Temporal and trophic partitioning promote coexistence between mesocarnivores in a Mediterranean landscape

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Abstract

The partition of the ecological niche can enhance the coexistence of predators due to differences in how they exploit three main resources: food, space, and time, the latter being an axis that remains often unexplored. We studied niche segregation in a Mediterranean mesocarnivore community in sites where the top predator, the Iberian lynx, is absent, addressing simultaneously two niche axes: the temporal and the trophic axes. Temporal overlap between prey and predator and potential competitors was analysed by comparing daily activity patterns of predators and prey species through data obtained by using 24 camera-traps deployed in three different sites of the Doñana National Park. We further examined the trophic dimension by compiling and analysing diet information in the study area and exploring trophic preferences between potential competitors. We found an overall temporal segregation between trophic generalist species while those species which showed higher values of temporal overlap differ largely in their trophic preferences. Furthermore, we observed an overall high degree of overlap between the activity patterns of predators and their putative prey (the common genet vs small mammals and the red fox vs European rabbit). Our study suggests that coexistence of the different species that compose the mesocarnivore assemblage in Mediterranean landscapes can be facilitated by the marked temporal segregation of the generalist species due to a divergence in the activity patterns, but also by differences in trophic preferences by specialist species when their activity patterns overlap.

Keywords

Diel activity, niche differentiation, interspecific competition, *Meles meles*, *Vulpes vulpes*, *Genetta genetta*, *Herpestes ichneumon,* Doñana, predator-prey

Introduction

Understanding the mechanisms that promote coexistence of species with similar ecological requirements is a central topic in community ecology, where competitive interactions between species have the potential to affect diversity patterns by limiting or promoting coexistence (Chesson 2000). In order to mitigate the negative impact of interspecific competition, species often partition resources along three main niche dimensions (temporal, trophic and spatial), which eventually results in niche differentiation (Schoener 1974). Most studies concerning species coexistence focused on the differential use of habitat and food resources; nonetheless, the differential use of the diel cycle may enhance coexistence of same-sized species, particularly among predator species (Di Bitetti et al. 2009, Wang and Fisher 2012).

Diel activity patterns are cyclical behavioural patterns which can be influenced by several factors (i.e., prey availability or thermoregulatory strategies) (Lode 1995, Maloney et al. 2005). Within mammals, a large variability and plasticity in their activity patterns has been documented (Bennie et al. 2014). This diversity of diel cycles could be due to the plastic nature of behavioural responses to different pressures which could induce marked variations in daily rhythms among different scenarios (Ensing et al. 2014, Gaynor et al. 2018). Broadly, activity patterns displayed by mammals are determined by circadian endogenous boundaries (Kronfeld-Schor and Dayan 2003) which are particularly shaped in carnivores by external factors (Zielinski 1986, Monterroso et al. 2014) setting a context-dependency in their diel cycle use. Hence, the co-occurrence of species that compete for a certain resource has the potential to produce shifts in the daily activity patterns of competitively surrogate species. For example, crab-eating and pampas foxes have been reported to change their daily foraging activity in sympatric areas where both species are present (switching from diurnal to

58 nocturnal), compared to allopatric areas where only one fox species is present (Di Bitetti et
59 al. 2009).

60 In addition, predators' activity patterns also could be influenced by rhythms of prey
61 activity where an arms race occurs through the temporal axis. Predators could adjust their
62 rhythms of daily activity to those hours of the day in which the availability of prey increases,
63 producing a synchrony between the daily activity patterns of the predator and their prey
64 (Foster et al. 2013), while at the same time, prey species could generate a temporal mismatch,
65 centering their activity at times when there is a lower risk of predation (Fenn and Macdonald
66 1995). Consequently, high temporal overlaps between carnivores and their putative prey have
67 been reported (Linkie and Ridout 2011) while in other predator-prey systems an asynchrony
68 was found in their respective activity peaks (Arias-Del Razo et al. 2011, Díaz-Ruiz et al.
69 2016). As a consequence, the daily activity of a given predator could be a result of a cost-
70 benefit trade-off between maximizing their activity during periods with high prey availability
71 (benefit) but also higher mortality risk due to encounters with intraguild competitors (cost)
72 (Santos et al. 2019).

73 Interspecific interactions play an important role in structuring a mammalian
74 community (Holt et al. 1994), especially in carnivores where competition not only arises for
75 exploiting the same resource simultaneously, but also for the risk associated with intraguild
76 predation. Indeed, interspecific relationships between different predators can be modulated
77 through direct or indirect competition. An example of a direct interaction is intraguild
78 predation (IGP), a type of interference competition where a predator species kills another
79 predator, or where both species prey upon each other (Polis et al. 1989, Palomares and Caro
80 1999). IGP is mediated mainly by species' biological characteristics such as body size, prey

availability as well as their trophic ecologies (Linnell and Strand 2000), being specially reported on top-predators (Palomares and Caro 1999).

The effects that top predators exert on surrogate competitors can be diverse, from abundance reductions and distributional shifts (in space and time) (Newsome et al. 2017, Jiménez et al. 2019) to behavioural modifications through restriction of their activity patterns (Wang and Fisher 2012). Apex predators play a key role in ecosystem functionality due to their regulatory role on prey populations (top-down control) and their extinction frequently triggers cascading effects through direct and indirect interactions among trophic levels (Terborgh et al. 2010). An effect of apex predator's extinction is the eventual ecological release of medium-sized carnivore populations, leading to increases in the distribution and abundance of their populations (Prugh et al. 2009) ; a phenomenon coined '*mesopredator release*' by Soulé et al. (1988), which has been repeatedly documented (Brashares et al. 2010).

In the Iberian Peninsula, the Iberian lynx (*Lynx pardinus*) exerts its role as a top-predator on the populations of surrogate competitors (Palomares et al. 1996, 1998). Sizeable reductions of mesocarnivore abundance have been reported after the reintroduction of the Iberian lynx (Jiménez et al. 2019), reinforcing the idea that the coexistence between these carnivores is supported by spatial structuring where the probability of occurrence of the lynx is negatively associated with the presence of mesopredators (Palomares et al. 1996, Monterroso et al. 2020). In Doñana National Park, the carnivore guild is composed by a habitat and trophic specialist top predator (the Iberian lynx, *Lynx pardinus*) and mesocarnivores such as the red fox (*Vulpes vulpes*), the European badger (*Meles meles*) and the Egyptian mongoose (*Herpestes ichneumon*), which are characterized by a wide niche breadth due to their generalist behaviour concerning habitat selection and trophic preferences.

105 The negative effects that the Iberian lynx has on these mesocarnivores occur mainly through
106 intraguild predation, particularly on Egyptian mongooses (*Egyptian mongoose)*, common
107 genets (*Genetta genetta)* and red foxes (*Vulpes vulpes*) (Palomares et al. 1996, Palomares and
108 Caro 1999, and references therein). However, aggressive interactions between the different
109 mesocarnivores remain quite unknown since most of the documented IGP interactions in
110 these scenarios were associated to the Iberian lynxes against surrogate competitors, and not
111 between mesopredator species (Valverde 1957, Palomares et al. 1996, Fedriani et al. 1999).
112 Therefore, in areas where the Iberian lynx is not present, indirect relationships may become
113 more relevant between these mesopredators since coexistence seems not to be mediated by
114 spatial features of their respective ecological niches (Soto and Palomares 2015).

115 Indirect competitive interactions can arise through competition for exploitation, which
116 occurs when one of the species consumes trophic or spatial resources more efficiently and
117 reduces their availability to the rest of the species (e.g., Holt et al. 1994). Within
118 mesocarnivore communities, these interactions can modulate activity patterns in order to
119 reduce spatial or temporal overlap between species with similar trophic requirements (Bu et
120 al. 2016). Empirical data in this respect are surprisingly very limited for the Mediterranean
121 area, where situations of mesopredator release may be common due to recent historical
122 reductions in the Iberian lynx populations. Yet, most previous studies have focused on spatial
123 avoidance as the main mechanism allowing the mesocarnivore coexistence, and only recently
124 has the focus shifted towards temporal segregation (Barrull et al. 2014, Monterroso et al.
125 2014, Vilella et al. 2020).

126 The main purpose of this study is to evaluate the ecological factors that allow the
127 coexistence of mesocarnivore species in the Doñana National Park without the presence and
128 influence of a top-predator, focusing in particular on the temporal segregation of four species

of mesocarnivores: the red fox (*Vulpes vulpes*), the European badger (*Meles meles*), the common genet (*Genetta genetta*), and the Egyptian mongoose (*Herpestes ichneumon)*. Thus, this study aims: 1) to explore the relationship between mesocarnivores along the trophic niche axis; 2) to determine the diel activity patterns of predator and prey species and their synchrony; and 3) to quantify the temporal overlap or segregation between potential competitors. Following a niche partitioning conceptual framework, we hypothesize that there would be greater temporal segregation in those species that have a higher degree of overlap in their respective trophic niches, while species that have similar use of the diel cycle should show differentiated trophic preferences in order to promote coexistence by reducing competition along temporal or trophic niche axes.

Material and methods

Study area

This study was carried out in Doñana National Park (37º1'N, 6º 33'W) in three 1-ha sites characterized by juniper stands (*Juniperus phoenicea* subsp. *turbinata)* of different age and ecological succession stages. The selected sites represent a gradient of habitat maturity in terms of ecological succession that ranges from an advance front of juniper stands to mature stands with a higher degree of vegetation cover: "*Sabinar de Colonización*" (SABCOL) represents an early stage with 2030 junipers/ha, "*Sabinar del Ojillo*" (SABOJI) is regarded as an intermediate stage with 9010 junipers/ha and "*Sabinar del Marqués*" (SABMAR) constitutes the final stage with 10520 junipers/ha (Figure S1, Supplementary information).

