09)	0.23	0.93
<i>C.familiaris</i> & <i>S.concolor</i>	0.31 (0.05)	0.31 (0.05)	0.91 (0.002)	0.88	-
<i>F.species</i> & <i>C.ferox</i>	0.85 (0.03)	0.85 (0.03)	0.98 (0.05)	0.65	-
<i>F.species</i> & <i>F.fossana</i>	-	-	-	-	-
<i>F.species</i> & <i>E.goudotii</i>	0.43 (0.03)	0.07 (0.03)	1.90 (0.21)	0.63	4.21
<i>F.species</i> & <i>G.elegans</i>	-	-	-	0.56	-
<i>F.species</i> & <i>G.fasciata</i>	-	-	-	0.42	-
<i>F.species</i> & <i>S.concolor</i>	0.13 (0.04)	0.13 (0.04)	1	0.61	-
<i>V.indica</i> & <i>C.ferox</i>	-	-	-	0.82	-
<i>V.indica</i> & <i>F.fossana</i>	0.33 (0.11)	0.72 (0.31)	0.50 (0.26)	0.80	0.57
<i>V.indica</i> & <i>E.goudotii</i>	0.11 (0.05)	0.64 (0.19)	0.22 (0.06)	0.74	0.97
<i>V.indica</i> & <i>G.elegans</i>	0.14 (0.06)	0.86 (0.27)	0.26 (0.01)	0.23	1.22
<i>V.indica</i> & <i>G.fasciata</i>	0.11 (0.08)	0.89 (0.22)	0.21 (0.01)	0.83	4.45
<i>V.indica</i> & <i>S.concolor</i>	-	-	-	0.29	-

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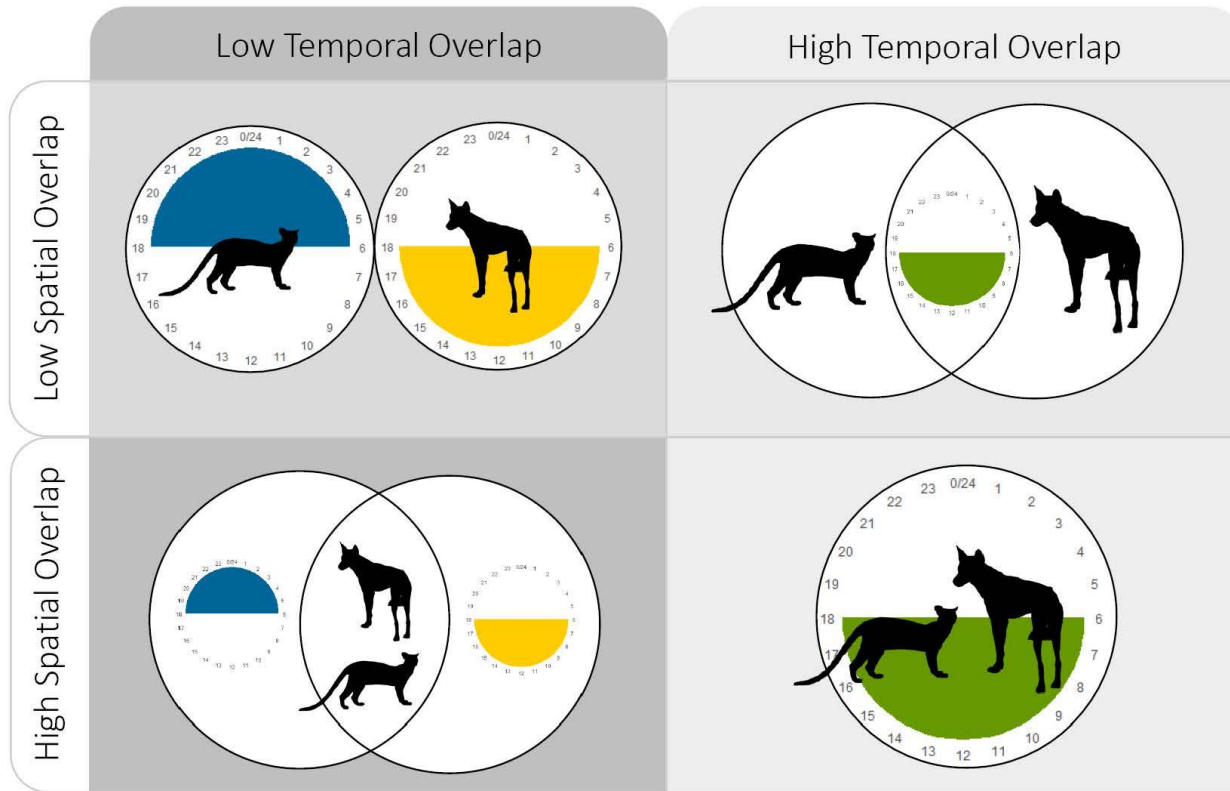


Figure 1.

