

Mediterranean mesocarnivores in spatially structured managed landscapes: community organisation in time and space

Gonçalo Curveira-Santos^{a,b,*}, Tiago A. Marques^{c,d}, Mats Björklund^a, Margarida Santos-Reis^b

^a Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18-D, SE-752 36, Uppsala, Sweden.

^b cE3c - Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências da Universidade de Lisboa, Ed. C2, Campo Grande, 1749-016 Lisboa, Portugal.

^c Centre for Research into Environmental and Ecological Modelling, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, KY16 9LZ, UK.

^d Centro de Estatística e Aplicações da Universidade de Lisboa, Faculdade de Ciências da Universidade de Lisboa, Ed. C6 - Piso 4, Campo Grande, 1749-016 Lisboa, Portugal

E-mail addresses: goncalo-cs@hotmail.com (Gonçalo Curveira-Santos)*; tam2@st-andrews.ac.uk (Tiago A. Marques); mats.bjorklund@ebc.uu.se (Mats Björklund), mmreis@fc.ul.pt (Margarida Santos-Reis).

* Corresponding author.

Abstract

In the multi-functional and biodiverse cork oak landscapes of Iberia (Montado), agro-silvo-pastoral practices promote landscape heterogeneity and create intricate habitat and resource availability patterns. We used camera-traps to investigate the temporal and spatial organisation of a mesocarnivore community in a Montado landscape in central Portugal. The target carnivore assemblage was largely dominated by three generalist species – the red fox *Vulpes vulpes*, the European badger *Meles meles* and the Egyptian mongoose *Herpestes ichneumon* – while remaining community members – the common genet *Genetta genetta* and the feral cat *Felis silvestris* spp. – exhibited restricted distributions. Interspecific differences in activity rhythms and habitat use were particularly marked among widespread species. Low temporal overlap was reported between the diurnal mongoose and predominantly nocturnal red fox and badger. For the latter two species, contrasting differences in habitat use were associated with anthropogenic-induced environmental heterogeneity. Whereas the red fox used more intensively Montado areas preserving dense shrubby understory and avoided semi-disturbed mosaics of sparse shrubs, the badgers displayed the opposite pattern. Our findings add to previous evidence suggesting that the spatial structure created in highly managed landscapes, particularly the diversity of resulting understory structures, promotes the abundance and spread of generalist mesocarnivore species. These may benefit from the surplus of resource amount (e.g. prey) and the creation of different human-made habitats conditions that provide particular combinations of ecological resources favourable to each species requirements. We concur the common view that maintaining understory heterogeneity in Montado landscapes, menaced by current intensification and extensification trends, is important where carnivore persistence is a relevant conservation goal, but alert for potential effects on carnivore assemblages structuring and impacts for specialist species less tolerant to disturbance.

Keywords: Community structure; Carnivora; Agro-Forestry systems; Montado; Landscape heterogeneity; Camera-trapping

1. Introduction

Multifunctional landscapes across the Mediterranean basin harbour a great proportion of this region's biodiversity (Cox and Underwood, 2011). Such biodiversity value is largely associated with the environmental heterogeneity preserved in centuries-old traditional agro-environmental systems, now menaced by intense and rapid environmental, economic and social changes (Pinto-Correia and Mascarenhas 1999, De Aranzabal et al. 2008). Intensification schemes in most productive regions led to the loss of semi-natural habitats while the abandonment of marginal farming areas promoted scrub encroachment and afforestation. These pervasive trends prompted population declines of several species, thus generating a need for management prescriptions most favourable to biodiversity conservation within managed landscapes (Benton et al. 2003, Henle et al. 2008, Wade et al. 2008). However, the implementation of successful agri-environmental schemes is conditional on our ability to foresee how alternative management choices affect the structure and functioning of the system and key functional groups (Benton et al. 2003).

Studies assessing wildlife responses to management options in human-dominated environments (e.g. agricultural landscapes *sensu lato*) often target species richness (e.g. Silva et al. 2008, Godinho et al. 2011, Gonçalves et al. 2011, Leal et al. 2011), or single threatened species (e.g. Lozano et al. 2003, Pita et al. 2006), overlooking guild-level approaches focused on species-specific responses and community organisation. Such knowledge is particularly important for groups of functional importance, such as mammalian carnivores, directly and indirectly associated with biodiversity patterns (Creel et al. 2001, Ray et al. 2005, Prugh et al. 2009, Roemer et al. 2009, Ripple et al. 2014). Iberian carnivore guilds have been the focus of extended research on community structuring processes across space, time, and food resources, in natural or semi-natural habitats (e.g. Fedriani et al. 1999, Carvalho and Gomes 2004, Monterroso et al. 2014). However, less attention was given to carnivore communities exposed to anthropogenic pressures (but see Pereira et al. 2012, Barrull et al. 2013, Cruz et al. 2015), particularly within a context of highly managed landscapes, such as those deriving from agricultural and/or pastoral practices. Anthropogenic-induced environmental heterogeneity may create surplus of resource variety and availability, providing adequate ecological conditions for a wide range of carnivore species (Rosalino et al. 2009, Verdade et al. 2011).

Nevertheless, local carnivore populations may vary in their ability to exploit the existing resources or cope with the associated disturbance (De Angelo et al. 2011). Therefore, augmented environmental heterogeneity may induce differential selective behaviours among sympatric species within the same trophic level, thus altering community organisation patterns (Rosenzweig 1981).

