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

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Abstract

1. 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 often remains unexplored.

2. 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.

3. Temporal overlap between prey and predator and between 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.

4. 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).

5. 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 between generalist species, but also by differences in trophic preferences by specialist species when their activity patterns overlap with other

mesocarnivores. Our findings reinforce that idea that the coexistence mechanisms underlying community structure are multidimensional.

Keywords

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

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 result in niche differentiation (Schoener, 1974). Most studies concerning species coexistence focus 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 & 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 may in turn 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 & Dayan, 2003), which, particularly in carnivores, are shaped by external factors (Monterroso et.al., 2014; Zielinski, 1986), and thus their diel cycle use is context-dependent. 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 nocturnal), compared to allopatric areas where only one fox species is present (Di Bitetti et al., 2009).

In addition, predators' activity patterns could also adjust their daily activity rhythms to those hours of the day in which the availability of prey increases (Foster et al., 2013), while, at the same time, prey species could generate a temporal mismatch by centering their activity at times when there is a lower risk of predation (Fenn & Macdonald, 1995). Consequently, high temporal overlap between carnivores and their putative prey have been reported in some predator-prey systems (Linkie & Ridout, 2011), whereas in others an asynchrony was found in their respective activity peaks (Arias-Del Razo et al., 2011; Díaz□Ruiz et al., 2016). As a consequence, the daily activity of a given predator could be a result of a cost-benefit trade-off between maximizing their activity during periods with high prey availability (benefit) but also higher mortality risk due to encounters with intraguild competitors (cost) (Santos et al., 2019).

Interspecific interactions play an important role in structuring a mammalian community (Holt et al., 1994), especially in carnivores where competition not only arises as a consequence of exploiting the same resource simultaneously, but also due to the risk associated with intraguild predation. Intraguild predation (IGP) is an antagonistic interaction where a predator species kills another predator, or where both species prey upon each other

(Palomares & Caro, 1999; Polis et.al., 1989), being specially reported on top-predators against surrogate competitors (Palomares & Caro, 1999). The IGP's effects in competitors can be diverse, from abundance reductions and distributional shifts (in space and time) (Jiménez et al., 2019; Newsome et al., 2017) to behavioural modifications through restriction of their activity patterns (Wang & Fisher, 2012). Because apex predators play a key role in ecosystem functioning due to their regulatory role on populations of prey and medium-sized carnivores (top-down control), their extinction frequently triggers cascading effects through direct and indirect interactions among trophic levels (Terborgh et. al., 2010). Hence, the collapse of top predators can lead to an eventual increase of the distribution and abundance of medium-sized carnivore populations, a phenomenon coined '*mesopredator release*' by Soulé et al. (1988) that has been repeatedly documented (Prugh et al., 2009; 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., 1998; Palomares et.al., 1996). 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 (Monterroso et.al., 2020; Palomares et al., 1996). 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 in terms of habitat and trophic preferences. This assemblage is completed by the common genet (*Genetta genetta*), with a considerably narrower diet. The negative effects that the Iberian lynx has on these mesocarnivores occur mainly through intraguild predation, particularly on Egyptian mongooses (*Egyptian* *mongoose)*, common genets (*Genetta genetta)* and red foxes (*Vulpes vulpes*) (Palomares et al. 1996, Palomares & Caro 1999, and references therein).

However, IGP interactions between the different mesocarnivores remain quite unknown (Palomares et al., 1996; Valverde, 1957). In areas where the Iberian lynx is not present, coexistence between mesopredators does not seem to be mediated by spatial structuring (Soto & Palomares, 2015) and thus indirect competitive interactions may become more relevant. In this sense, differences in activity shifts of mesocarnivores with similar trophic requirements would alleviate resource overlap. Empirical data in this respect are surprisingly very limited for the Mediterranean area, where situations of mesopredator release may be common due to recent historical reductions in the Iberian lynx populations. Yet, most previous studies have focused on spatial avoidance as the main mechanism allowing the mesocarnivore coexistence, and only recently has the focus shifted towards temporal segregation (Barrull et al., 2014; Monterroso et al., 2014; Vilella et al., 2020).

Hence, the main purpose of this study is to evaluate the ecological factors that allow the coexistence of mesocarnivore species in the Doñana National Park without the influence of a top-predator, focusing on the temporal segregation of four mesocarnivore species: 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 would 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, ranging from mature stands with a higher degree of vegetation cover to an advance front of juniper stands with lower vegetation cover. "*Sabinar del Marqués*" (SABMAR) constitutes the most mature stage with 10520 junipers/ha, "*Sabinar del Ojillo*" (SABOJI) is at an intermediate stage with 9010 junipers/ha, and "*Sabinar de Colonización*" (SABCOL) represents the colonization front stage with 2030 junipers/ha (Supplementary Fig. S1).

Data collection

We deployed eight camera traps per site that were rotated periodically through 35 randomly selected focal juniper plants. Juniper plants were selected at random in each of five subplots within each of the three main sites, with the subplots distributed regularly throughout the main plot. The structure of this habitat consists of paths of variable width between juniper individuals, where the cameras were installed at 1-m height focusing on the ground and the bottom of the plant. Camera trap models employed in this study were Browning Dark Ops Pro XD and Bushnell Aggressor. Camera traps were active for ca. 10 days in each of these rotations and then changed to other 8 locations, thus ensuring that the whole site was sampled in 5 weeks. Following this procedure, we obtained data from a total set of 24 camera traps sampling the three sites during two campaigns: October 2018 - May 2019 and October 2019 - June 2020. No attractants were used over the two years of sampling.