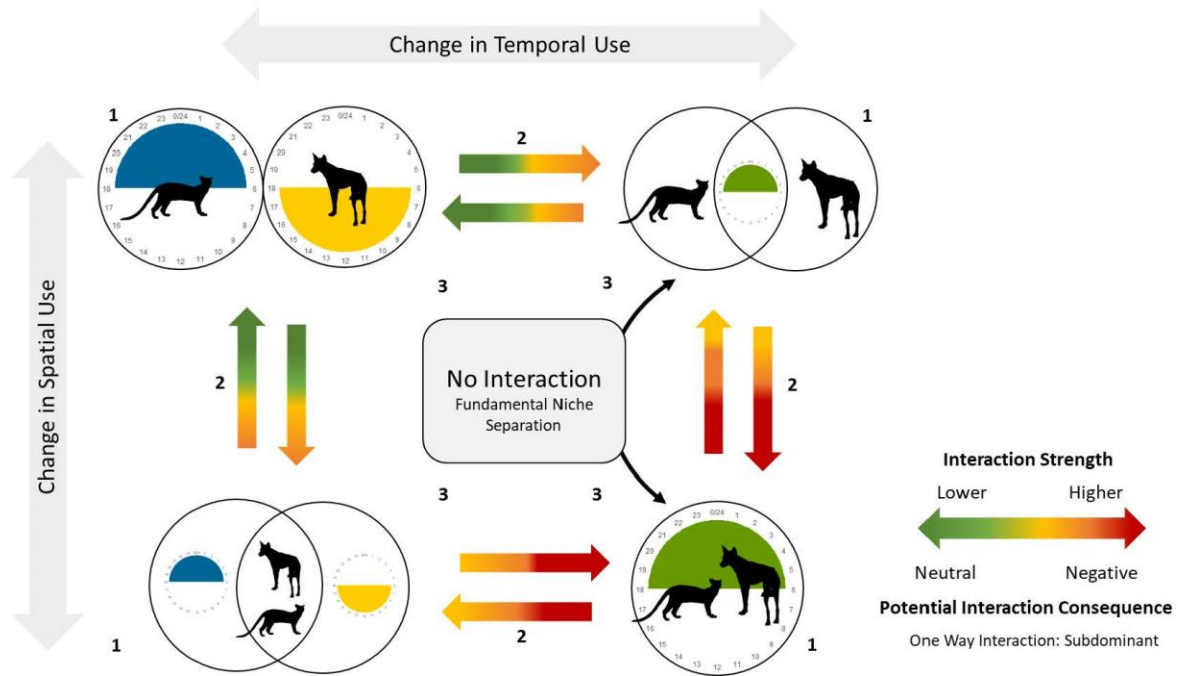


Figure 2.