Unique to the Mediterranean region, the Iberian cork oak (*Quercus suber*) and/or holm oak (*Quercus rotundifolia*) woodland - or “Montado” (“Dehesa” in Spanish) – is the last major wood-pasture system in Europe (Blondel and Aronson 1999), representing a sustainable multi-use system well-adapted to the local edapho-climatic constraints. Centuries of agro-silvo-pastoral practices have transformed the native Mediterranean scrubland into spatially complex agroecosystems, where extensive and heterogeneous cork/holm oak woodlands, shaped by different management options (e.g. grazed and non-grazed areas), are interspersed with other production lands and remnant semi-natural vegetation (Pinto-Correia and Mascarenhas 1999). Management actions within oak woodlands prevent shrub encroachment, either by grazing or mechanical means of varied intensity, while dense vegetation is preserved in less accessible areas or those set aside for wildlife conservation; thus creating highly heterogeneous and spatially structured landscapes mainly in regard to differences in understory structure and density. This variety of cover types (compositional heterogeneity) and their intricate spatial patterning (configurational heterogeneity) promotes complex habitat mosaics and resource availability patterns (Farhig et al. 2011), the maintenance of which depends on continuous management at the farmstead level (Gonçalves et al. 2011). Due to its structural complexity, the Montado agroecosystem holds high species richness and maintains a balance between human activity and biodiversity preservation, being recognized as a high nature value farmland (Pinto-Correia and Vos 2004).

In spite of carnivores being reported as sensitive to human disturbance (Gittleman et al. 2001) all ten mesocarnivore species with resident populations in southern Portugal persist in the intensively managed Montado landscapes (Santos-Reis et al. 1999). Nonetheless, most studies aimed to understand how human-induced environmental heterogeneity relate to carnivore diversity patterns (Pita et al. 2009, Rosalino et al. 2009, Gonçalves et al. 2011), while anthropogenic influence as a community-structuring force within carnivore assemblages remains unclear. Here, we investigated the

spatio-temporal structure of a mesocarnivore assemblage in a Montado farmstead in central Portugal. We assessed interspecific differences among coexisting species in circadian activity and habitat use to reveal how community organisation patterns relate, directly or indirectly, to features of a landscape shaped by management actions. Specifically, we hypothesized: i) activity and temporal overlap patterns to be similar to reports for other Iberian natural and semi-natural areas (Monterroso et al. 2013, 2014), in accordance with our target species behavioural habits and low levels of direct disturbance in the study area; and ii) the existence of interspecific differences in habitat use patterns, reflecting each species ecological requirements, i.e. a community exhibiting a spatial structure supported by human-induced environmental heterogeneity.

2. Materials and methods

2.1. Study area and target community

This study was conducted in the forested area (“Charneca” – 100 km²) of the largest agro-forestry farmstead in Portugal - Companhia das Lezírias S.A. (180 km²). The study area is representative of the agro-silvo-pastoral cork-oak systems with a vast geographic extension across the Mediterranean basin (Aronson et al. 2009). The farmstead has been intensively managed since its foundation in 1836, in the Charneca primarily for silviculture and pastoral practices, and varied management options gave rise to a complex and heterogeneous landscape (Fig. 1). The cork oak Montado woodland (~61 km²) is the dominant land-cover, occurring in pure or mixed patches with maritime pine (*Pinus pinaster*), and with variable composition and density of understory structures (dense, sparse and absent; Fig SA1). This mosaic is complemented by interspersed maritime pine stands (~14 km²), and scattered patches of eucalyptus (*Eucalyptus globulus*) and scrublands. Croplands (rice fields and irrigated plots) cover the remaining area (Gonçalves et al. 2011). More than 35 km of watercourses cross the study area, of which ca. 11 km are permanent and associated with fully developed arboreal and shrubby strata of riparian vegetation (Ferreira and Aguiar 2006). The majority of the forested area (~55 km²) is used for biological cattle raising. From late September until late February/March, around 1,500 cows roam within the “Charneca”, organized into 50-300 head herds that rotate among grazing plots of up to 4 km² (Gonçalves et al. 2011); in Spring cattle are

guided to the farmstead's marshy areas (called "Lezíria", c.a. 20 km North-east), with richer soils and pastures, where they reside until late Summer.

The study area supports a diverse mesocarnivore community, including eight out of the ten mesocarnivore species occurring in the Portuguese Montado (Santos-Reis et al. 1999, Gonçalves et al. 2011). Our target community comprised the five most abundant species found locally (Gonçalves et al. 2011): two native species (red fox *Vulpes vulpes* and European badger *Meles meles*), two exotic, naturalized, species (common genet *Genetta genetta* and Egyptian mongoose *Herpestes ichneumon*), originating from Africa (Gaubert 2016), and the feral cat (*Felis silvestris* spp.). The designation "feral cat" arises from uncertain species identification in a population of wild-phenotype cats roaming free across the landscape, independently of human settlements, and includes genetically confirmed first generation hybrids of European wildcat (*Felis silvestris silvestris*) and its domestic counterpart (*Felis silvestris catus*) (Gonçalves et al. 2011).

2.2. Carnivore sampling

From November 2013 to March 2014, we monitored the activity and use of space of local mesocarnivores with camera-trapping surveys. Carnivore surveys were constrained to the Autumn-Winter period due to logistic limitations. We used 54 passive infra-red cameras placed individually in trapping stations evenly distributed across the landscape according to a stratified approach based on land-cover representativeness of main habitat types (Fig. 1). Distance between trapping stations averaged 836 m (SD=169 m; max=1445 m; min=576 m). No bait was used but cameras were positioned on animal trails, attached to trees or artificial stakes at 30-40 cm above ground level (Swann et al. 2004). To facilitate species identification, cameras were set to take three sequential photographs once triggered (at 1 s intervals). Consecutive records of the same species at the same site were deemed independent when there was at least 30 min interval between them, unless multiple individuals could be distinguished by appearing simultaneously in the same photograph sequence. This independence interval was chosen following previous studies (e.g. Davies et al. 2011) and ongoing work on guild specific independence intervals suggesting short permanence time for carnivore species (J. Sanderson, pers. comm.). Cameras operated for the entire study period and

trapping stations were visited every 15 days for camera verification and battery/memory card replacement. Sampling effort resulted in a total of 6,496 effective trap-days (average trap-days / station =120, SD=11).