Data collection

We located eight camera traps per site that were rotated periodically through 35 randomly selected focal juniper plants. Juniper locations were selected at random in each of

152 five subplots within each of the three main sites, with the subplots distributed regularly
153 throughout the main plot. The structure of this habitat consists of paths between juniper
154 individuals, so the cameras were installed at 1-m height focusing on the ground and the
155 bottom of the plant. Camera traps were active for ca. 10 days in each of these rotations and
156 then changed to other 8 locations, thus ensuring that the whole site was sampled in 5 weeks.
157 Following this procedure, data were obtained from a total set of 24 camera traps sampling the
158 three sites during two campaigns: the first one from October 2018 to May 2019 and the
159 second one from October 2019 to June 2020.

160 The diel activity cycle of each species was characterized by pooling the total number
161 of detections across all cameras during the whole study period. In order to avoid data
162 dependency, in our analyses we discarded consecutive detections of a given species within a
163 site (Davis et al. 2011, Monterroso et al. 2014). Since the area covered by our study sites is
164 limited (ca. 1 ha/site), we set a period of 15 min between consecutive detections of a given
165 species within a study site, which is a reasonable time period for a species to abandon the
166 site. Moreover, in such cases where a given individual was detected repeatedly without
167 leaving the camera detection zone, only the time of its first detection was considered. In
168 analyses we used either the total, absolute number of records (e.g., to compare the relative
169 frequency of sunrise, day, dusk, and nocturnal records within a given site) or the relative
170 frequency of records expressed as number per camera-day (e.g., when comparing across sites
171 that received different sampling intensity).

172 Target species consisted mainly of mesopredators which occur in Doñana National
173 Park and their respective prey species. The mesocarnivore guild in the study area is
174 composed by the Egyptian mongoose (*Herpestes ichneumon*), the red fox (*Vulpes vulpes*), the
175 Eurasian badger (*Meles meles*) and the common genet (*Genetta genetta*) (Valverde 1967).

Large top predators either extinct or at low density in the area include the wolf (*Canis lupus*) and the Iberian lynx (*Lynx pardinus*) (Valverde 1967). Simultaneously, other species recorded during the course of this study were considered as possible prey items for predators such as lagomorphs (mainly European rabbits, *Oryctolagus cuniculus*), small mammals and birds such as *Alectoris rufa*. Detections from ungulates (mainly *Cervus elaphus* and *Sus scrofa*) were not included in the analysis as their presence in mesocarnivore diets is frequently associated with carrion consumption, with direct predation being recorded sporadically on very young individuals (Valverde 1967). No attractants were used over the two years of sampling.

Trophic overlap data

With the aim of exploring trophic overlap between the predators mentioned above, we extracted diet information from a set of studies carried out in Doñana National Park (Table S1, Supplementary information). We searched WOS and Google Scholar for studies that reported trophic preferences of the four mesocarnivores in Doñana National Park using the following search string: (trophic OR diet) AND (*Vulpes vulpes* OR *Genetta genetta* OR *Meles meles* OR *Herpestes ichneumon*) AND (Doñana). The selection of studies was aimed at compiling all the trophic information available for the four species at different locations in the Doñana National Park to better estimate the entire trophic spectra of each of the different species. Given that the four target species are commonly reported as opportunists in their feeding behaviour, this approach was taken in order to capture the natural variability in dietary composition across the whole Doñana study area and its marked seasonal component.

To avoid pseudo-replication issues, we selected those studies in which the data come from strictly different samples and periods. From each study, period and species, we extracted the percentage of occurrence of food items. In order to estimate trophic overlap

200 between mesocarnivores, we carried out a correspondence analysis (CA) using the percentage
201 of occurrence of each prey item for each predator. The CA ordered the different diet studies
202 (cases) relative to the prey species composition reported by each study, resulting in an
203 ordination of the studies corresponding to each mesopredator species, based on their
204 similarity of prey species composition. We used the coordinates on the first two CA axes
205 corresponding to each diet study to build convex polygons spanning each mesopredator group
206 of studies. In this way, these polygons illustrate the range of dietary variation shown by each
207 mesopredator species in relation to the diet composition of other species.

208 **Camera trap data analysis**

209 Time and date were extracted from each detection of every camera trap to estimate
210 daily activity patterns and temporal overlap between mesocarnivores and their potential prey
211 and between mesocarnivore potential competitors. As time and dates are variables with a
212 circular nature, diel activity cycles were estimated using non-parametric Kernel density plots
213 which provide a density function of the daily activity pattern of a given species (Rowcliffe et
214 al. 2014). Raw data were subsampled in order to carry out analyses only for those species
215 with more than 10 detections (Fisher 1995, Gerber et al. 2012).

216 To determine the daily activity pattern of the species we resorted to the classification
217 used by van Schaik and Griffiths (1996) by which species are classified according to the
218 number of independent detections obtained as: diurnal (> 90% of the detections occurring
219 during the daylight), nocturnal (> 90% of the detections obtained at night), crepuscular (>
220 90% of their detections occur at dawn or dusk) or cathemeral if their activity pattern is
221 distributed uniformly throughout the daily cycle. We tested whether the target species
222 actually show a certain activity pattern and deviate from a random pattern using the Rao
223 Spacing Test (U) (Rao 1976).

Moreover, as the present study has been carried out over two years, daylight can vary from one detection to another and induce bias to our results. Species could adjust their daily activity levels depending on the day length, thus not taking this aspect into account when dealing with strictly diurnal or nocturnal species could lead to the misinterpretation of the results and the underestimation of peaks of daily activity (Vazquez et al. 2019). Therefore, we carried out a double average anchoring time transformation to take into account the mean average sunrise and sunset times for the study area (Vazquez et al. 2019).

We evaluated the extent of temporal segregation between mesopredators using the overlap coefficient (Δ) described by Ridout and Linkie (2009). This coefficient ranges from 0 to 1, where 0 values represent completely different diel activity patterns while 1 represents the maximum overlap between both species. Ridout and Linkie (2009) have reported different estimators of the degree of overlap between the daily activity curves and tested which of them represent a better estimate of the temporal overlap as a function of the sample size. Briefly, Δ_1 represents accurately the degree of overlap between two curves when the smallest size of the two samples is less than 50 detections while Δ_4 best fits when the smallest sample size exceeds 75 detections. Following Ridout and Linkie (2009), we used Δ_1 for those cases in which sample size was lower than 75 detections, and Δ_4 when sample sizes were equal or greater than 75 detections.

Once the overlap coefficients between the different species were estimated, 99% confidence intervals were calculated through smoothed bootstrap analysis with 10,000 replicates. Moreover, the significance of differences in pairwise comparisons of daily activity patterns were evaluated by using the non-parametric Mardia-Watson-Wheeler test (MWW) which allows us to detect whether two circular samples differ significantly from each other (Batschelet 1981). However, deciding whether a certain degree of temporal overlap is high or

low based solely on this coefficient is somewhat subjective. Therefore, we followed Monterroso et al. (2014) and used percentiles to establish threshold levels of overlap for our discussion. Thus, when $\Delta >$ 75th percentile, a high temporal overlap exists between both species, while $\Delta \leq$ 50th percentile values show a low degree of overlap. Intermediate values of these percentiles, 50th $< \Delta \leq$ 75th, were interpreted as moderate levels of overlap.

Statistical software

All analyses were conducted in R Statistical Software 3.6.2 (R Core Team 2020). Data handling was done with the package "dplyr" (Wickham et al. 2020); the correspondence analysis (CA) was carried out with "*FactoMineR*" package (Lê et al. 2008); kernel density functions, overlap coefficients (Δ) and their respective confidence intervals were calculated with the package "*overlap*" (Ridout and Linkie 2009), and MWW and Rao Spacing tests were conducted using the "*circular*" package (Agostinelli and Lund 2017). Finally, in order to calculate mean average sunrise and sunset times and perform average anchoring transformation we used the "*activity*" package (Rowcliffe 2019).

Results

Trophic segregation among mesocarnivores

The correspondence analysis explains approximately 66% of the variability of mesocarnivore diets through the first two dimensions (Figure 1). Axis 1, which explains 51.6% of the variation, discriminates the set of mesocarnivores into two separate groups: species whose diet is mainly omnivorous (red fox and European badger) and those with essentially carnivorous diets (common genet and Egyptian mongoose). The red fox and the European badger showed very close values due to their frugivorous behaviour and the predominant consumption of lagomorphs and invertebrates. Simultaneously, axis 2, which

271 explains 15% of the trophic variation, is generated by variation between the diets of the
272 Egyptian mongoose and the common genet, with the latter having a trophic preference for
273 small mammals followed by a secondary intake of birds. However, the second dimension of
274 the correspondence analysis does not discern between the trophic niches of the red fox and
275 the European badger, indicating that there is a greater trophic overlap between these two
276 omnivorous species with respect to the rest of the mesocarnivore guild. Finally, the convex
277 polygons represent the more ample trophic diversification of the generalist species (red fox,
278 European badger and Egyptian mongoose) whose range of prey types tends to be
279 considerably wider compared with the common genet and its specialist feeding behaviour
280 (Figure 1).