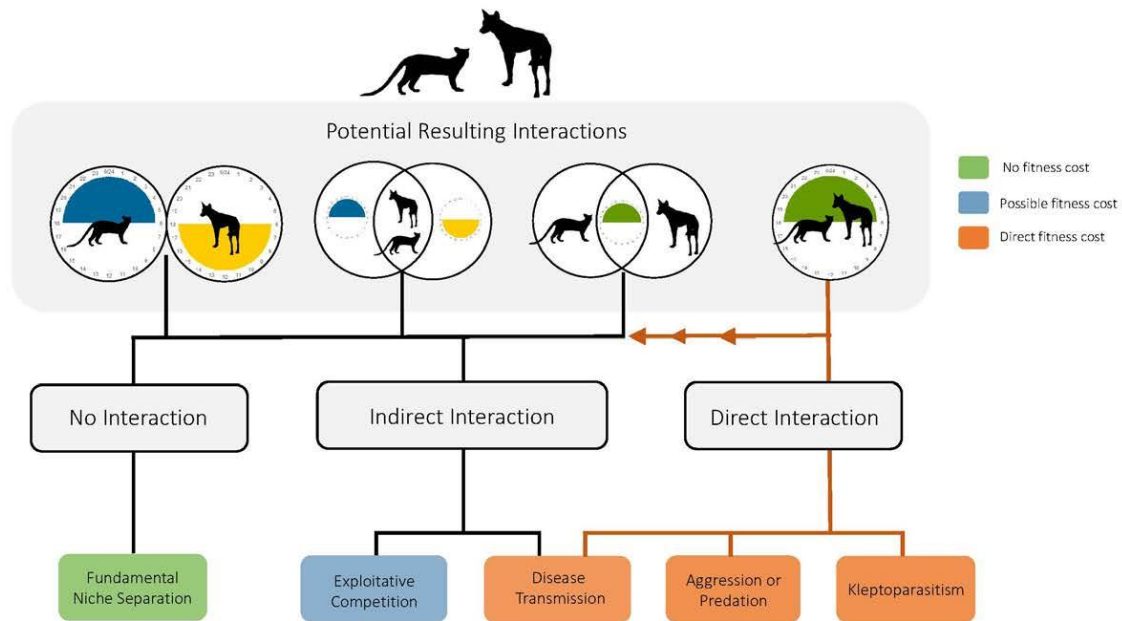
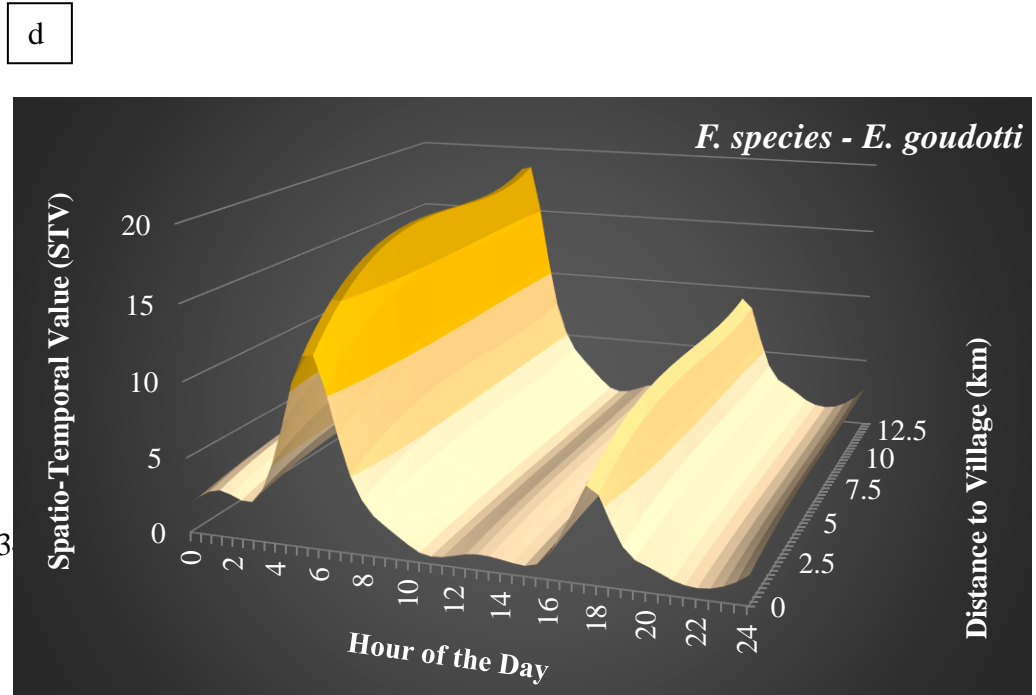