2.3. Diel activity patterns and temporal overlap

Date and time were recorded for each independent photograph. Capture times were converted to solar time to facilitate ecological interpretation (Foster et al. 2013). Each record was regarded as a random sample belonging to an underlying distribution, describing capture probability as a function of time of day. The correspondent probability density function of this distribution represents the activity pattern and was estimated non-parametrically using a kernel density approach (Ridout and Linkie 2009). As a complement to estimated activity curves, we used Jacob's selectivity index (JSI, Jacobs 1974) to analyse individual species strength of selection for specific periods of the diel cycle - Night, Day, Dusk, and Dawn; as defined in Foster et al. (2013) (Supp. Table 1).

Temporal overlap was assessed on species pairwise comparisons of activity patterns using the species pair overlap coefficient $\Delta 1$ (Ridout and Linkie 2009): $\Delta 1$ ranges from 0 for no overlap to 1 for complete overlap. Estimator 95% CIs were obtained as percentile intervals from 500 bootstrap samples. Analyses were implemented in R V.2.15.1 (R Development Core Team 2011, Vienna) using available scripts from Ridout and Linkie (2009). We consider three qualitative classes of overlap as defined by Monterroso et al. (2014): "Low" ($\Delta 1 < 0.66$); "Moderate" ($0.66 \leq \Delta 1 \leq 0.76$) and "High" ($\Delta 1 > 0.76$). Reference values 0.66 and 0.76 correspond respectively to the 50th and 75th percentiles of an overall sample of pairwise comparisons obtained from activity patterns of Iberian mesocarnivores across several locations and seasons.

2.4. Patterns of habitat use

We used N-mixture models (Royle 2004, Royle et al. 2005) to infer habitat use patterns from the relation between a set of environmental covariates and space-use estimates of each target species, while accounting explicitly for variations in detectability, i.e. formally accommodating the imperfect detection process underlying the collection of animal counts. N-mixture models are a class of

hierarchical models that use spatio-temporal replicated count data to simultaneously model spatial variation in abundance and detection error (see Methods [Royle 2004, Royle et al. 2005]). We produced species-specific detection histories, using the number of independent captures over nine consecutive 14-day sampling occasions, to generate the basic count matrix. The count n_{ij} on trap i ($i=1,2,\dots,54$) and occasion j ($j=1,2,\dots,9$) was given by the sum of random variables x_{dij} representing the number of independent captures on day d at trap i and occasion j , i.e. $n_{ij}=\sum_{d=1}^{14} x_{djk}$. Periods with incomplete sampling days due to camera malfunction were assigned a “missing value (NA)” status, albeit less than 0.05% of all sampling periods. We modelled spatial variation in “abundance” states (λ) using the negative-binomial variant of the N-mixture model to better accommodate extra-Poisson variation present in our data.

Habitat use patterns (habitat selection) manifest in distinct ways and are inherently dependent on the scale of analysis. Since we sampled at a fine spatial scale while focusing on generalist species capable of exploiting a variable habitat set, differential habitat preferences can occur as a function of distinct levels of habitat use intensity; i.e. differences in the frequency of use of different habitats between species spatially co-occurring across the landscape. Although parameterized originally to represent local population size, λ does not need to be interpreted as abundance per se (Mackenzie et al. 2006). Irrespectively of the number of individual animals generating the counts at each site, λ estimates can be interpreted as a relative measure of intensity of habitat use for a given species. It is possible to accommodate spatial variability in λ by modelling this surface as a function of environmental covariates, allowing identifying the main predictors of a species’ pattern of habitat use. To make interspecific comparisons possible, despite the subjective nature of this measure, we adopted a conservative approach focused on parameters influencing the estimates obtained rather than the estimates themselves.

2.4.1 Environmental covariates

Literature-based ecological requirements of the target species were taken into consideration to select a set of predictor variables of mesocarnivore patterns of habitat use. We divided covariates into

three categories: 1) HABITAT (land-cover features pertinent for refuge, resting and foraging); 2) DISTURBANCE (relevant local sources of anthropogenic-derived pressure that may influence species behaviour); 3) PREY (availability of key food resources) (see Table 1 for a full description).

Covariates were measured within a 325 m radius buffer around each camera-trap station to reflect species preferences at the core-area level, considering the minimum mean core-area size described among target species (0.34 km² for the common genet, Santos-Reis et al. 2004).

Habitat covariates were collected as the land-cover proportion of the six main habitat types, based on a GIS database available for the study area (see Gonçalves et al. 2011 for details on land-cover data); updated in September 2013 to include landscape changes resulting from recent management actions (Fig. 1). Land-cover metrics were obtained using software Quantum GIS (version 1.8.0 Lisboa). A principal component analysis (PCA, Zuur et al. 2007) was used to reduce dimensionality of HABITAT covariates. PCA scores of the three first axes, explaining 92% of the total variance, were incorporated as predictors in the modelling process (Supp. Table 2, variable loadings presented in Table 1): PC1 captures the contrast between Montado with dense (+, i.e. positive loadings) and sparse (-, i.e. negative loadings) shrubs; PC2 reflects the contrast of Montado with shrub cover (dense or sparse, +) and absent understory (-); PC3 contrasts Montado areas (+) with other habitats (pine stands and scrublands, -). Due to the ecological relevance of riparian vegetation (Matos et al. 2009, Santos et al. 2011), it was included as a separate covariate within the HABITAT category, despite its reduced land-cover representativeness. Additionally, the Simpson's Landscape diversity index was computed as a quantitative measure of habitat heterogeneity.