The diel activity cycle of each species was characterized by pooling the total number of detections across all cameras during the whole study period. In order to avoid data dependency, we discarded consecutive detections of a given species within a site (Davis, Kelly, & Stauffer, 2011; Monterroso et al., 2014). When multiple photographs of the same species were taken within a 15-min interval, we considered them as a single capture event to ensure capture independence. Since the area covered by our study sites is limited (ca. 1 ha/site), we deem 15 min a reasonable time period for a species to abandon the site. In cases where a given individual was detected repeatedly without leaving the camera detection zone, only the time of its first detection was considered. In our analyses we used either the total, absolute number of records per species (e.g., to compare the relative frequency of sunrise, day, dusk, and nocturnal records within a given site) or the relative frequency of records expressed as number of photographs per species per camera-day (e.g., when comparing across sites that received different sampling intensity).

Our target species consisted of the four mesopredators which occur in Doñana National Park namely the Egyptian mongoose, the red fox, the European badger and the common genet (Valverde, 1967), and their respective prey species. Large top predators such as the wolf (*Canis lupus*) and the Iberian lynx (*Lynx pardinus*) were not present in our study sites. Potential prey species include lagomorphs (mainly European rabbits, *Oryctolagus cuniculus*), small mammals and birds such as the red partridge *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).

Conversely, we did not have sufficient detections from the other lagomorph present in RBD (*Lepus granatensis*, N = 3) to include them in this study.

Trophic overlap data

We searched on Web of Science (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 (predator species) AND (Doñana), where “predator species” was substituted by one of the mesopredator species considered in this study when performing the search. We also gathered diet data for the common genet by consulting experts (P. Ferreras). The selection of studies contains all the trophic information available for the four species at different locations in the Doñana National Park and reflects the entire trophic spectra of each of the different species (Supplementary Table S1). We collected all food items per species and study without pooling seasons or periods in order to capture the natural variability in dietary composition across the whole Doñana study area and its marked seasonal component.

Some studies reported information collected in previous studies (e.g., Martín et al. (1995) and Fedriani et al. (1998), or Palomares and Delibes (1991b) and Palomares (1993)). To avoid pseudo-replication issues, we kept only those studies where the data strictly belong to different samples and periods. From each study, period and species, we extracted the frequency of occurrence of food items in mesopredator faeces. In order to estimate trophic overlap between mesocarnivores, we carried out a correspondence analysis (CA) using the frequency of occurrence of each prey item for each predator. The CA ordered the different diet studies (cases) relative to the prey species composition reported by each study, resulting in an ordination of the studies corresponding to each mesopredator species based on their similarity of prey species composition. We used the coordinates on the first two CA axes corresponding to each diet study to build convex polygons spanning each mesopredator group of studies. Convex polygons illustrate the range of dietary variation shown by each mesopredator species in relation to the diet composition of other species.

Camera trap data analysis

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

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

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. Following Ridout and Linkie (2009), we used Δ_1 for cases with a sample size lower than 75 detections, and Δ_4 when sample size was 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, we evaluated differences in pairwise comparisons of daily activity patterns using the non-parametric Mardia-Watson-Wheeler test (MWW, Batschelet, 1981). Further, we used percentiles to establish threshold levels of overlap. Thus, $\Delta>$ 75th percentile indicates a high temporal overlap between both species, $\Delta \leq$ 50th percentile a low degree of overlap and, finally, intermediate values of these percentiles, 50th $<\Delta \leq$ 75th, denote moderate levels of overlap (Monterroso et al. 2014).

All analyses were conducted in R Studio 1.2.5033 Statistical Software (R Core Team, 2020). The correspondence analysis (CA) was carried out with "*FactoMineR*" package (Lê, Josse, & Husson, 2008); kernel density functions, overlap coefficients (Δ) and their respective confidence intervals were calculated with the package "*overlap*" (Ridout & Linkie, 2009); MWW and Rao Spacing tests were conducted using the "*circular*" package (Agostinelli & Lund, 2017). Finally, we calculated mean average sunrise and sunset times and performed the average anchoring transformation with the "*activity*" package (Rowcliffe, 2019).

Results

Trophic segregation among mesocarnivores

The first two dimensions of the correspondence analysis explained 62% of the variability of mesocarnivore diets (Fig. 1). Axis 1, which explained 34.5% of the variation, clearly discriminates the trophic preferences of the European badger and the common genet due to their eminently omnivorous and carnivorous diets, respectively, but not from the rest of the mesocarnivores. The red fox and the European badger showed very close values due to their frugivorous behaviour and the predominant consumption of lagomorphs and invertebrates. Meanwhile, the Egyptian mongoose had the wider trophic preferences, with an intermediate position between the omnivorous diets of the European badger and the red fox, and the carnivorous diet of the common genet. Simultaneously, axis 2, which explained 27.3% of the trophic variation, is generated by variation between the diets of the red fox and the common genet, with the latter preferring small mammals followed by birds as main food items. However, the second dimension of the correspondence analysis does not discern between the trophic niches of the red fox, the European badger and the Egyptian mongoose, indicating that there is a greater trophic overlap between these three species with respect to the common genet. Further, convex polygons indicate the ampler trophic diversification of the generalist species (red fox, European badger and Egyptian mongoose) whose range of prey types tends to be considerably wider compared with the common genet (Fig. 1).