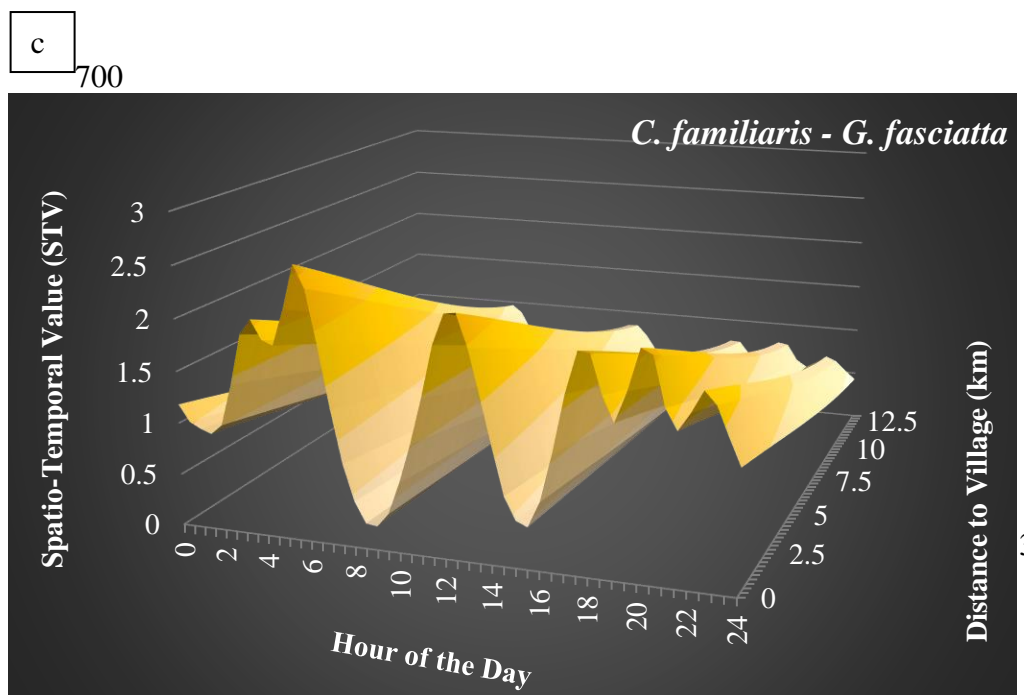
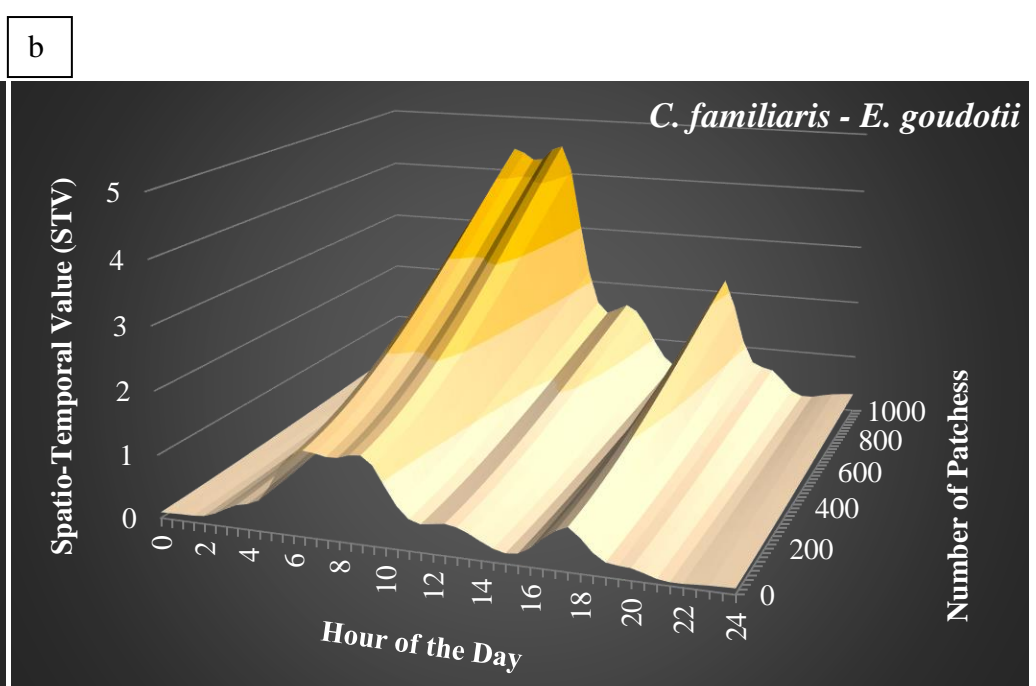