To complement the indirect effect of anthropogenic disturbance represented in land-cover variables, we included a covariate representing cattle presence during the sampling period, the most relevant source of direct disturbance. With this variable we intended to account for possible avoidance behaviours of carnivores to cattle presence (Mullen et al. 2013). Movement of herds inside the “Charneca” is registered by the farmstead’s Agricultural Livestock Department, which contains information on each herd and issues a control map every time a herd is transferred to a new plot. Cattle presence at the plot level was calculated, given by the number of livestock units (*LSU*) placed in a grazing plot of known size (ha), during a known number of days (*n_days*), according to the equation

$LSU/(ha \times n_days)$ (Gonçalves et al. 2011). LSU indexes were calculated for plots partially contained within the camera-traps buffer and for the survey time span (see Table 1).

Prey variables reflect relative abundance of main prey species - European rabbits (*Oryctolagus cuniculus*) and small mammals - of the majority of the target mesocarnivores (Santos et al. 2007, Delibes-Mateos et al. 2008a). Rabbit relative abundance was estimated through latrine counts (Beja et al. 2007) in fixed 500 m transects per each 1×1 km UTM quadrats covering the entire study area in November 2014, presented as a kilometric index of abundance. Relative small mammal abundance was estimated from 2013 live-trapping surveys, performed according to a stratified sampling scheme based on main habitat types' representativeness (Gonçalves et al. 2011).

Covariate relationships were assessed by pairwise Spearman's correlation. For highly correlated pairs ($r>0.7$) the less biologically meaningful variable was discarded to avoid multicollinearity among predictor variables (Dormann et al., 2013). This led to the removal of small mammal abundance predictor, highly correlated with PC1 ($r>0.9$) (Supp. Table 3).

2.4.2. Modelling procedure

The modelling procedure followed a two-step approach. First, we assessed individual HABITAT and DISTURBANCE covariates influence on detection probability while keeping λ constant, i.e. $\lambda(\cdot)$, $\rho(\text{covariate})$. Second, the best-fitting detection model was kept fixed and combined with candidate models representing realistic biological hypotheses (sensu Burnham and Anderson 2002) regarding covariates possibly influencing mesocarnivores' intensity of habitat use. The candidate model set included, the null model (λ constant), univariate models of HABITAT, DISTURBANCE and PREY covariates, and combined models of HABITAT and covariates of remaining categories (see Supp. Table 4). Prior to model selection, we used the Pearson chi-square statistic (1000 parametric bootstrap samples) to assess the goodness-of-fit of the most parameterized (global) model. Provided models exhibited good fit, models were ranked according to the Akaike Information Criterion corrected for small sample size (AICc), and parameter estimates averaged for models with $\Delta AICc < 2$ (Burnham and Anderson 2002). Otherwise, AICc was adjusted for an over-dispersion factor (\hat{c}) and the Quasi-AICc (QAICc) was used (Mackenzie and Bailey 2004). Spatial

autocorrelation in species counts was not accounted for in modelling, as no evidence for a significant spatial structure was found in a preliminary analysis based on the Moran (I) index (Moran 1950). The effect of covariates included in the most parsimonious models was considered to be well-supported when 90% unconditional CIs of the averaged beta coefficient estimates did not overlap zero. The same procedure was repeated for each target species. N-mixture models were implemented in R V.2.15.1 (R Development Core Team 2011, Vienna) using the ‘unmarked’ package (Fiske and Chandler 2011).

3. Results

A total of 1,645 independent captures of the targeted mesocarnivore species was obtained over 6,496 effective trap-days (25 captures / 100 trap-days). Three species, the red fox (623 captures), the European badger (554 captures), and the Egyptian mongoose (303 captures), were widespread in the study area (naïve occupancies > 0.8). In contrast, genets (97 captures) and feral cats (68 captures) were captured at low rates, in less than 40% of the trapping stations.

3.1. Diel activity patterns and temporal overlap

Species activity patterns are depicted in Fig. 2 (see Supp. Table 1 for JSI results). Apart from the mongoose, that showed diurnal activity (JSI Day = 0.61), other species displayed predominantly nocturnal habits; either exclusive (badger and genet [JSI Night > 0.70], with limited activity at dusk), or complemented by the use of crepuscular periods (red fox [JSI Night = 0.46; JSI Dusk = 0.24]). Despite sharing a negative preference for the daytime period, feral cat activity across remaining diel cycle periods lacked any strong selection patterns (JSI's < 0.30), suggesting a cathemeral behaviour.

Regarding interspecific pairwise measures of activity overlap (Fig. 3), low temporal overlap was observed between the mongoose and all other species, as expressed by the low $\Delta 1$ values (range $\Delta 1 = 0.12 - 0.43$). Among mesocarnivores exhibiting a pronounced nocturnal behaviour, $\Delta 1$ values ranged from 0.67 (moderate overlap) to 0.91 (high overlap). Moderate temporal overlap was found between badgers, the species with the strongest nocturnal habits, and the feral cat ($\Delta 1 = 0.67$) and the red fox ($\Delta 1 = 0.74$), mesocarnivore species with crepuscular behaviour and some day time activity. All remaining species pairs showed high levels of activity overlap ($\Delta 1 = 0.80$).

3.2. Patterns of habitat use

Goodness-of-fit tests for all species, except the badger, suggested the models fit the data adequately (p-values > 0.1) and therefore AICc values were used. The global model of badger habitat use revealed a significant lack of fit (p-value < 0.05) and a considerable degree of over-dispersion (\hat{c} = 1.97), hence QAICc was used for this species.

We identified “HABITAT” effects for the detectability of four species (Table 2, Supp. Table 5). Riparian vegetation cover was positively associated with detection probability of red foxes, mongooses and genets. Badger detectability related to contrasts in understory cover between Montado patches coded in the covariate PC2, being higher in Montado patches with absent understory. Feral cat detection probability was negatively influenced by the presence of cattle in the vicinity of the camera-station.