281 *Camera trapping results and diel activity patterns*

282 Results obtained in this study come from a total of 531 effective sampling days. All
283 sites were sampled with same number of cameras per site and a similar effort (number of
284 days): $\bar{x}$ ± SD = 80.3 ± 28.3 d for SABCOL; 80.4 ± 27.3 d for SABOJI and 86.8 ± 26.0 d for
285 SABMAR. Thus, sampling effort was quite evenly distributed among sites. Broadly, a total
286 of 2786 detections were obtained throughout the study period, of which 96 (3.44%) could not
287 be identified at the species level. Among all detections, 16% corresponded to
288 mesocarnivores, 28.7% to prey species (e.g. rabbit, partridge, small mammals…), 15% to
289 ungulates and 38.7% to passeriformes (Table S2, Supplementary information).

290 Regarding target species, detections accounted for by the red fox represented a total of
291 301 of which 55% were in SABCOL, while the rest of the detections were evenly distributed
292 between the other two sites. A large amount of the detections obtained from this species were
293 linked to its nocturnal habits while the rest were distributed throughout the periods with
294 daylight, demonstrating a cathemeral activity pattern with a tendency towards bimodality

295 (U = 142.26; p-value < 0.05) (Table S3, Supplementary information). Conversely, detections
296 of European badgers were very scarce in the three study sites, showing a predominantly
297 nocturnal activity pattern, with 77% of the detections occurring at night and the rest during
298 the dawn or dusk periods (U = 178.95; p-value < 0.01). Likewise, the activity pattern shown
299 by the common genet was strictly nocturnal (95% of the records produced during nighttime;
300 U = 165.81; p-value < 0.01) and linked to SABCOL where 62% of its detections took place.
301 Finally, detections of Egyptian mongooses were mainly concentrated in the SABOJI (54%)
302 while the other two sites maintained the same proportion of records, showing a marked
303 diurnal activity pattern in each of them (92% of the detections occurred during daylight; U =
304 199.78; p-value < 0.01) (Table S3, Supplementary information).

305 For prey species, most of the detections corresponded to the European rabbit
306 (*Oryctolagus cuniculus*), the red-legged partridge (*Alectoris rufa*) and small mammals.
307 European rabbits were detected 650 times with an even distribution between SABOJI and
308 SABMAR, while SABCOL had only 6 detections during the entire sampling period (Table
309 S2, Supplementary information). Rabbit detections were distributed throughout the day,
310 setting it as a cathemeral species with distinct activity peaks around sunrise and sunset (U =
311 156.97; p-value < 0.01) (Table S3, Supplementary information). Conversely, we did not have
312 sufficient detections from the other lagomorph present in RBD (*Lepus granatensis*, N = 3) to
313 include them in this study.

314 Small mammals accounted for a total of 98 detections, mainly associated with
315 SABMAR and detected only during nighttime (U = 198.27; p-value < 0.01). Red-legged
316 partridges were mainly detected in SABCOL (89% of detections) with a markedly diurnal
317 activity pattern (U = 226.53; p-value < 0.01) (Table S3, Supplementary information). Finally,

318 detections of ungulates present in the area (mainly *Cervus elaphus* and *Sus scrofa*)
319 represented approximately 14% of the total number of detections.

320 *Predator and prey diel activity patterns*

321 Broadly, the activity patterns and their corresponding overlap differed between
322 predators and the potential prey items in the study area. The European rabbit showed a high
323 degree of overlap with the red fox ($\Delta_4 = 0.84$), followed by a moderate overlap with the
324 European badger ($\Delta_1 = 0.62$). Conversely, both the common genet and the Egyptian
325 mongoose showed low overlap coefficients ($\Delta_1 = 0.47$ and $\Delta_1 = 0.44$, respectively) with
326 rabbit activity patterns (Figure 2).

327 We found a high temporal overlap between the activity patterns of small mammals
328 (with most detections at night) and the European badger ($\Delta_1 = 0.89$) and the common genet
329 ($\Delta_1 = 0.76$). In turn, the red fox showed a moderate temporal overlap with small mammals (Δ_4
330 $= 0.68$), while the Egyptian mongoose showed a total temporal segregation with respect to the
331 detected micromammals ($\Delta_1 = 0.14$). Activity patterns of red-legged partridges overlapped
332 with those of the Egyptian mongoose ($\Delta_1 = 0.82$) while showing a large temporal segregation
333 with European badgers ($\Delta_1 = 0.08$) and common genets ($\Delta_1 = 0.03$) (Figure 2).

334 European rabbit activity patterns differed significantly between SABOJI and
335 SABMAR (W = 32.69; p-value < 0.01) (Figure 3). Conversely, the red fox showed shifts in
336 activity patterns between different sites with varying rabbit availability, with a predominantly
337 nocturnal activity in SABCOL and a tendency towards bimodal activity patterns in SABOJI
338 and SABMAR. Significative differences were found between activity patterns of red foxes
339 from SABCOL and SABMAR (W = 11.14; p-value < 0.01) while no differences were found
340 between SABCOL - SABOJI (W = 3.97; p-value = 0.137) or SABOJI - SABMAR (W =
341 2.44, p-value = 0.295). The temporal overlap for the European rabbit and the red fox was $\Delta_1 =$

342 0.79 for SABOJI and $\Delta_1 = 0.73$ for SABMAR while the temporal overlap between European
343 rabbit and Egyptian mongoose was $\Delta_1 = 0.49$ for SABOJI and $\Delta_1 = 0.37$ for SABMAR
344 (Figure 3). No statistically significant differences were found between activity patterns of the
345 Egyptian mongoose between SABCOL - SABOJI (W = 1.09; p-value = 0.58), SABCOL -
346 SABMAR (W = 2.06; p-value = 0.36) and SABOJI - SABMAR (W = 0.40; p-value = 0.82)
347 (Figure 3).

348 *Temporal overlap and segregation between mesocarnivores*

349 The mesocarnivore assemblage in the study area is composed mainly by two
350 predominantly nocturnal species, a strictly diurnal species and a species with a cathemeral
351 activity pattern. The average overlap and standard deviation of the activity patterns of the
352 different species was $\Delta_1 = 0.48$ and SD = 0.29, which reflect a low, although variable,
353 temporal overlap among these potential competitors. The average overlap values ($\Delta_1 \pm$ SD) of
354 a species with respect to the set of potential competitors were: 0.59 ± 0.15 for the fox; 0.57 ±
355 0.34 for the badger; 0.50 ± 0.36 for the genet and 0.24 ± 0.18 for the Egyptian mongoose.

356 Strictly nocturnal species (European badger and common genet) showed a high
357 overlap coefficient without significant differences between their activity patterns ($\Delta_1 = 0.79$;
358 W = 1.89, p-value = 0.386). On the contrary, the Egyptian mongoose, due to its diurnal
359 habits, showed a strong and significant temporal segregation with the European badger ($\Delta_1 =$
360 0.16; W = 41.75, p-value < 0.01) and the common genet ($\Delta_1 = 0.08$; W = 65.79, p-value <
361 0.01) (Figure 4). Simultaneously, the cathemeral activity pattern of the red fox sustained
362 intermediate levels of temporal segregation with the common genet ($\Delta_1 = 0.57$; W = 24.96; p-
363 value < 0.01) and the European badger ($\Delta_1 = 0.71$; W = 8.44; p-value = 0.014) and a low
364 overlap with the Egyptian mongoose ($\Delta_1 = 0.44$; W = 73.48; p-value < 0.01) (Figure 4).

365 Among study sites, temporal overlap between the red fox and the Egyptian mongoose was
366 Δ_1= 0.41 for SABCOL, Δ_1 = 0.45 for SABOJI and Δ_1 = 0.36 for SABMAR (Figure 3).

367 Discussion

368 In this study we explore how the sympatry of mesocarnivores in the Doñana National
369 Park could be mediated by temporal or trophic segregation when there is a greater overlap in
370 any of these two niche axes. Our study explores the mechanisms underlying the structure of
371 Mediterranean mesocarnivore communities, which have been traditionally focused on spatial
372 responses (Fedriani et al. 1999, Soto and Palomares 2015, Monterroso et al. 2020, but see
373 Barrull et al. 2014, Monterroso et al. 2014, Vilella et al. 2020), by providing new insights on
374 the importance of temporal segregation at facilitating co-occurrence by reducing resource
375 overlap. Overall, we found a moderate level of temporal segregation within the
376 mesocarnivore guild in our study area, which was composed by two strictly nocturnal species
377 - the European badger and the common genet (Palomares and Delibes 1994, Rodríguez et al.
378 1996, Camps 2008), one diurnal - the Egyptian mongoose (Palomares and Delibes 1992) and
379 one with plasticity in its daily activity pattern - the red fox, which ranges from diurnal
380 (Cavallini and Lovari 1994) to nocturnal habits (Baker et al. 2007).

381 The highest values of temporal overlap occurred between the European badger and the
382 common genet due to their predominantly nocturnal activity patterns. However, they
383 markedly differ in their respective trophic niches, with a segregation between them due to
384 preferential consumption of small mammals by the common genet. Indeed, the common
385 genet had a high temporal overlap with small mammals, its main prey item, which were
386 detected mostly at night. The common genet consumes almost all species of rodents and
387 insectivores, but it is certainly a specialized predator on *Apodemus sylvaticus*, the main prey
388 of its diet when this item is available (Palomares and Delibes 1991a, Virgós et al. 1999). This

synchrony between predator and prey is an expected outcome of Optimal Foraging Theory constraints (MacArthur and Pianka 1966), by which an animal will try to maximize its prey intake by showing an efficient foraging pattern. Predators whose diet is eminently specific are expected to maximize synchrony of their daily activity patterns to their main and most profitable prey (Pyke et al. 1977). However, this pattern would not be so marked in predators whose feeding behaviour is opportunistic and depends on the availability and accessibility of several prey types (Pyke et al. 1977), which is the case of the rest of mesocarnivores studied.