Species detections and diel activity patterns

Results obtained in this study come from a total of 531 effective sampling days. All sites were sampled with the same number of cameras per site and a similar sampling effort (number of days): x□ ± SD = 80.3 ± 28.3 d for SABCOL; 80.4 ± 27.3 d for SABOJI and 86.8 ± 26.0 d for SABMAR. Broadly, 2786 detections in total were obtained throughout the study period, of which 96 (3.44%) could not be identified at the species level. Among all detections, 16% corresponded to mesocarnivores, 28.7% to prey species, 15% to ungulates and 38.7% to passeriformes, which were not included in this study (Supplementary Table S2).

Regarding our target species, we recorded 301 detections of the red fox, with 54.8% of them in SABCOL and the rest of the detections evenly distributed between the other two sites (SABOJI: 23.9%; SABMAR: 21,3%). A large amount of the detections obtained from this species were linked to its nocturnal habits while the rest were distributed throughout daylight periods, demonstrating a cathemeral activity pattern with a tendency towards bimodality ($U = 142.26$; p-value < 0.05) (Supplementary Table S3). Conversely, detections of European badgers were very scarce in the three study sites (total: 22 detections), with 77% of the detections occurring at night and the rest during the dawn or dusk periods ($U = 178.95$; p-value < 0.01). As for the common genet, its activity pattern was strictly nocturnal (95% of the records produced during nighttime; $U = 165.81$; p-value < 0.01), with most detections occurring in SABCOL (62% of detections). Finally, detections of Egyptian mongooses were mainly concentrated in the SABOJI (61%) while the other two sites maintained the same proportion of records (ca. 20%), showing a marked diurnal activity pattern in each of them (92% of the detections occurred during daylight; $U = 199.78$; p-value < 0.01) (Supplementary Table S3).

For prey species, most of the detections belonged to the European rabbit ($N = 650$ detections). Rabbit detections concentrated similarly between SABOJI and SABMAR, while SABCOL had only 6 detections during the entire sampling period (Supplementary Table S2).

Overall, the distribution of rabbit detections spanned throughout the day, with distinct activity peaks around sunrise and sunset (U = 156.97; p-value < 0.01) (Supplementary Table S3).

Small mammals (*Mus spretus* and *Apodemus sylvaticus*) were detected 98 times, mainly in SABMAR and only during nighttime (U = 198.27; p-value < 0.01). Finally, red-legged partridges were mostly detected in SABCOL (89% of detections) and showed a markedly diurnal activity pattern (U = 226.53; p-value < 0.01) (Supplementary Table S3).

Predator and prey diel activity patterns

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

We found a high temporal overlap between the activity patterns of small mammals (with most detections at night) and the European badger ($\Delta_1 = 0.89$) and the common genet ($\Delta_1 = 0.76$), respectively. In turn, the red fox showed a moderate temporal overlap with small mammals ($\Delta_4 = 0.68$), while the Egyptian mongoose showed a total temporal segregation with respect to the detected micromammals ($\Delta_1 = 0.14$). Activity patterns of red-legged partridges overlapped with those of the Egyptian mongoose ($\Delta_1 = 0.82$), but not with those of European badgers ($\Delta_1 = 0.08$) and common genets ($\Delta_1 = 0.03$) (Fig. 2).

European rabbit activity patterns differed significantly between SABOJI and SABMAR (W = 32.69; p-value < 0.01) (Fig. 3). Meanwhile, red fox, but not the Egyptian mongoose, showed different responses in terms of diel cycle among sites with different rabbit availability. The red fox showed a predominantly nocturnal activity in SABCOL, where rabbits were absent, and a tendency towards bimodal activity patterns in SABOJI and SABMAR. Red fox activity patterns differed significantly between SABCOL and SABMAR ($W = 11.14$; p-value < 0.01), while no differences were found between SABCOL - SABOJI ($W = 3.97$; p-value $= 0.137$) or SABOJI - SABMAR ($W = 2.44$, p-value $= 0.295$). In turn, no statistically significant differences were found between activity patterns of the Egyptian mongoose between SABCOL - SABOJI ($W = 1.09$; p-value $= 0.58$), SABCOL - SABMAR ($W = 2.06$; p-value $= 0.36$) and SABOJI - SABMAR ($W = 0.40$; p-value $= 0.82$) (Fig. 3). The temporal overlap between the activity patterns of the European rabbit and the red fox was $\Delta_1 = 0.79$ for SABOJI and $\Delta_1 = 0.73$ for SABMAR, while the temporal overlap between European rabbit and Egyptian mongoose was sensibly lower ($\Delta_1 = 0.49$ for SABOJI and $\Delta_1 = 0.37$ for SABMAR) (Fig. 3).