Habitat use models for target mesocarnivore species revealed distinct interspecific habitat preferences (Table 2, Supp. Table 5). HABITAT covariates were included in the most parsimonious models for all species. Model-averaged estimates supported the contrasting effects of PC1 on foxes and badgers, with estimates of fox habitat use intensity increasing with cover of Montado patches with dense shrubby understory and decreasing in Montado areas with sparse shrubs, while the reverse was found for badgers. Riparian vegetation cover was positively selected by both the red fox and the genet. For the latter, cover of riparian stretches was the only suitable factor explaining this species habitat use patterns, with a marginally well-supported effect. Landscape diversity had a well-supported influence on two species, with badgers favouring homogeneous areas and mongooses preferring heterogeneous sites. Although present in some of the most parsimonious models, the large SEs obtained for the remaining HABITAT variables (i.e. PC2 and PC3) hindered the accurate assessment of these predictors influence. Concerning prey variables, model-averaged estimates revealed a positive and strong effect of local rabbit abundance on habitat usage intensity estimates of the red fox, mongoose and feral cat. For the feral cat, rabbit abundance was the only suitable predictor. Finally, cattle presence had a well-supported negative influence on habitat use intensity estimates of the red fox, while not showing any relation with other species habitat preferences.

4. Discussion

Our results allowed the identification of spatio-temporal community organisation patterns, mediated by interspecific differences in activity and habitat use among local mesocarnivores. The three most widespread and dominant predators in the area – foxes, badgers and mongooses – exhibited distinct preferences for the diel cycle periods, with moderate to low levels of temporal activity overlap, and contrasting differences in habitat use, closely associated with anthropogenic-induced environmental heterogeneity. Remaining community members, which exhibited restricted distributions, denoted high temporal overlap and similar habitat preferences with more common species. These findings exemplify how heterogeneous agroecosystems may favour the persistence of generalist Iberian carnivores at high local densities (Pita et al. 2009, Sobrino et al. 2009) and add to the existing body of evidence advocating the functional ecological role of fine-grained habitat complexity for Mediterranean mammals in human-dominated environments (Mangas et al. 2008, Muñoz et al. 2009, Rosalino et al. 2009, Gonçalves et al. 2011).

4.1. Spatio-temporal organisation of the Mesocarnivore community

Observed patterns of target species activity were consistent with previous findings obtained in Iberian natural and semi-natural habitats, with species falling into three separate classes from a behavioural perspective (Monterroso et al. 2014): diurnal - mongoose; facultative nocturnal – red fox and feral cat; strictly nocturnal - badger and genet. These differential activity rhythms along the diel cycle translated into the low or moderate temporal overlap observed in six out of 10 pairwise comparisons, mainly associated with the contrasting diurnal habits of mongooses relative to the other species. Foxes differed from badgers in their increased use of crepuscular periods, possibly to track the activity of the European rabbit (Monterroso et al. 2013). Furthermore, partially asynchronous activity peaks between most target mesocarnivores suggest a sequential use of the diel cycle (Di Bitetti et al. 2010), possibly to reduce direct interference. Similar temporal overlap patterns have been reported for other Mediterranean mesocarnivore communities and interpreted as behavioural strategies of temporal niche partitioning (Monterroso et al. 2014); a process suggested to promote competitive coexistence

within carnivore assemblages (Schoener 1974, Ritchie and Johnson 2009, Di Bitetti et al. 2010, Gerber et al. 2012). Nevertheless, the functional implications of the observed temporal preferences in the context of intraguild relationships may depend on species-specific strategies (e.g. diet and foraging strategies) and do not necessarily translate responses to competitive interactions.

All mesocarnivore species exhibited unique combinations of environmental covariates driving their patterns of habitat use, a fact suggesting that species-specific habitat preferences are spatially structuring the local community. Nevertheless, rabbit abundance had a pervasive positive effect on the spatial patterns of three species, the red fox, mongoose and feral cat. This corroborates the previously described role of rabbits as the main prey species of mammalian predators in the Iberian Peninsula (Delibes-Mateos et al. 2008a) and indicates mesocarnivores in our study area indirectly benefit from management practices directed at promoting rabbit populations (e.g. management for heterogeneous habitats and supplementary feeding; Delibes-Mateos et al., 2008b).

The red fox and the badger displayed the most contrasting habitat preferences, associated with variable understory density within the Montado matrix. Whereas the red fox used more intensively Montado patches preserving a dense understory, and less frequently semi-disturbed areas with sparse shrubs, badgers displayed the opposite pattern. Despite the recognized importance of shrub cover for Mediterranean carnivores (Mangas et al. 2008, Gonçalves et al. 2011), above a certain threshold of understory density, distinct species may profit from variable shrub structures in dissimilar manners. Distinctive understory cover promotes differential patterns of prey availability. While denser understories increase the diversity and abundance of small mammals (Muñoz et al. 2009, Gonçalves et al. 2011), an important item in fox's diet (Santos et al. 2007), ground-beetle abundance was shown to be higher in semi-disturbed mosaics of cork-oak woodlands (Silva et al. 2008), possibly favouring badgers, an important insect consumer in the study area (Hipólito et al. 2016). Moreover, badger (small height, short limbs) movement is constrained by dense vegetation, while agile predators such as the fox are less likely to be affected. Hence, the open areas and aggregated shrub mosaic may favour badgers by offering simultaneous foraging and refuge opportunities (Rosalino 2004). The difference in habitat preferences appear to be driven by the behavioural and morphological traits of the selected

species. However, we cannot discard a direct response to interspecific competition. Both hypotheses are not mutually exclusive, but rather complementary.