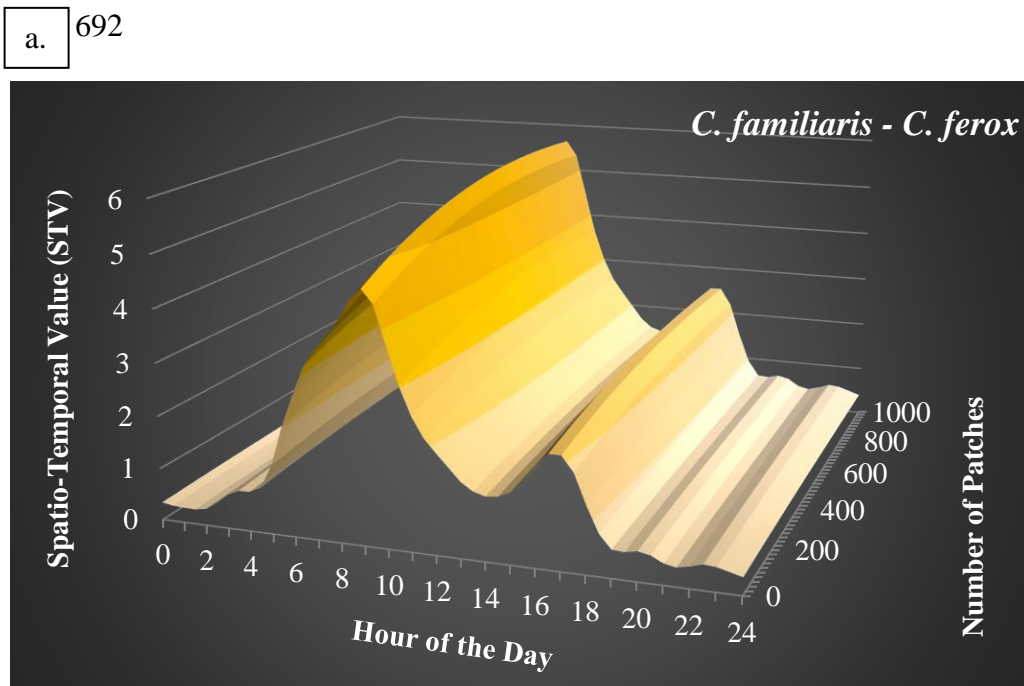
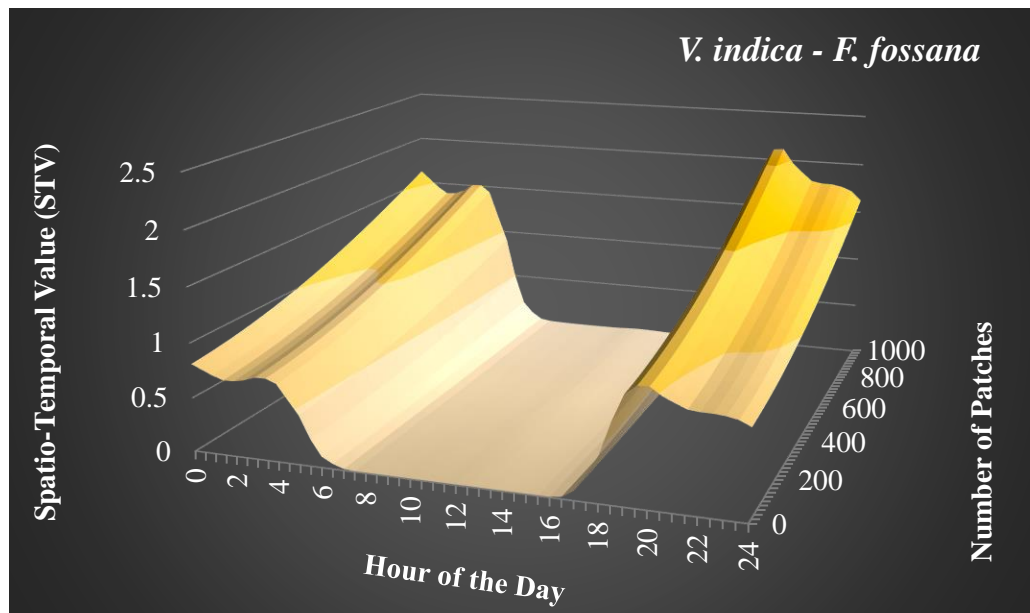