Temporal overlap and segregation between mesocarnivores

The average overlap and standard deviation of the activity patterns of the different species was $\Delta_1 = 0.48$ and $SD = 0.29$, which reflect a low, although variable, temporal overlap among these potential competitors. The average overlap values ($\Delta_1 \pm SD$) of a species with respect to the set of potential competitors were: 0.59 ± 0.15 for the fox; 0.57 ± 0.34 for the badger; 0.50 ± 0.36 for the genet and 0.24 ± 0.18 for the Egyptian mongoose.

Strictly nocturnal species (European badger and common genet) showed a high overlap coefficient and no significant differences between their activity patterns ($\Delta_1 = 0.79$; $W = 1.89$, p-value $= 0.386$). In contrast, the Egyptian mongoose showed a strong and significant temporal segregation with the European badger ($\Delta_1 = 0.16$; $W = 41.75$, p-value < 0.01) and the common genet ($\Delta_1 = 0.08$; $W = 65.79$, p-value < 0.01) (Fig. 4). Simultaneously, we found that the activity pattern of the red fox had intermediate levels of temporal segregation with the common genet ($\Delta_1 = 0.57$; W = 24.96; p-value < 0.01) and the European badger ($\Delta_1 = 0.71$; W = 8.44; p-value = 0.014) and a low overlap with the Egyptian mongoose ($\Delta_1 = 0.44$; W = 73.48; p-value < 0.01) (Fig. 4). Among study sites, temporal overlap between the red fox and the Egyptian mongoose was Δ_1= 0.41 for SABCOL, Δ_1 = 0.45 for SABOJI and Δ_1 = 0.36 for SABMAR (Fig. 3).

Discussion

In this study we explore the mechanisms underlying the structure of Mediterranean mesocarnivore communities living in sympatry in a mesopredator release scenario. We show that mesocarnivore coexistence could be mediated by temporal or trophic segregation when there is a greater overlap in any of these two niche axes. Unlike previous studies which have been traditionally focused on spatial responses (Fedriani et al. 1999, Soto and Palomares 2015, Monterroso et al. 2020, but see Barrull et al. 2014, Monterroso et al. 2014, Vilella et al. 2020), our study provides new insights on the importance of temporal segregation at facilitating co-occurrence by reducing resource overlap. Overall, we found a moderate level of temporal segregation within the mesocarnivore guild in our study area, which was composed by two strictly nocturnal species - the European badger and the common genet (Camps, 2008; Palomares & Delibes, 1994; Rodríguez et al., 1996), one diurnal - the Egyptian mongoose (Palomares & Delibes, 1992) and one with plasticity in its daily activity pattern - the red fox, which ranges from diurnal (Cavallini & Lovari, 1994) to nocturnal habits (Baker et al., 2007).

The highest values of temporal overlap occurred between the European badger and the common genet due to their predominantly nocturnal activity patterns. However, they showed marked differences in their respective trophic niches, mostly because of the preferential consumption of small mammals by the common genet. The common genet consumes almost all species of rodents and insectivores, but it is certainly a specialized predator on *Apodemus sylvaticus* when this prey is available (Palomares & Delibes, 1991a; Virgós et al., 1999). According to the Optimal Foraging Theory (MacArthur & Pianka, 1966), predators maximize its prey intake by showing an efficient foraging pattern. In the case of predators with specialized diets such as the genet, they optimize their foraging behaviour by maximizing synchrony of their daily activity patterns to their main and most profitable prey (Pyke et al., 1977), as shown by our results. 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 for the rest of the mesocarnivores studied.

The three other species that constitute the Doñana mesocarnivore assemblage are known for their generalist feeding habits (Fedriani et al., 1999; Palomares, 1993; Rau, 1987). Yet, we found trophic segregation of the Egyptian mongoose with respect to the red fox and the European badger, 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 antagonistic encounters.

The ecological plasticity and the ample spectra of resource use shown by these species in their trophic and habitat niche axes suggest a scenario with potentially reduced interspecific competition (Fedriani et al., 1999; Monterroso et al., 2020; Palomares, 1993).

However, the temporal segregation of these species may become more relevant in situations where those two niche axes exhibit ample overlap. For example, a reduction in the abundance and availability of its main trophic resources at a given moment may lead to increasing competition for the consumption of available secondary resources. A clear example is the reported reduction in the consumption of European rabbits after a sudden population collapse due to the emergence of the rabbit hemorrhagic disease (RHD) (Ferreras et. al., 2011), which resulted in an increased trophic overlap among most generalist carnivore species. In such cases, time partitioning becomes the main mechanism to facilitate coexistence by reducing competitive stress in resource use among these species (Barrientos & Virgós, 2006).