The persistence of genet in the study area, with a low-dense population, is particularly associated with riparian vegetation. Santos-Reis et al (2004) documented this previously and Galantinho and Mira (2009) showed that the strength of selection for this habitat type is dependent on the quality of the surrounding matrix. The expected habitat associations with Montado woodlands were unclear for this species. This might have been a result of a detection bias caused by the genet's arboreal behaviour (Santos-Reis et al. 2004), an effect not captured while modelling detectability. This species preference for riparian habitats was shared with the red fox, while riparian stretches were positively associated with the detectability of both these species and that of the mongoose. In Mediterranean ecosystems, riparian habitats are acknowledged as crucial landscape elements, acting as food provisioning habitats and movement corridors (Matos et al. 2009, Santos et al. 2011, 2016a), sustaining higher levels of carnivore species richness compared to the adjacent matrix (Virgós 2001a). However, while riparian habitats may benefit the entire community, our results suggest genet's persistence in our study area is fully dependent of this environment, showing full time use (i.e. residency), while for other species, such as the red fox, its function is only complementary to that of the surrounding matrix.

Unexpectedly, only the red fox negatively responded to direct disturbance associated with cattle presence at the plot level, although it also negatively influenced detectability rates of feral cats. Previous studies have shown that badgers actively avoid cattle while foraging (Mullen et al. 2013), and similar behaviour was expected for the study area and from ecologically similar species. Livestock shapes local vegetation structure and, consequently, patterns of food provisioning, both important determinants of mesocarnivores' habitat preferences (Gonçalves et al. 2011); these indirect effects can potentiate or mask species response to cattle disturbance. Grazing pressure prevents shrub encroachment and decreases local small mammal abundance and diversity (Gonçalves et al. 2011), both factors associated with red fox habitat use. Contrastingly, mosaics of sparse shrubs created by cattle presence offer environmental conditions favourable for badgers (Silva et al. 2008, discussed

above), which might override a potential direct negative response of this species. The ability of other sympatric species to cope with such disturbance pressure remains an open question.

Moreover, species-habitat relationships are not constant but dependent on environmental variability and species phenology. In the Mediterranean region, water shortage during the driest months decreases food availability (e.g. fruits and small mammals; Rosalino and Santos-Reis 2001, Santos et al. 2007) which, coupled with seasonality of anthropogenic activities (e.g. cattle rotation schemes), can induce different spatial preferences. Moreover, individual's spatio-temporal activity can change along its life cycle (e.g. breeding and non-breeding season), in response to changes in ecological requirements or tolerance to disturbance (Blanco 1998, Monterroso et al. 2014). Therefore, a more complete assessment of community organisation patterns would benefit from a seasonal perspective particularly if it includes summer surveys, the most detrimental season for carnivores in drier Mediterranean areas.

4.2. Human-induced environmental heterogeneity and community organisation

Our findings concur with the general view that the diversity of medium-sized Iberian carnivores in multifunctional landscapes is positively influenced by increased environmental heterogeneity, as a result of management actions beyond land uses (Beja et al. 2009, Pita et al. 2009, Rosalino et al. 2009, Gonçalves et al. 2011). Specifically, we add to previous evidence by suggesting that the environmental mosaicism in spatially structured managed landscapes positively influences generalist mesocarnivores, particularly those with wide space and food niches, able to quickly exploit the additional variety of ecological resources (Sobrino et al. 2008, Pita et al. 2009), ultimately profiting from an increase in habitat carrying capacity (Verdade et al. 2011).

Human-induced environmental heterogeneity may increase resource quantity at the landscape scale (e.g. prey abundance; Delibes-Mateos et al. 2008b, Silva et al. 2008) and expand resource diversity (e.g. food and habitat; Virgós 2001b, Santos et al. 2016b). Mesocarnivore species may profit from this by using heterogeneous areas (as shown by the observed preference of mongooses for areas with high habitat diversity) and/or by selecting habitats that provide particular combinations of favourable ecological resources (Santos et al. 2011). We show that even habitat-generalist species

such as the red fox and the badger, which usually share habitat preferences and extensively overlap in space (Fedrianni et al. 1999, Barrull et al. 2013, Cruz et al. 2015), exhibited contrasting small-scale preferences for human-made habitats. These opposing habitat associations were mediated by structural contrasts within the Montado woodland shrubby strata, which are the outcome of multiple management practices (e.g. grazing but also shrub clearance or cork removal), variable in space and with combined and long-lasting shaping effects (Pinto-Correia and Vos 2004). It is possible that such pattern contributes to reduce interspecific competition and potentiate high-density sympatry of species within the same trophic level, as observed for foxes and badgers within our study landscape (Levin 1974, Fahrig 2003). Therefore, future studies, besides assessing population densities, should aim to identify the mechanisms mediating the differential habitat selective behaviours observed (i.e. distinguishing dissimilar habitat requirements and interference competition) and test for small-scale spatial segregation patterns (i.e. spatial niche partitioning, Fisher et al. 2013), to evaluate how differential associations to human-made habitats may shape local intra-guild competitive interactions (Linnell and Strand 2000, Creel et al. 2001, Schoener et al. 2009).