The rest of the species that constitute the Doñana mesocarnivore assemblage are known for their generalist feeding habits (Rau 1987, Palomares 1993, Fedriani et al. 1999). However, we found a distinct trophic segregation of the Egyptian mongoose with respect to the red fox and the European badger, due to its eminently carnivorous behaviour, with plant material (e.g., fleshy fruits) virtually absent from its diet. Meanwhile, the trophic overlap between European badger and red fox was the highest within the mesocarnivore community due to their omnivorous behaviour based on the consumption of fleshy fruits, invertebrates and lagomorphs. Despite their reduced differences in terms of spatial and trophic niche, these species showed a marked temporal segregation, displaying distinct activity patterns: nocturnal, cathemeral and diurnal, which could ease coexistence by exploiting similar resources at different times and thus reducing intraguild encounters.

The ecological plasticity and the ample spectra of resource use shown by these species in trophic and habitat niche axes suggest a scenario with potentially reduced interspecific competition (Palomares 1993, Fedriani et al. 1999, Monterroso et al. 2020). However, the temporal segregation of these species may become more relevant, given that the other two axes of their respective ecological niches can exhibit ample overlap. These situations could be produced due to a reduction in the abundance and availability of its main trophic resources

413 at a given moment, increasing competition for the consumption of secondary resources
414 available. A clear example is the reduction in the consumption of European rabbits after a
415 sudden population collapse due to the emergence of the rabbit hemorrhagic disease (RHD)
416 (Ferreras et al. 2011), which resulted in an increased trophic overlap among most generalist
417 carnivore species. In such cases, time partitioning becomes the main mechanism to facilitate
418 coexistence by reducing competitive stress in resource use among these species (Barrientos
419 and Virgós 2006).

420 The European rabbit in the study area accounts for a very high percentage of the diet
421 of Egyptian mongooses (Palomares and Delibes 1991b) and also for European badgers. Some
422 authors even point out a possible specialization of badgers in this type of prey, a contentious
423 assertion which has been debated (Martín et al. 1995, Revilla and Palomares 2002). The
424 activity pattern of European rabbits matches those previously reported, showing a bimodal
425 pattern with peaks of activity at sunrise and sunset (Villafuerte et al. 1993, Monterroso et al.
426 2013, Díaz-Ruiz et al. 2016). However, rabbit availability differed between study sites since
427 during both sampling periods we did not obtain almost any detections in the least mature,
428 early successional juniper colonization front, the "*Sabinar de Colonization*" site. Conversely,
429 detections in "*Sabinar del Marqués*" and "*Sabinar del Ojillo*" were considerably more
430 frequent, which would reflect the differences in terms of prey availability among different
431 study sites. Such differences may be due to habitat requirements since, at the landscape scale,
432 the ideal habitat for rabbits is a juxtaposition of ecological units where the refuge areas are
433 intermingled with others where herbaceous food is more abundant (Monzón et al. 2004,
434 Dellafiore et al. 2014). The "*Sabinar de Colonización*" (SABCOL) represents a
435 Mediterranean scrubland in an early ecological stage composed mainly by a low-density
436 population of *J. phoenicea* (2030 junipers/ha) and therefore, a low vegetation cover which
437 does not fulfil rabbit habitat preferences. Meanwhile, "*Sabinar del Marqués*" (SABMAR)

438 and "*Sabinar del Ojillo*" (SABOJI) are sites characterized by late successional mature
439 vegetation and high vegetation cover, which may serve as refuge for rabbits. In these two
440 sites, we found differences between the diel cycle use of rabbits, showing two activity peaks
441 in SABOJI and only one crepuscular activity peak in SABMAR. Interestingly enough, the
442 activity pattern displayed by the red fox, showed a unimodal pattern with an activity peak
443 around midnight in SABCOL, but shifted towards bimodality in sites where the rabbit was
444 present, putatively to match the activity patterns of this prey and thus increase the probability
445 of encounter.

446 In SABMAR, the European rabbit had the lowest value of temporal overlap with its
447 main predators (red fox and Egyptian mongoose) since it concentrated its activity around
448 dusk periods while, in SABOJI, its bimodal pattern increased the overlap. This situation may
449 be a reflection of an anti-predatory behaviour of the European rabbit since, despite showing
450 two possible activity peaks in its daily cycle, its activity in SABMAR is centered at time
451 periods in which it does not overlap with its main predators. Meanwhile, in SABOJI, the
452 bimodal activity of the fox is less marked than in the SABMAR, matching with the activity
453 peaks of the rabbits and increasing the temporal overlap. In this way, the intensity of the red
454 fox activity could trigger a shift in the activity patterns of the European rabbit given that an
455 increase in the dawn activity of the predator in SABMAR is counteracted by rabbits which
456 display only one activity peak at twilight. This observation could support the Risk Allocation
457 Hypothesis by which a temporal mismatch between activity patterns of a prey species and its
458 predator could be due to a higher perception of mortality risk that drives anti-predatory
459 behaviours along the time axis (Lima and Bednekoff 1999). A similar situation has been
460 previously observed among other species of lagomorphs and canids, where the bimodal
461 patterns of the Black-tailed jackrabbit (*Lepus californicus*) and the desert cottontail
462 (*Sylvilagus audubonii*) showed a single peak of activity overlapping with the activity of their

463 predator, the coyote (*Canis latrans*), supporting the idea that these prey species are able to
464 shift their activity with a temporary mismatch that allows them to reduce predation risk
465 (Arias-Del Razo et al. 2011).

466 Regarding the differences between the plasticity of the activity patterns of the red fox
467 and the Egyptian mongoose, they may be due to differences in foraging strategies. The
468 European rabbit is a profitable prey for the generalist mesopredators in Doñana (Rau 1987,
469 Palomares and Delibes 1991b, Martín et al. 1995, Ferreras et al. 2011) but each predator
470 displays different hunting and consumption strategies of this prey item. Egyptian mongooses
471 and European badgers are species that preferentially consume younger rabbit age classes
472 since their foraging strategy consists of digging in burrows even though they can actively
473 hunt them (Palomares and Delibes 1991b, Martín et al. 1995). Conversely, the red fox resorts
474 to a foraging strategy based mainly on the pursuit of prey items, although it also excavates in
475 rabbit burrows (Fedriani et al. 1999). Thus, these distinct foraging strategies could allow the
476 Egyptian mongoose and European badgers to maintain a temporal asynchrony with the prey's
477 activity patterns while the red fox would be forced to track and match the activity pattern of
478 its prey.

479 The observational nature of this study does not allow us to establish a clear causal
480 relationship in the observed patterns of the different species (i.e., temporal avoidance
481 between competitors). Future research should address differences of rabbit availability for
482 predators through the study of their respective abundances among study sites, as well as the
483 relative abundances of each mesopredator by accounting for the probability of detection in
484 occupancy models. Unfortunately, our sample size did not allow us to fit these models. In
485 these situations, camera trap data could be complemented with other census methods (i.e.
486 pellet counts or track censuses). Complementarily, the study of the trophic relationships

between potential competitors could be evaluated by studying the diet composition through the collection, identification and analysis of faecal samples in the different study sites simultaneously to the camera-trapping surveys. Nevertheless, our study addresses for the first time the interspecific relationships among the 4 species of mesocarnivores present in Doñana National Park by integrating together the different patterns of daily activity and their respective overlap, as well their trophic ecologies, since previous efforts have focused on niche differentiation along other axes (spatial; (Palomares and Delibes 1991c, Palomares et al. 1996, Soto and Palomares 2015); and trophic, (Palomares and Delibes 1991a, Fedriani et al. 1999, Ferreras et al. 2011)).

Conclusions

The activity patterns of mesopredators are ultimately restricted by the circadian boundaries, but at the same time can be slightly modulated by interspecific interactions with both prey and potential competitors. Our results show that the coexistence of the different species that compose the mesocarnivore assemblage in the Doñana National Park can be facilitated by the temporal segregation among generalist species due to a divergence in the activity patterns (nocturnal, diurnal and cathemeral) but also by differences in trophic preferences among specialist species, as suggested in previous studies (Palomares and Delibes 1991c, Fedriani et al. 1999, Soto and Palomares 2015).

Our study further suggests that in order to clarify the coexistence mechanisms underlying community structure, it is necessary to consider a multidimensional perspective, addressing simultaneously the differences in multiple axes of the ecological niches. In markedly seasonal habitats like Doñana, with patchy vegetation including ample gradients of vegetation cover and successional status, even subtle differences in daily activity such as those documented here represent multiple ways to facilitate sympatry of coexisting

mesopredator species. These effects might prove crucial for such coexistence in settings where the loss of apex predators may lead to mesopredator release, triggering increased densities and resource overlap. Recent scenarios of rewilding with top predators may represent ideal conditions to experimentally examine these effects of mesopredator release in biodiverse carnivore guilds like those of the Mediterranean habitats studied here.

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Author contributions

ABL conceived the original idea; IF performed the analyses, designed the figures and led the writing of the manuscript; JI and PJ designed the methodology; JI and IF compiled the camera-trap data and IF collected the diet data. All authors contributed critically to subsequent drafts and the final version of the manuscript.