The European rabbit in the study area accounts for a very high percentage of the diet of Egyptian mongooses (Palomares & Delibes, 1991b) and also for European badgers. Some authors even point out a possible specialization of badgers for this type of prey, a contentious assertion which has been debated (Martín et al., 1995; Revilla & Palomares, 2002). The activity pattern of European rabbits matches those previously reported, showing a bimodal pattern with peaks of activity at sunrise and sunset (Díaz□Ruiz et al., 2016; Monterroso et al., 2013; Villafuerte et al., 1993). However, rabbit availability differed between study sites, with almost no detections in the least mature, early successional juniper colonization front site (SABCOL), and frequent detections in the other more mature sites (SABMAR and SABOJI). Such differences may be due to its habitat requirements since, at the landscape scale, the ideal habitat for rabbits is a juxtaposition of ecological units where the refuge areas are intermingled with others where herbaceous food is more abundant (Dellafiore et al., 2014; Monzón et al., 2004). The colonization site (SABCOL) represents a Mediterranean scrubland in an early ecological stage composed mainly by a low-density population of *J. phoenicea* (2030 junipers/ha) and therefore, a low vegetation cover which does not fulfil rabbit habitat preferences. Meanwhile, SABMAR and SABOJI are sites characterized by late successional mature vegetation and high vegetation cover, which may serve as refuge for rabbits. In these two sites, we found differences between the diel cycle use of rabbits, showing two activity peaks in SABOJI and only one crepuscular activity peak in SABMAR.

Interestingly enough, the activity pattern displayed by the red fox, showed a unimodal pattern with an activity peak around midnight in SABCOL, but shifted towards bimodality in sites where the rabbit was present, putatively to match the activity patterns of this prey and thus increase the probability of encounter. This was particularly obvious in SABOJI, where the temporal overlap between fox activity and that of the rabbits was the highest. Yet, this strategy was less beneficial in SABMAR, where an increase in the red fox activity around dawn may have triggered an anti-predatory behaviour in the European rabbit, which displayed only one activity peak at twilight, thus leading to low temporal overlap. This observation is in line with the Risk Allocation Hypothesis by which a temporal mismatch between activity patterns of a prey species and its predator could be due to a higher perception of mortality risk that drives anti-predatory behaviours along the time axis (Lima & Bednekoff, 1999). Previous studies with Black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*) and the coyote (*Canis latrans*), have shown that lagomorphs are able to shift their activity in order to reduce predation risk by the coyote (Arias-Del Razo et al., 2011).

Dissimilarities in the plasticity of the activity patterns of the red fox and the Egyptian mongoose may be explained by their different foraging strategies. Although, the European rabbit is a profitable prey for the generalist mesopredators in Doñana (Ferreras et al., 2011; Martín et al., 1995; Palomares & Delibes, 1991b; Fedriani, 1996), each predator displays different hunting and consumption strategies of this prey item. Egyptian mongooses and European badgers are species that preferentially consume younger rabbits by digging in burrows (Martín et al., 1995; Palomares & Delibes, 1991b). Conversely, the red fox resorts to a foraging strategy based mainly on the pursuit of prey items, although it also excavates in rabbit burrows (Fedriani et al., 1999). Thus, these distinct foraging strategies could explain why the Egyptian mongoose and European badgers display temporal asynchrony with the prey's activity patterns while the red fox is expected to track and match the activity pattern of its prey.

Hence, our study addresses for the first time the interspecific relationships among the four mesocarnivores species present in Doñana National Park by integrating together the different patterns of daily activity and their respective overlap, as well their trophic ecologies. Yet, these results should be taken with caution as the observational nature of this study does not allow us to establish a clear causal relationship in the observed patterns of the different species (i.e., temporal avoidance between competitors). Future research should address variations in the relative abundance of mesopredators across sites with different rabbit availability. Unfortunately, our sample size was limited to address these questions and we recommend complementing camera trap data with other census methods (i.e. pellet counts or track surveys). Complementarily, 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.

Conclusions

The activity patterns of the different 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 (Fedriani et al., 1999; Palomares & Delibes, 1991c; Soto & 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 multiple axes of the ecological niche. 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 pathways to facilitate sympatry of coexisting mesopredator species. These mechanisms might prove crucial for coexistence in settings where the apex predator is absent and medium-sized carnivores live at high densities and show resource overlap. Recent scenarios of rewilding with top predators may represent ideal conditions to experimentally examine the effects of mesopredator release in diverse carnivore guilds like those of the Mediterranean habitats studied here.

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Author contributions

ABL conceived the original idea; IF collected the diet data, performed the analyses, designed the figures and wrote the first draft of the manuscript; JI and PJ designed the methodology; JI and IF compiled the camera-trap data. All authors contributed to the writing of the manuscript.

Data accessibility

Data and R codes used in this study are deposited in GitHub (https://github.com/IagoFerreiroArias/TempPart)