The maintenance of environmental heterogeneity in Montado agroecosystems is a major directive for biodiversity preservation in the Mediterranean, but contrasts with current intensification and extensification trends (Aranzabal et al. 2008). In the context of carnivore conservation within farmed landscapes, we reinforce the ecological value of understory heterogeneity associated with management practices. However, while it can favour generalist mesocarnivores, species less able to cope with disturbance may be negatively affected or become under intense competitive pressure from more tolerant ones (e.g. European polecat *Mustela putorius*, stone marten *Martes foina*; captured at low rates in this study) (Krauze-Gryz et al. 2012). Simultaneously, management directed at promoting habitat heterogeneity can overlook the requirements of specialist species (e.g. wildcat and, eventually, Iberian lynx *Lynx pardinus*) at the expense of non-native species expansion (Verdade et al. 2011). Such effects are subject to idiosyncrasies of local management and dependent on the local carnivore community composition. We argue future carnivore research in managed landscapes should prioritize species-centric responses to functional landscape heterogeneity (*sensu* Fahrig et al. 2011), contextualized at the assemblage level by considering its effects on interspecific competitive

interactions and community structuring (Fischer and Lindenmayer 2006). Such knowledge can guide the delineation of management policies in Montado agroecosystems when the management of carnivore populations is a relevant goal; either to protect species of conservation concern (Lozano et al. 2003), promote the functional conservation role of local top predators (Sergio et al. 2008), guide efforts to reduce the incidence of predation on game species (Beja et al. 2009) and those of conservation interest (e.g. ground nesting farmland birds, Pita et al. 2009), or potentiate carnivore aesthetic value in favour of public appeal for agri-environmental schemes (Kruuk 2002).

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Figure captions

Fig. 1. Study area location, main habitat types and camera-trapping sites in Companhia das Lezírias, Portugal. Land-cover is presented for the broadest effectively sampled area, as given by the largest home-range area reported among the target species (European badger, Rosalino 2004).

Fig. 2. Kernel density estimates representing diel activity patterns of target mesocarnivore species in Companhia das Lezírias, Portugal. Short vertical lines above the x-axis represent individual records. Throughout vertical lines mark averaged sunset and sunrise times (solid line), plus and minus 1 hour (dashed lines), delimiting the four diel periods: Night, Dawn, Day and Dusk (Forster et al. 2013).

Fig. 3. Overlap coefficient ($\Delta 1$) estimates and bootstrapped 95% CIs for all interspecific pairwise comparisons among target mesocarnivore species and qualitative measure of overlap (“High”, “Moderate”, “Low”) according to Monterroso et al. (2014) reference $\Delta 1$ values (dashed lines).

- 1 **Table 1.** Covariates used to assess mesocarnivore species patterns of habitat use in Companhia das Lezírias, Portugal. For the first five HABITAT covariates,
- 2 PC1, PC2 and PC3 correspond to the first three PCA axes, accounting for 50.7%, 22.6% and 18.7% of the total variance, respectively.

Covariate	Code	Units	PCA loadings			Description
HABITAT			PC1	PC2	PC3	
Montado with dense shrubs	MDS	PCA scores	0.65	0.34	0.41	Undisturbed cork oak stands or mixed woodland patches of <i>Quercus suber</i> and <i>Pinus pinaster</i> resembling natural Mediterranean habitats, with well-developed and dense (>60% cover) understory, dominated by <i>Ulex sp.</i> , <i>Cistus ladanifer</i> and <i>Cistus monspeliensis</i> .
Montado with sparse shrubs	MSS	PCA scores	-0.75	0.38	0.27	Semi-disturbed cork oak stands, with sparse understory (30%-60% cover) dominated by <i>Ulex sp.</i> , often aggregated to individual trees, with moderate grazing pressure levels.
Montado without shrubs	MNS	PCA scores	0.00	-0.86	0.23	Highly-disturbed cork oak stands, with reduced or absent understory (<30% cover) due to intense grazing pressure or direct shrub clearance activities for pasture cultivation. Ground mostly covered by natural or permanent biodiverse pastures.

Pine stands	MP	PCA scores	0.00	0.00	-0.83	<i>P. pinaster</i> stands of varying age with well-developed understory structure of mixed composition.
Scrubland	S	PCA scores	0.00	0.00	-0.10	Areas dominated by tall shrubs (>1m) of <i>C. ladanifer</i> and <i>C. monspeliensis</i> , with absent or sparse <i>Q. suber</i> and <i>P. pinaster</i> .
Riparian Vegetation	RIP	meters				Linear and narrow strips of dense vegetation adjacent to waterlines, composed primarily by willows (<i>Salix alba</i>), ashes (<i>Fraxinus angustifolia</i>), alders (<i>Alnus glutinosa</i>), hawthorns (<i>Crataegus monogyna</i>) and Blackberries (<i>Rubus fruticosus</i>).
Simpson's Landscape diversity index	Land div	0-1				Patch diversity within a buffer area of 350m radius around each trapping station; equals zero when the buffer area is totally integrated in just one patch and increases as the number of patch types and/or proportional distribution of patch types rise.

DISTURBANCE

Cattle presence	Cattle P	$LSU/(ha \times n_{days})$	Cattle presence index, given by the number of days (n_{days}) a number of livestock units (LSU) spent in a grazing plot of a given area (ha) during the sampling period, calculated as a function of grazing plot area within a buffer area of 350m radius around the camera-trap.
PREY			
Rabbit abundance	Rabbit	$n_{latrines/km}$	Weighted average per 500m transects in each 1×1km UTM square within a buffer area of 350 m radius around the camera-trap.
Small mammal abundance	SMammal	$n_{(relative\ abundance)}$	Small mammal relative abundance (index) for each land-cover type and calculated as a function of habitat proportion within a buffer area of 350m radius around the camera-trap.

1 **Table 2.** Model averaged beta coefficient estimates on the logit scale, standard errors (SE) and 90% confidence intervals (CI) for covariates included in the
2 best models for target mesocarnivore species habitat use in Companhia das Lezírias, Portugal.