Data and code accessibility

All data and R scripts used in this study are available in the GitHub repository:

https://github.com/IagoFerreiroArias/TempPart

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Figures

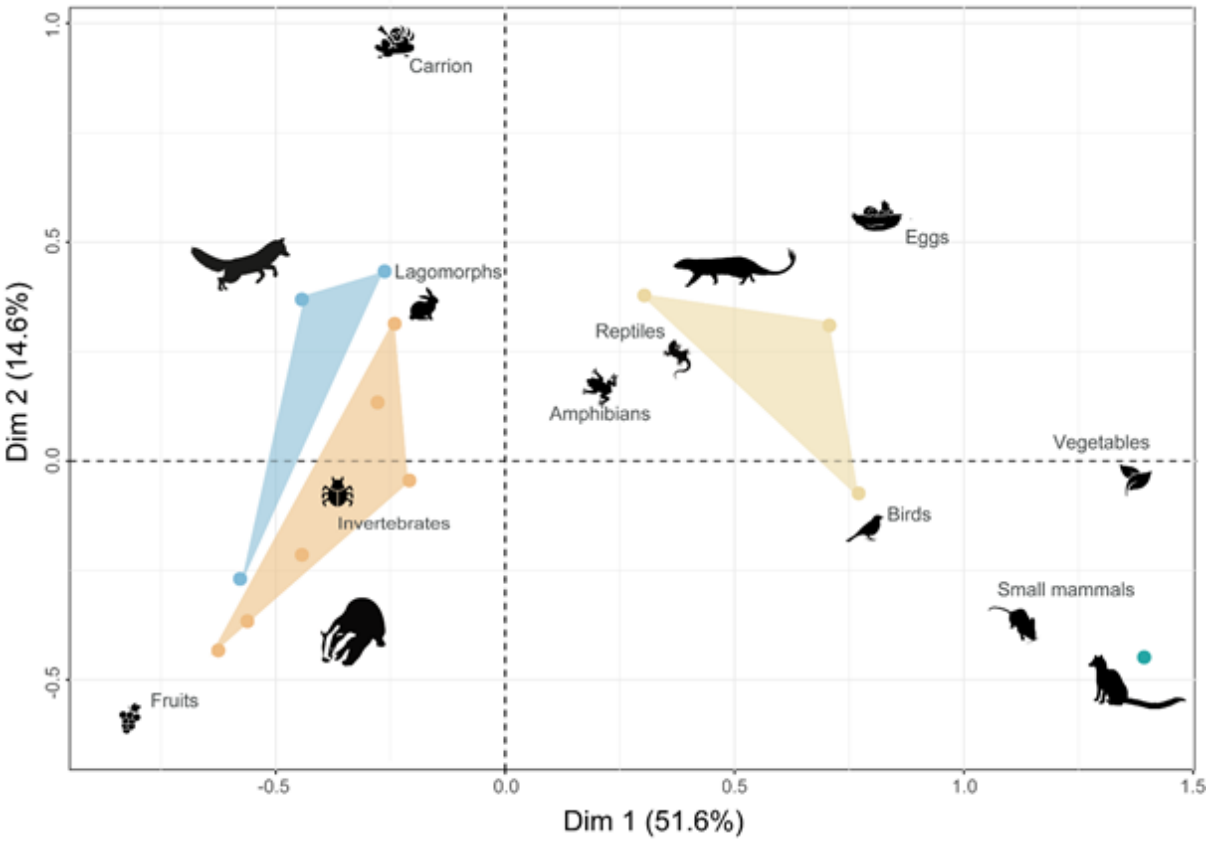


Figure 1. Niche segregation along the trophic axis among mesocarnivores in Doñana National Park. Convex polygons represent trophic niche breadth for generalist species. Since only one diet study could be used regarding common genet diet in the study area, convex polygons are omitted for this species. The CA first two dimensions (Dim 1, Dim 2) explain 66% of the variability in diet composition among species and studies. The first dimension separates mesocarnivores into two groups: species whose diet is predominantly carnivorous and species whose diet is omnivorous. The second dimension separates the Egyptian mongoose from the genet while indicating a greater trophic overlap between the diets of the red fox and the European badger.

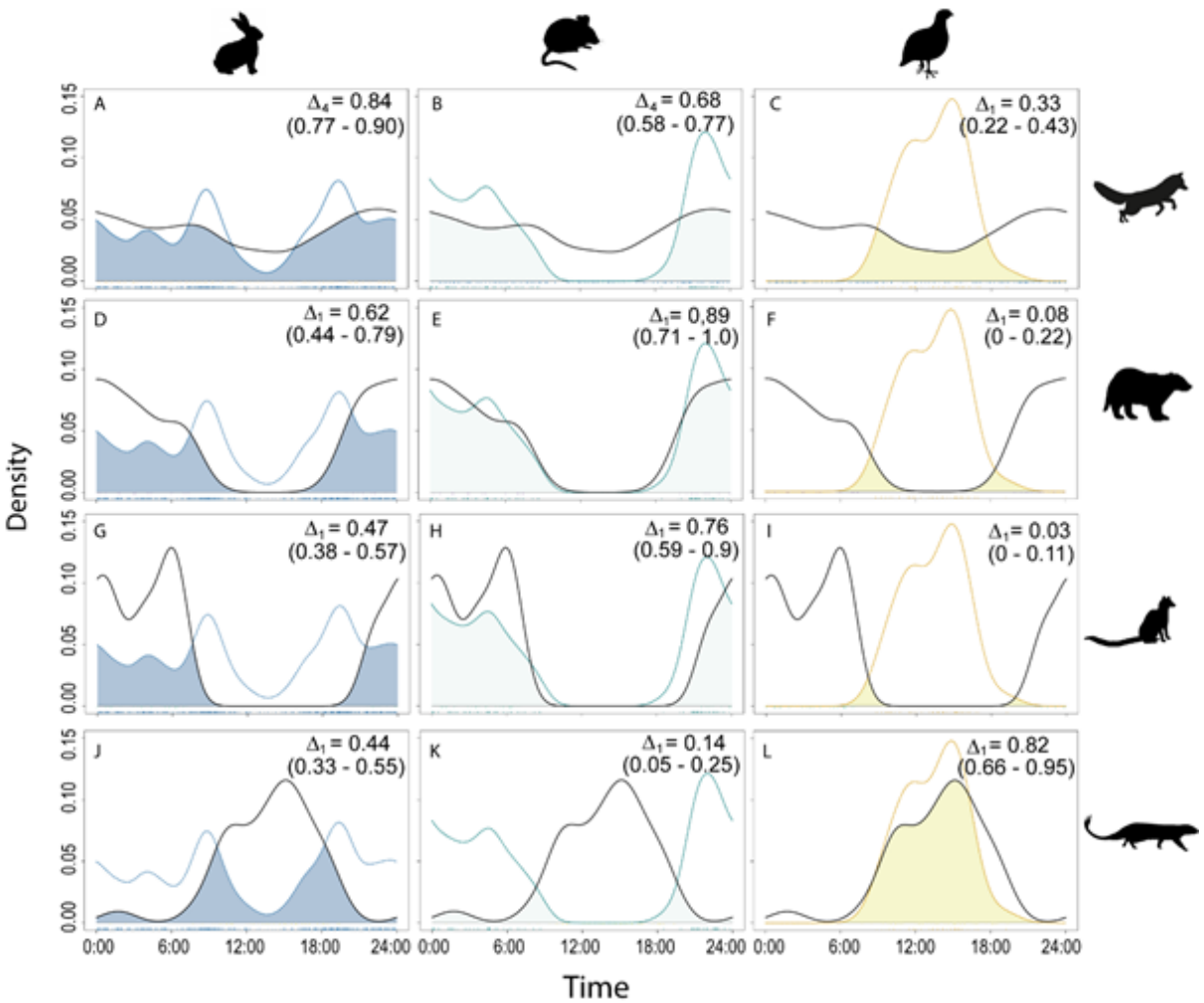


Figure 2. Pairwise comparisons of daily activity patterns between mesocarnivores (rows, top to bottom: red fox, badger, genet, and Egyptian mongoose) and their main prey items in the study area (columns, left to right: *Oryctolagus cunniculus*, small mammals, and *Alectoris rufa*). Coloured lines describe prey activity patterns (blue for European rabbit, green for small mammals and yellow for red-legged partridge) and black lines indicate predator's activity patterns. Overlap coefficients (Δ) and their respective 99% confidence intervals are shown in brackets.