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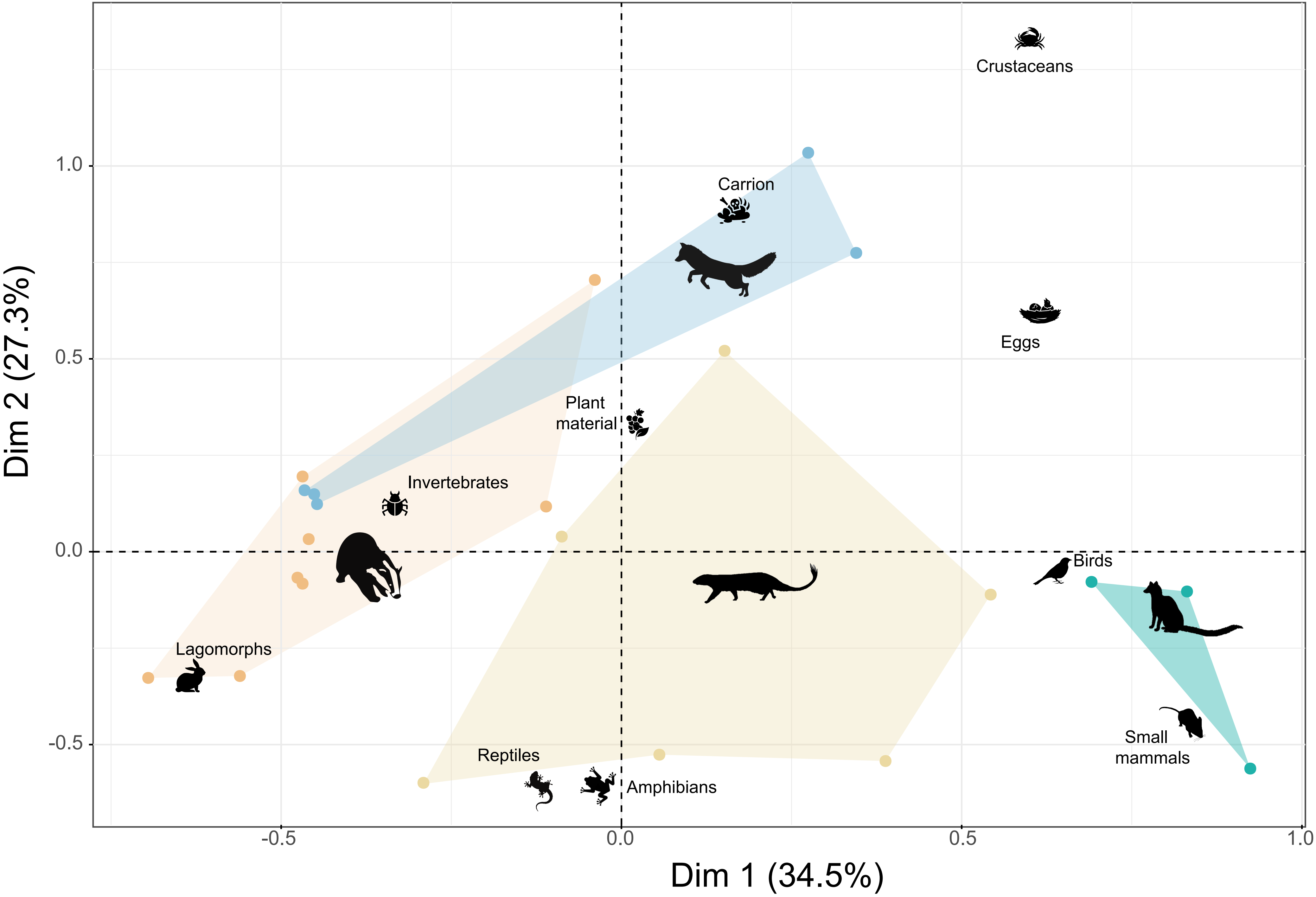
Figures

Figure 1. Niche segregation along the trophic axis among mesocarnivores in Doñana National Park. The first two CA dimensions (Dim 1, Dim 2) explain 66% of the variability in diet composition between species and studies. The first dimension represents a gradient of diet variability between the common genet and the European badger, while the second dimension separates the diet of the red fox and the common genet. Convex polygons represent trophic niche breadth.

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.