Species	Detection probability (p)			Intensity of habitat use (λ)						
	PC2	RIP	Cattle P	PC1	PC2	PC3	RIP	Land div	Rabbit	Cattle P
Red Fox		0.17 ± 0.11		0.21 ± 0.13			0.32 ± 0.13		0.26 ± 0.14	-0.25 ± 0.13
		[-0.01; 0.36]		[0.00; 0.43] ^a			[0.11; 0.53] ^a		[0.03; 0.50] ^a	[-0.47; -0.04] ^a
Badger	-0.44 ± 0.07			-0.35 ± 0.20				-0.42± 0.25		
	[-0.56; -0.32] ^a			[-0.67; -0.02] ^a				[-0.82; -0.01] ^a		
Mongoose		0.39 ± 0.20			0.16 ± 0.20			0.38 ± 0.20	0.37 ± 0.18	
		[0.06; 0.71] ^a			[-0.17; 0.48]			[0.05; 0.70] ^a	[0.07; 0.66] ^a	
Genet		0.43 ± 0.27		-0.33 ± 0.29	0.30 ± 0.32		0.64 ± 0.40	0.26 ± 0.35	-0.34 ± 0.29	
		[-0.02; 0.88]		[-0.81; 0.15]	[-0.24; 0.83]		[-0.01; 1.29]	[-0.32; 0.83]	[-0.82; 0.13]	
Feral cat			-1.16 ± 0.53		0.61 ± 0.57	0.43± 0.39			0.60 ± 0.24	
			[-2.04; -0.29] ^a		[-0.32; 1.54]	[-0.21; 1.07]			[0.21; 1.00] ^a	

^a – Indicates a well-supported effect (estimate unconditional β coefficient 90% CIs do not overlap zero).

Figure 1
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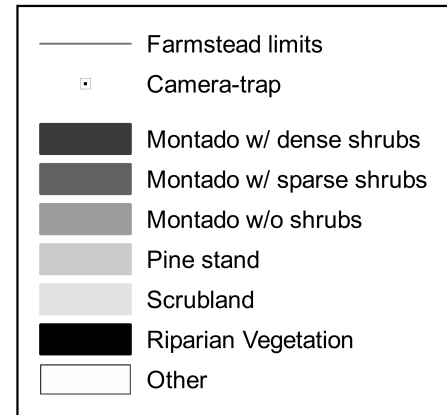
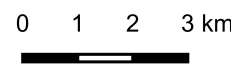


Figure 2

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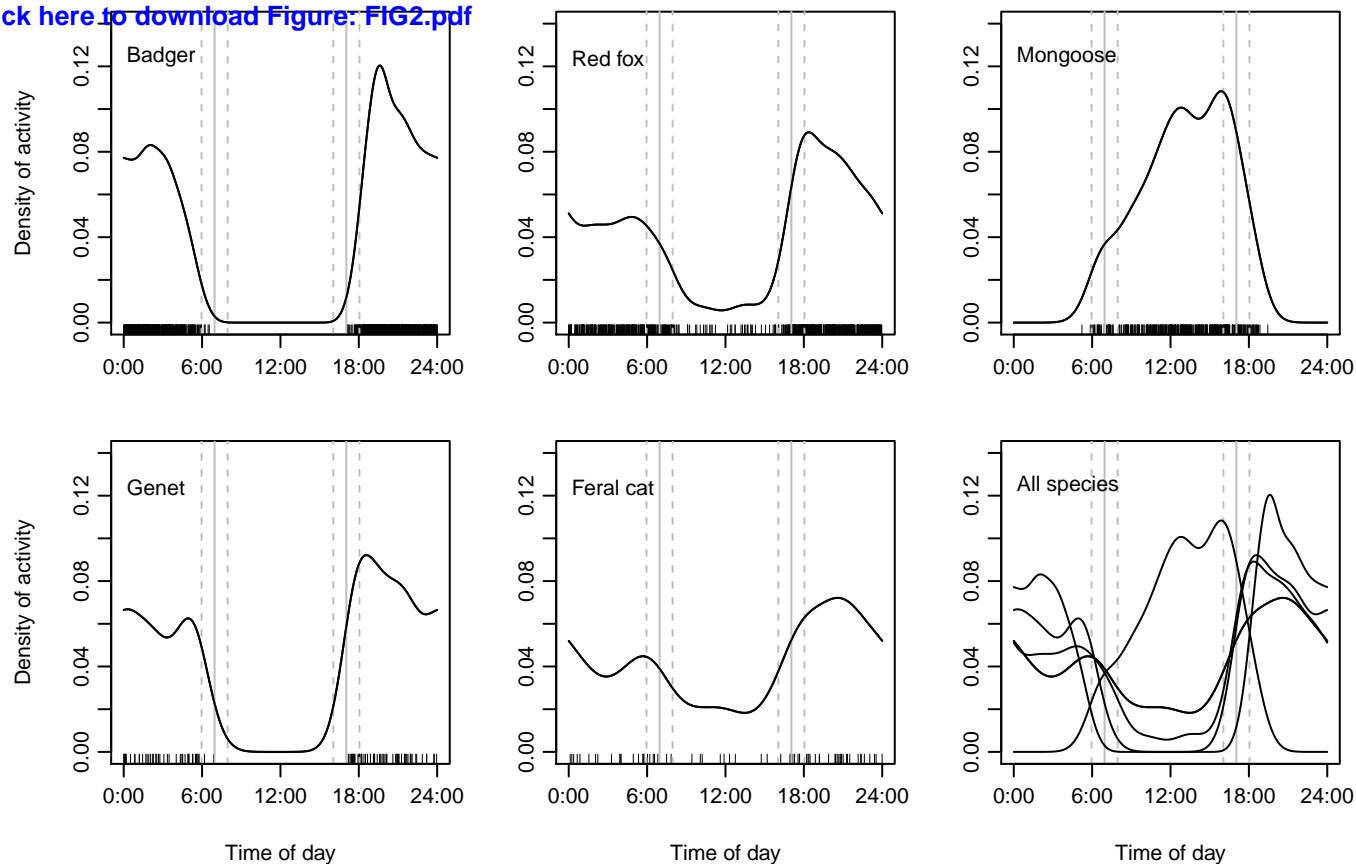


Figure 3

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