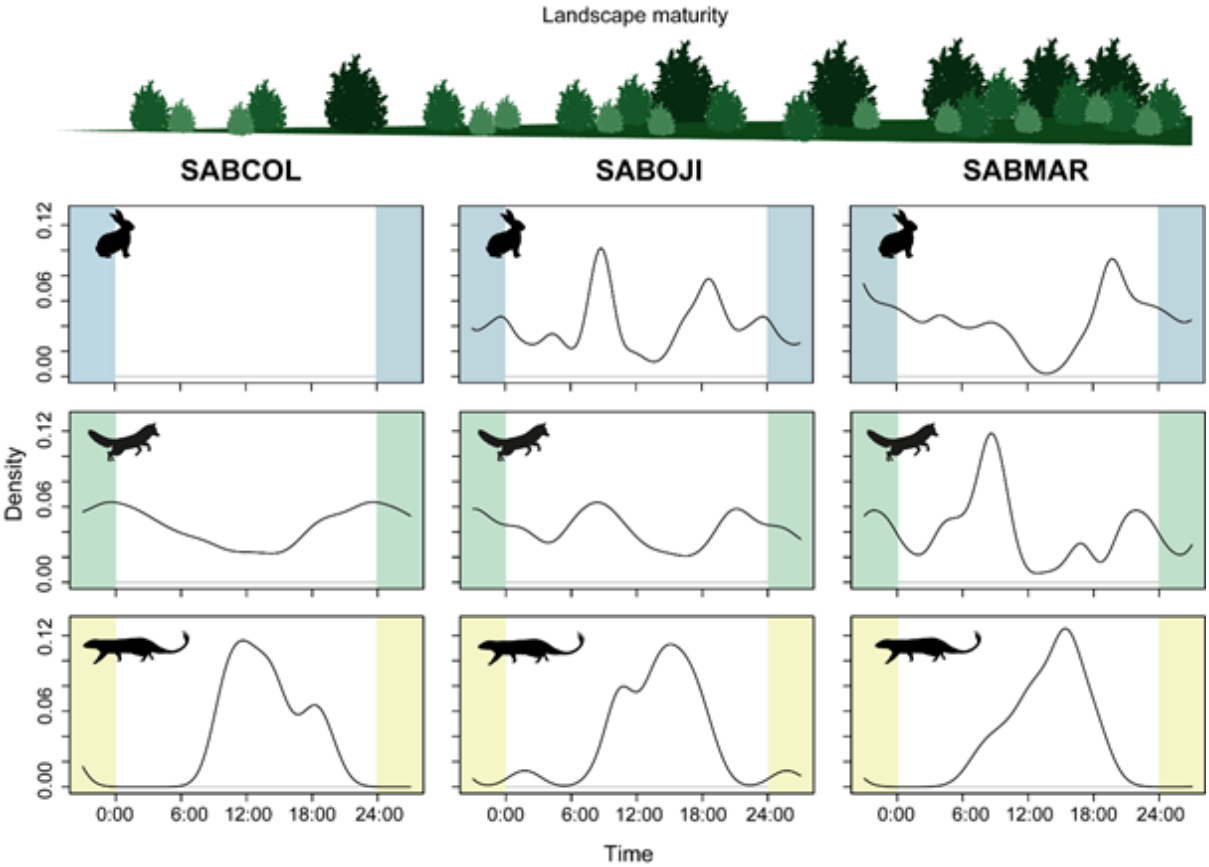


Figure 3. Diel activity patterns of two mesocarnivores (red fox and Egyptian mongoose; mid and bottom rows, respectively) and its main prey item (European rabbit, top row) along the gradient of ecological succession, from younger juniper stands (SABCOL) to mature, late successional stands (SABMAR).

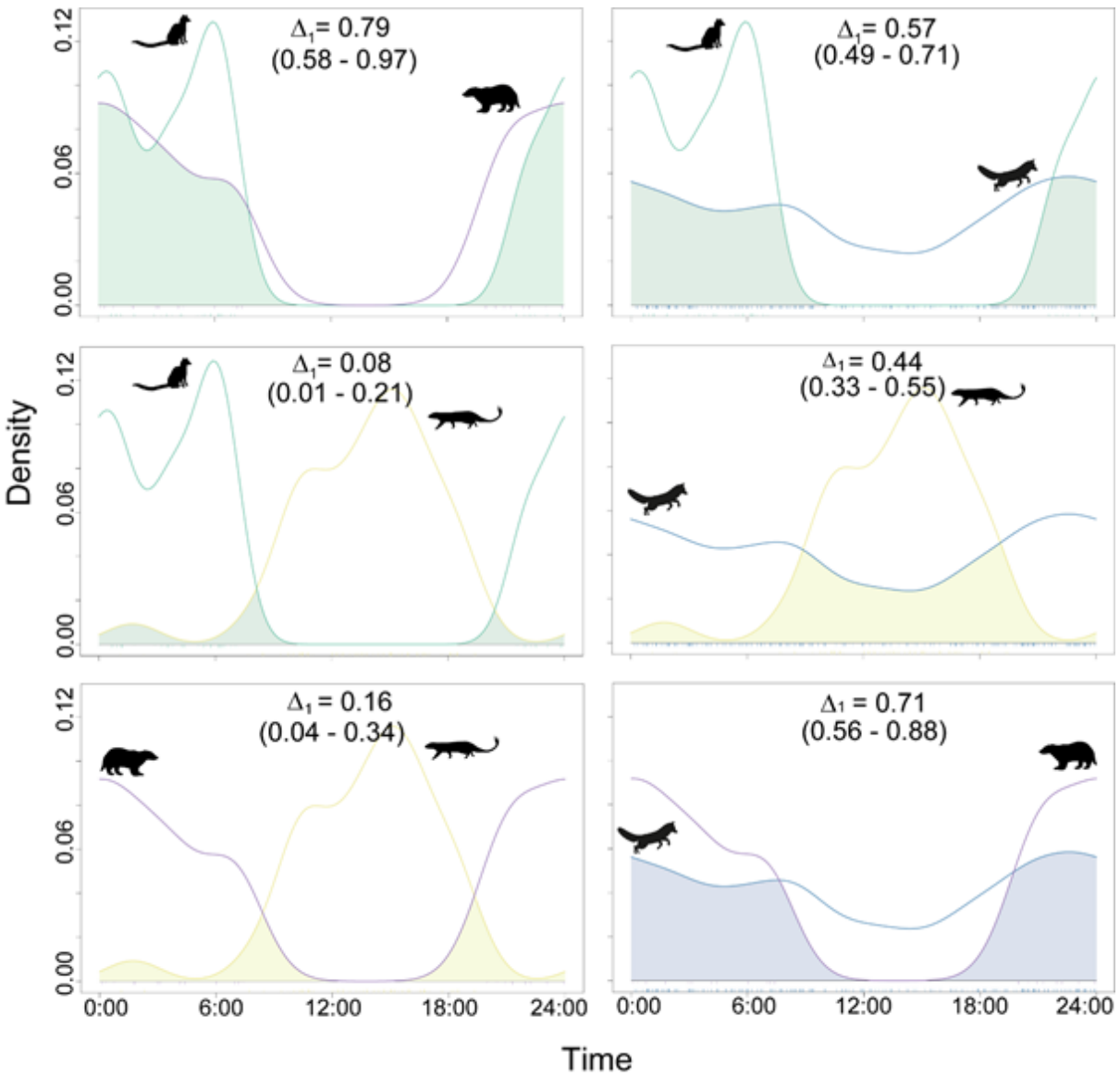


Figure 4. Kernel density plots and temporal overlap between mesocarnivores in the study area: common genet (green line), red fox (blue line), European badger (purple line) and Egyptian mongoose (yellow line). Overlap coefficients (Δ) and their respective 99% confidence intervals are shown in brackets.