Crustaceans
Carrion
Eggs
Plant material
Invertebrates
Birds
Lagomorphs
Small mammals
Reptiles
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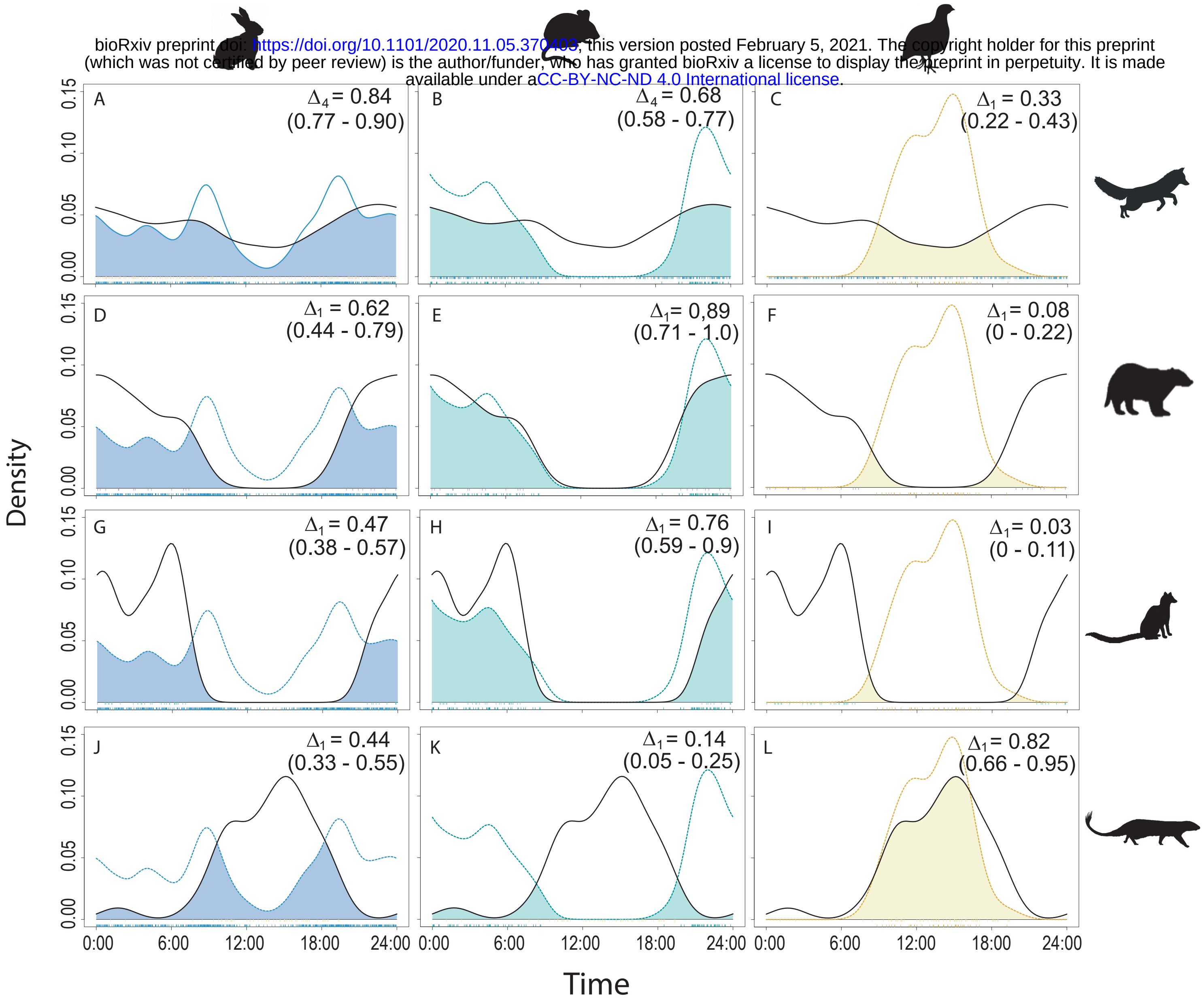
Dim 2 (27.3%)
Dim 1 (34.5%)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B
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(0.22 - 0.43)
D
$\Delta_1 = 0.62$
(0.44 - 0.79)
E
$\Delta_1 = 0,89$
(0.71 - 1.0)
F
$\Delta_1 = 0.08$
(0 - 0.22)
G
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H
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I
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J