Figure 3.

691 Figure 4.

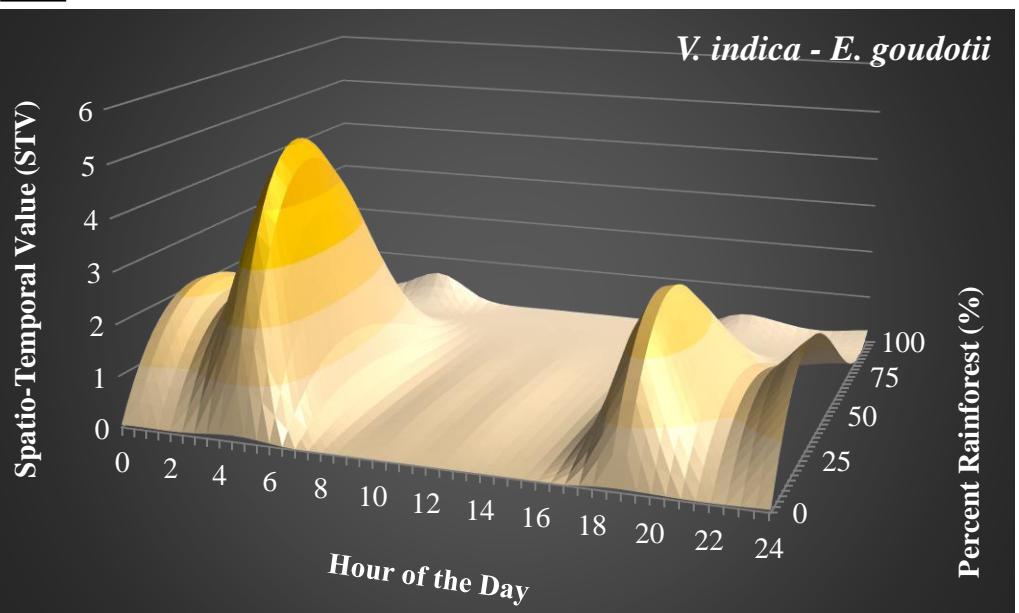


e

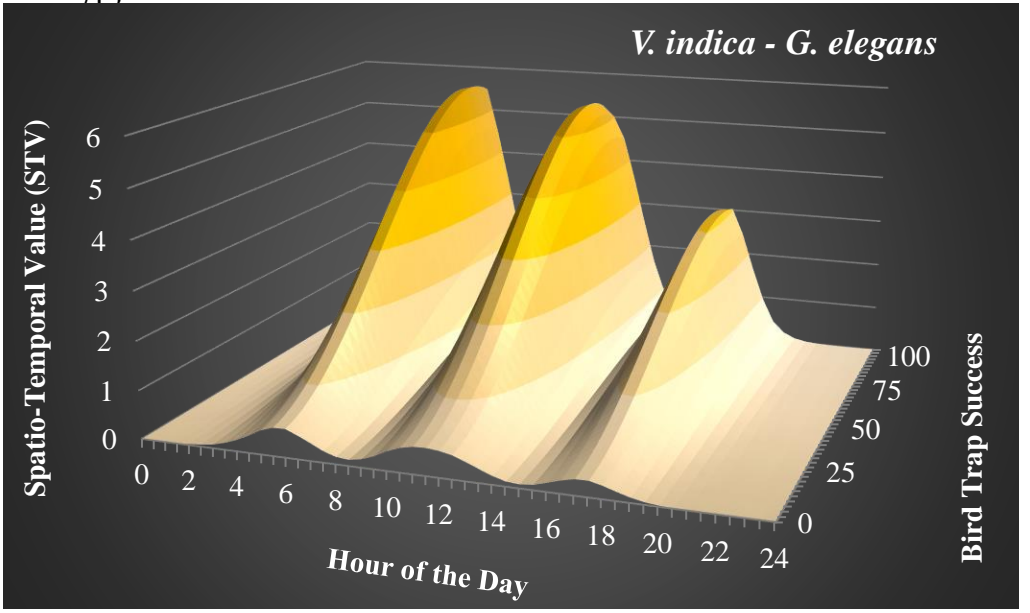


Spatiotemporal interactions

f



g



h