Supporting Information

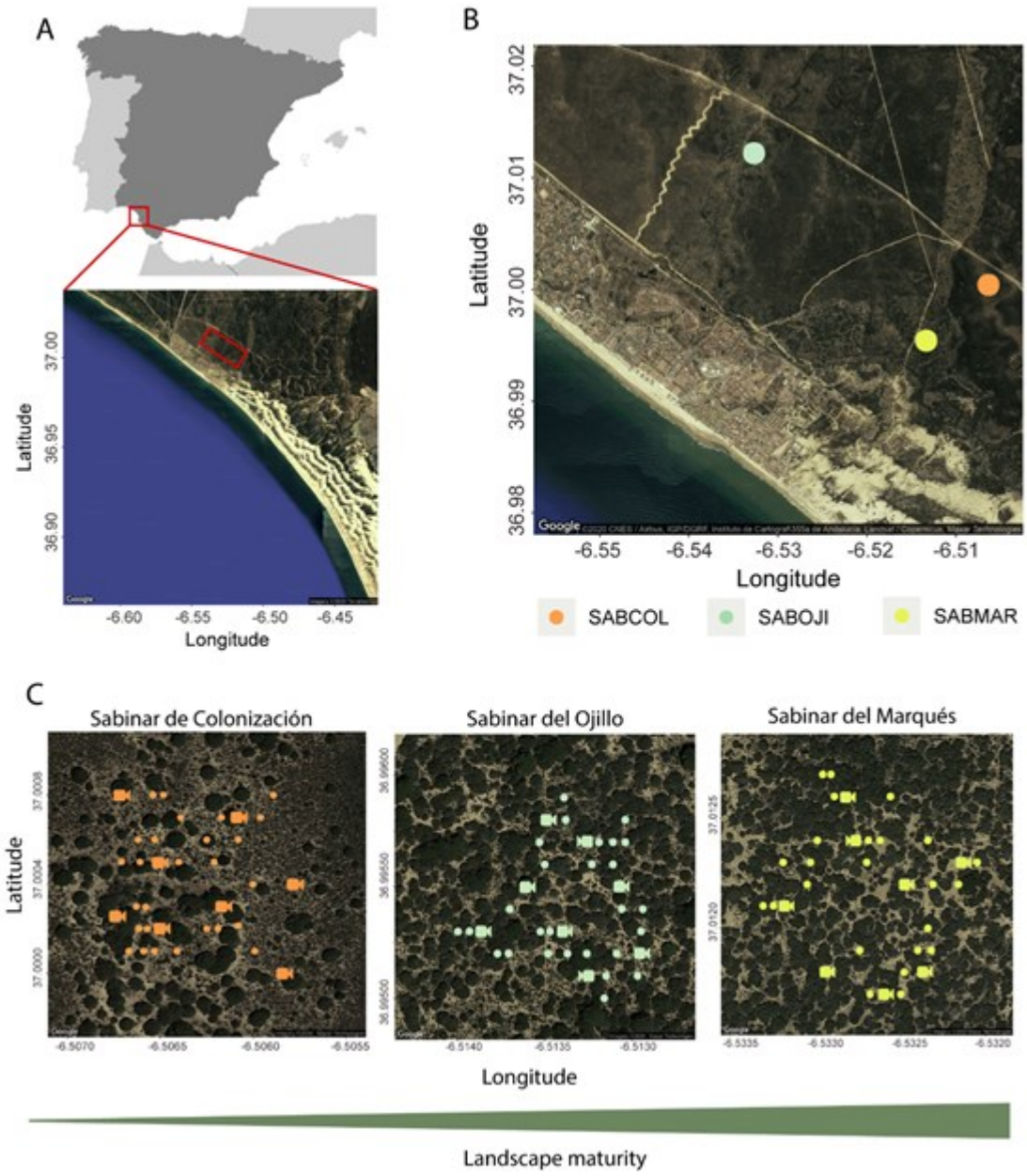
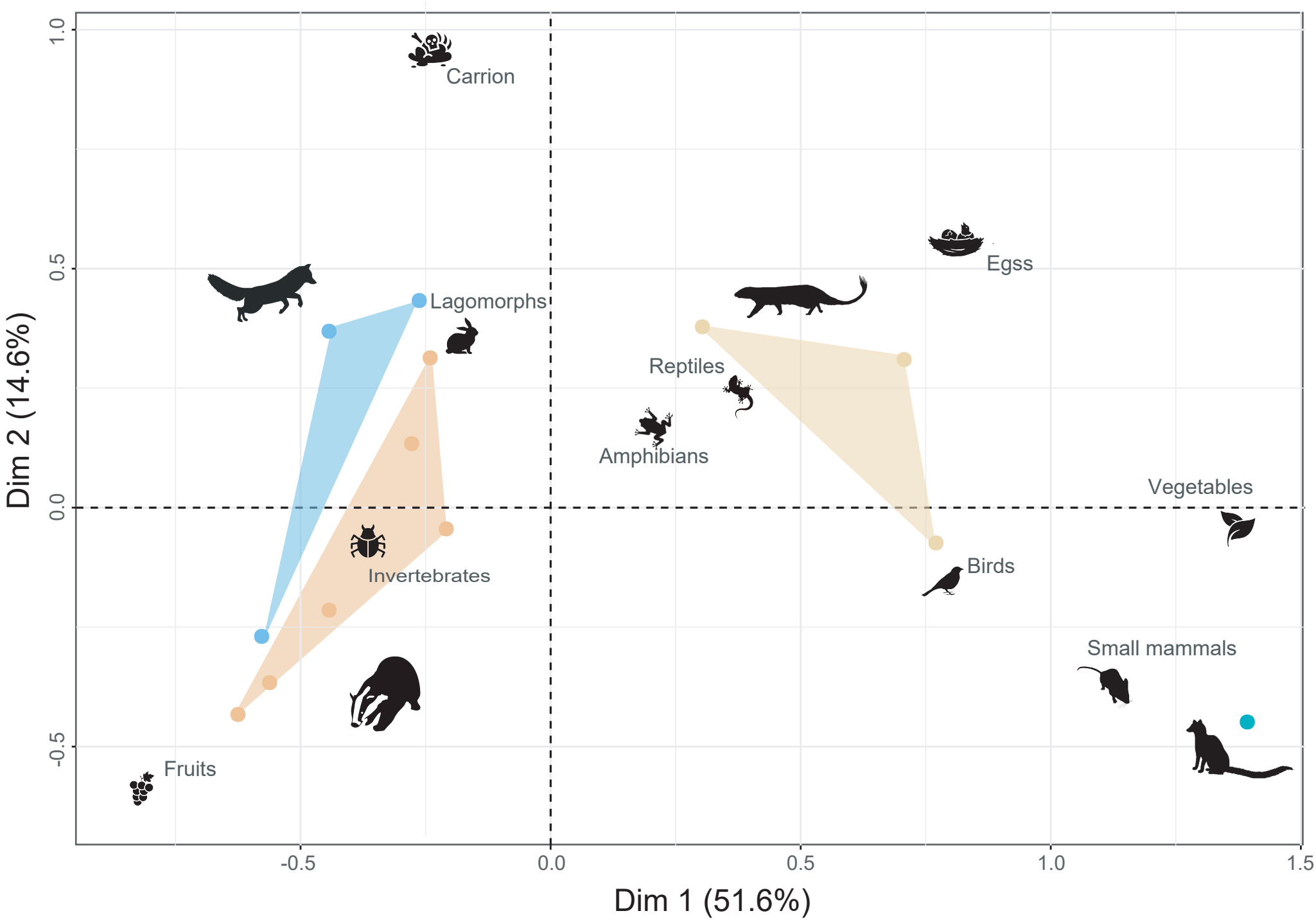


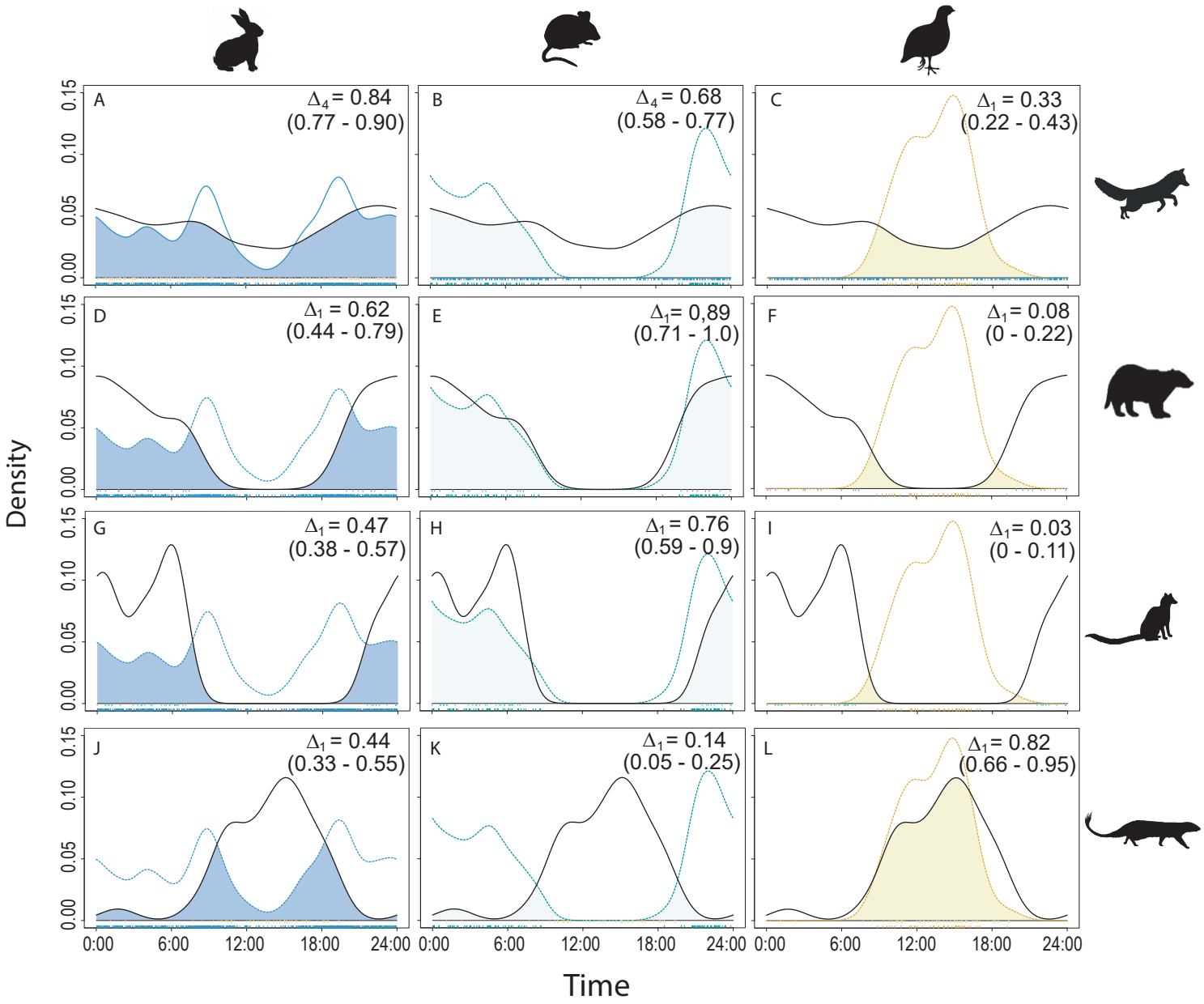
Figure S1. Study area showing: A, location of Doñana National Park and Doñana Biological Reserve (red rectangle); B, location of 3 sites selected (*Sabinar de Colonización* - *SABCOL*, *Sabinar del Ojillo* - *SABOJI* and *Sabinar del Marqués* - *SABMAR*) and C, location of camera trapping stations (points) and set of cameras active for ca. 10 days during a given sampling period.