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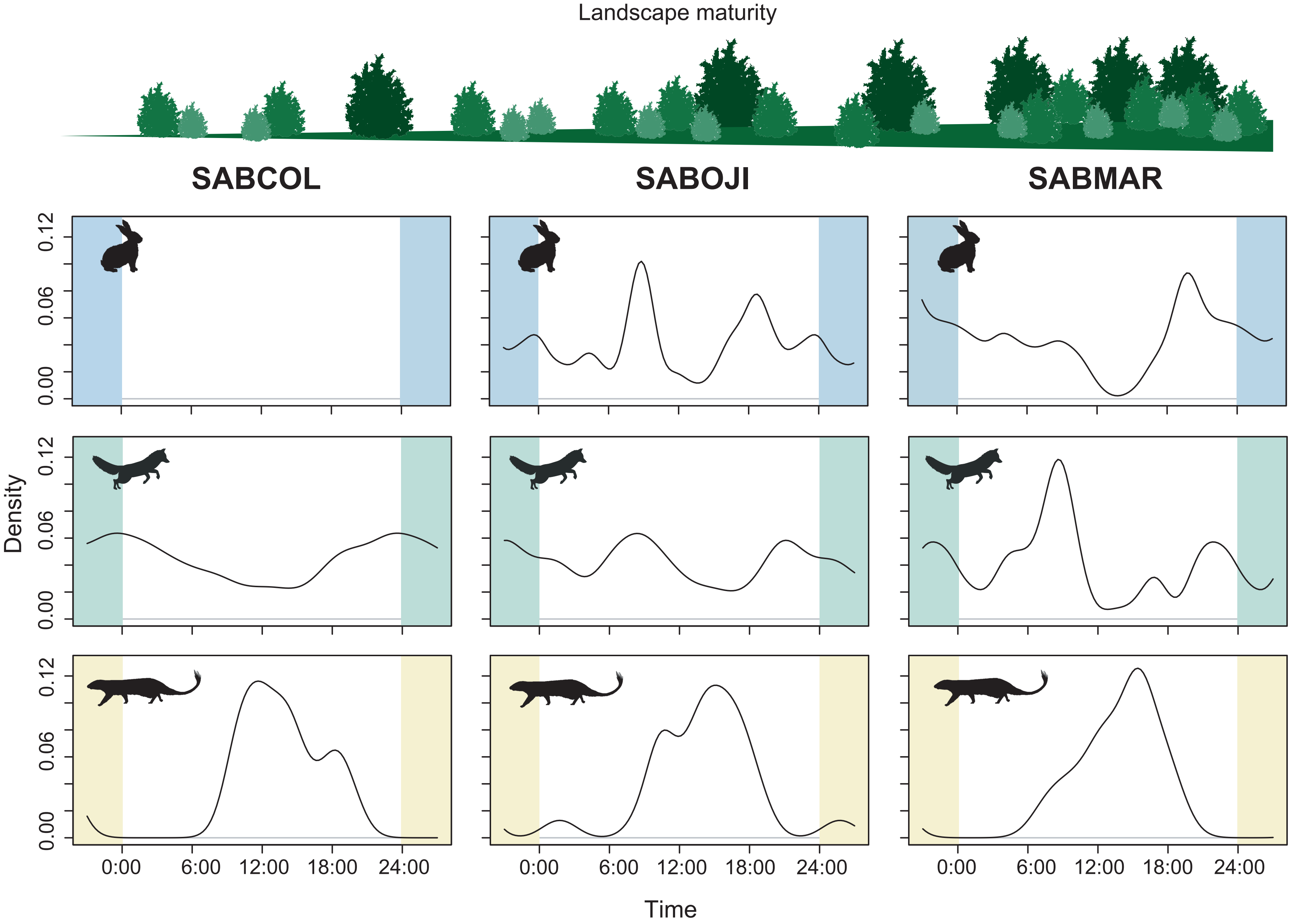
Landscape maturity
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SABOJI
SABMAR
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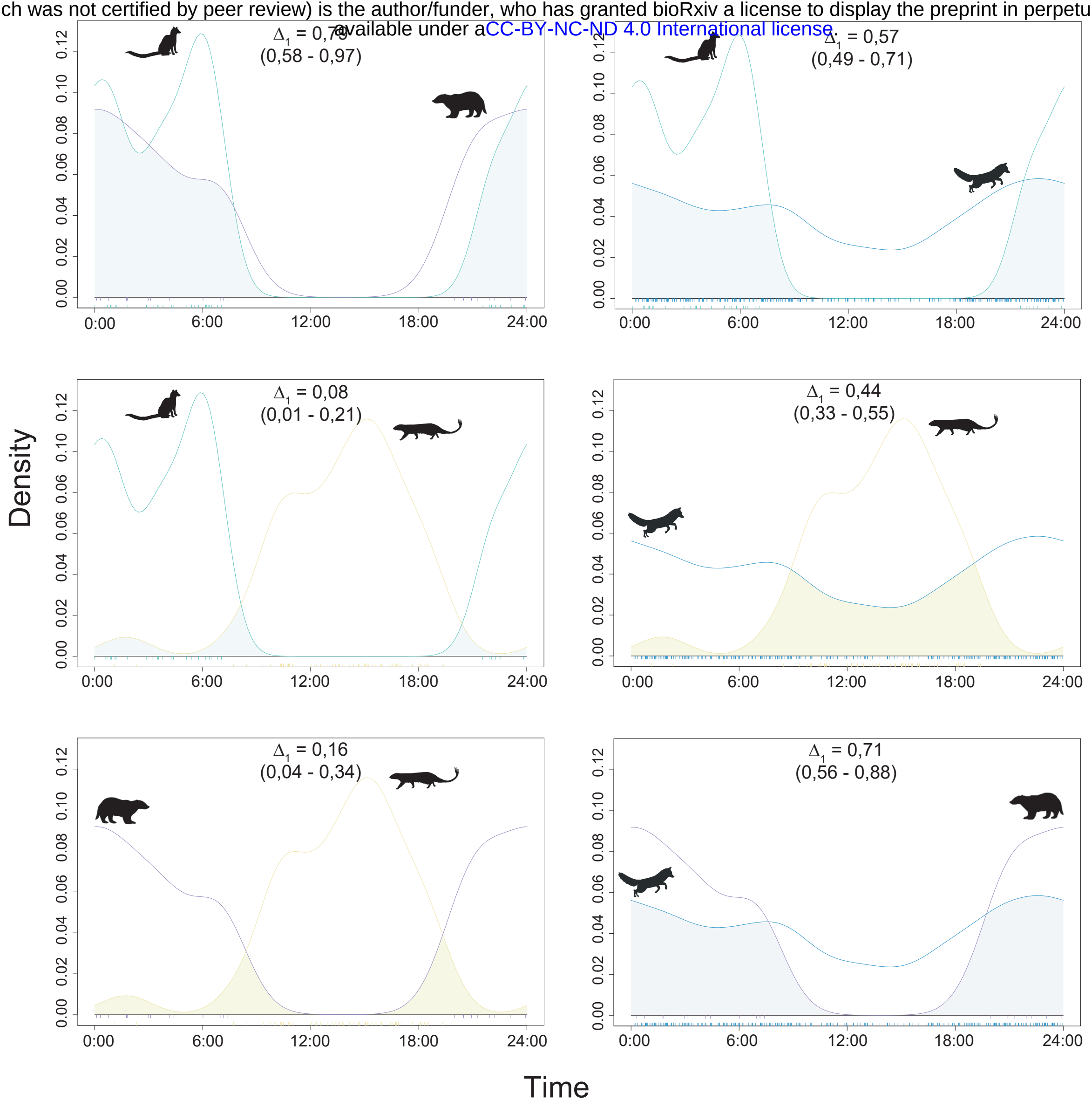
Time


Δ1 = 0,79
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Δ1 = 0,57
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Δ1 = 0,08
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(0,04 - 0,34)
Δ1 = 0,71
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Density
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