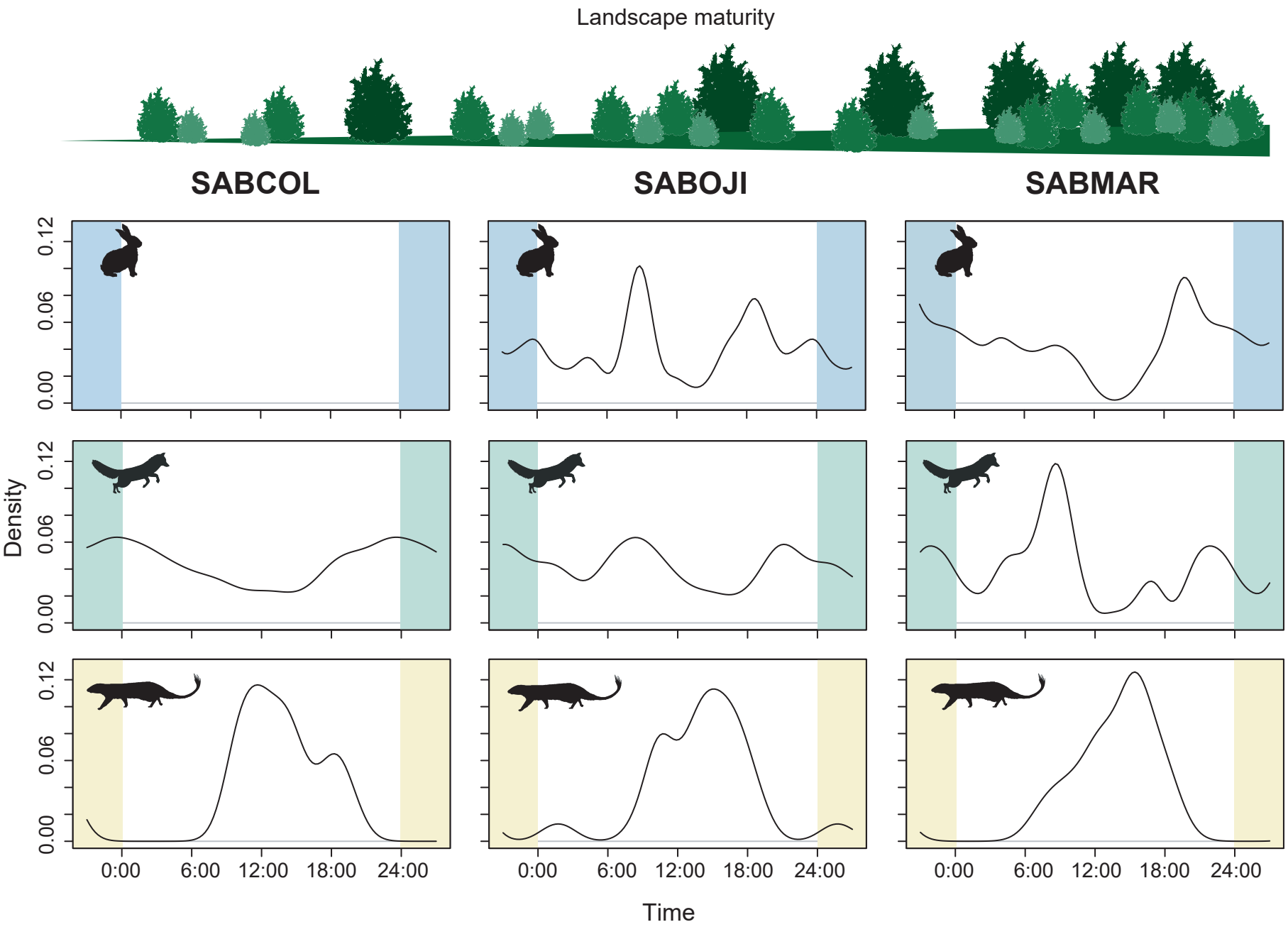
Table S1. Summary of the studies used to carry out the correspondence analysis and explore the trophic relationships between mesocarnivores. Repetition of the studies is due to the different data coming from different areas and/or periods sampled within the same study.

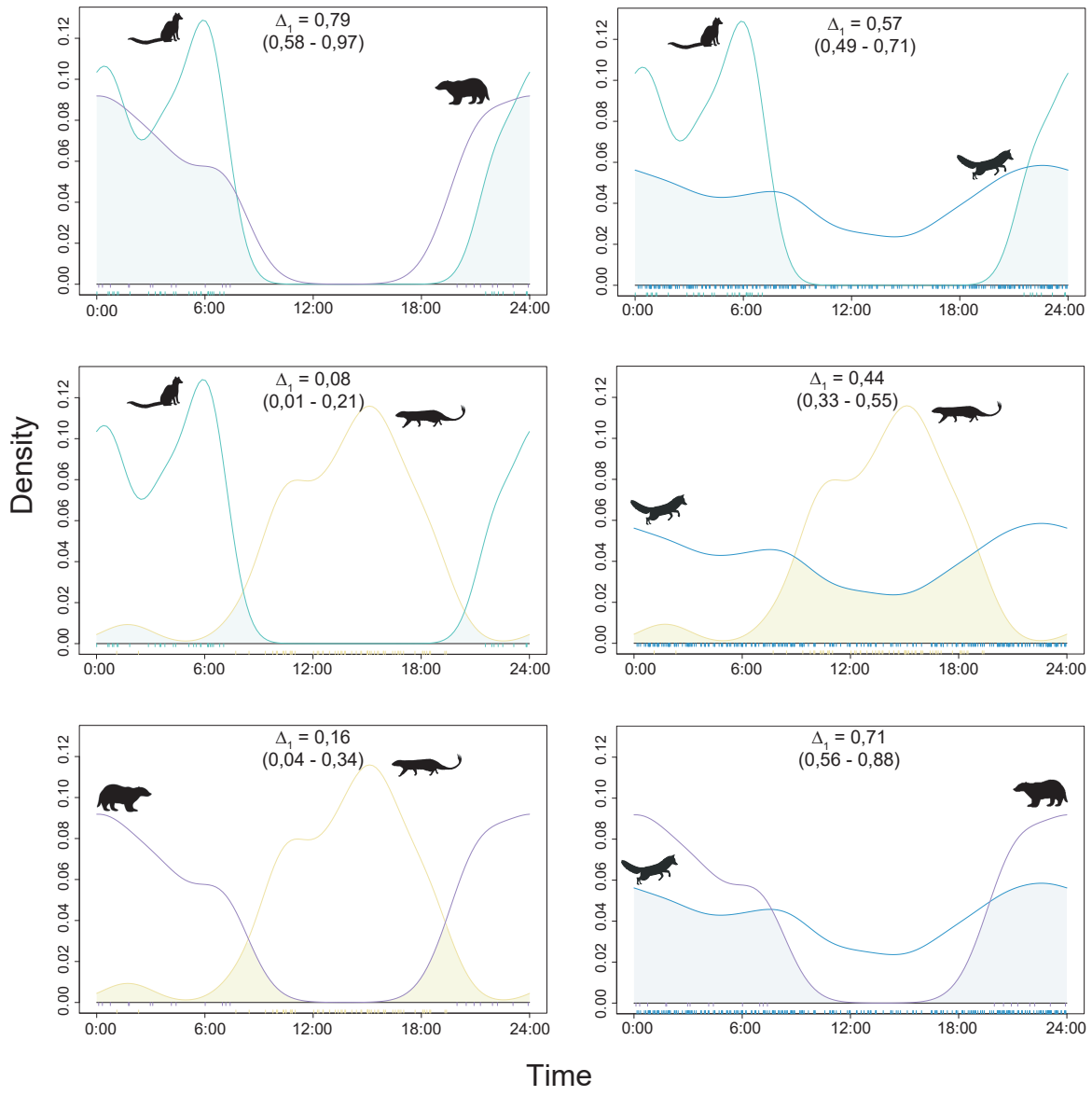
Table S2. Number of detections (N) of target species and trap success measured as number of detections of each species per 100 camera-days for each study site.

Table S3. Number of detections of target species across three sites selected. Dawn: 1 hour before and after sunrise; Day: 1 hour after sunrise until 1 hour before sunset; Dusk: 1 hour before and after sunset; Night: 1 hour after sunset and 1 hour before sunrise. We set sunrise as 8:00:00 and sunset as 20:00:00. Rao Spacing Test significance: p-value <0,01 **; p value <0,05 *. Sampling effort per site reported as mean and standard deviation ($\bar{x}$ ± SD) of camera-days.


Carrion
Egss
Lagomorphs
Reptiles
Amphibians
Vegetables
Invertebrates
Birds
Small mammals
Fruits
1.0
0.5
0.0
-0.5
-0.5
0.0
0.5
1.0
1.5
Dim 2 (14.6%)
Dim 1 (51.6%)


A
Δ_4 = 0.84
(0.77 - 0.90)
B
Δ_4 = 0.68
(0.58 - 0.77)
C
Δ_1 = 0.33
(0.22 - 0.43)
D
Δ_1 = 0.62
(0.44 - 0.79)
E
Δ_1= 0,89
(0.71 - 1.0)
F
Δ_1= 0.08
(0 - 0.22)
G
Δ_1 = 0.47
(0.38 - 0.57)
H
Δ_1 = 0.76
(0.59 - 0.9)
I
Δ_1= 0.03
(0 - 0.11)
J
Δ_1 = 0.44
(0.33 - 0.55)
K
Δ_1= 0.14
(0.05 - 0.25)
L
Δ_1= 0.82
(0.66 - 0.95)
Density
0.00
0.05
0.10
0.15
0:00
6:00
12:00
18:00
24:00
Time


Landscape maturity
SABCOL
SABOJI
SABMAR
Density
0.00
0.06
0.12
0:00
6:00
12:00
18:00
24:00
Time


Δ1 = 0,79
(0,58 - 0,97)
Δ1 = 0,57
(0,49 - 0,71)
Δ1 = 0,08
(0,01 - 0,21)
Δ1 = 0,44
(0,33 - 0,55)
Δ1 = 0,16
(0,04 - 0,34)
Δ1 = 0,71
(0,56 - 0,88)
Density
Time
0:00
6:00
12:00
18:00
24:00
0.00
0.02
0.04
0.06
0.08
0.10
0.12