

## Convocatoria AEET-SIBECOL de ayudas a proyectos de investigación ERC en ecología (11ª ed., 2021)

### 1. Datos de identificación.

<b>Título de la propuesta</b>	Coexistence of mesocarnivore species in High Nature Value farmlands: a tale of space, time, and food resources.
<b>Categoría</b>	Tomando la iniciativa
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### 2. Memoria Técnica. Actividades y resultados de investigación

#### 2.1. Introducción (Planteamiento, objetivos y justificación)

Portugal has an unexpected richness of mammalian carnivores, placing it among the European countries with highest carnivore species richness (Bencatel et al., 2018). This is partially due to the long-term human presence (Myers et al., 2000), as Mediterranean landscapes have been shaped by centuries of human activities, with farming as one of the historical land-uses. Interestingly, low intensity farming systems have long been recognised as important for biodiversity and wildlife conservation (EEA, 2004).

The *montado*, a High Nature Value farmland (HNVF), is a unique agro-forest ecosystem where the combination of patches with different biophysical characteristics leads to an increased gamma diversity (Sévêque et al., 2020). Here several mammalian carnivore species tend to coexist. However, coexistence theory states that two competing species must segregate, at least partially, along one or more axes of their ecological niche to allow stable coexistence (Letten et al., 2017). This partitioning can occur at the temporal, trophic and/or spatial level. Therefore, a species' niche is inherently a function of species interactions, and the capacity for species to coexist relies on both their niche overlap and their difference in fitness (Sales et al., 2021).

To better understand how mesocarnivore species coexist in these human altered landscapes, we propose an integrated study of the three partitioning niche axes: species' space

use, diel activity pattern and trophic niche. Most studies of the carnivore guild in Mediterranean landscapes have looked primarily at differences in habitat niche to explain species coexistence. However, it is particularly difficult to study communities of generalist species which can explore multiple food resources and adapt to less-than-optimal habitat conditions. Therefore, most studies find that coexistence is possible due to fine-scale habitat selection and/or small differences in activity peaks (Pereira et al., 2012; Soto & Palomares, 2015). However, few studies simultaneously investigate partitioning along the three axes of the ecological niche (Barrull et al., 2014).

With this work, we aim to (i) assess the influence of management practices on species space use and activity patterns, (ii) determine the drivers of species coexistence in these landscapes at the spatial, activity and trophic level and (iii) evaluate the potential for species interaction (e.g., competition). Also, by estimating the influence of forestry management practices, we will assess how these can influence community structure.

## 2.2. Descripción de la ejecución- Metodología

### *Data collection*

To achieve the proposed goals, we selected two study areas with contrasting management practices: Companhia das Lezírias (CL) and Serra de Grândola (SG). The CL is the largest agroforestry farmstead in Portugal with a sustainable forestry management. It is dominated by cork oak trees, interspersed by pine stands, scrubland patches, olive groves, and riparian vegetation, among other. In contrast, SG comprises several small private estates. The landscape is also characterised by cork oak *montado* with small patches of eucalyptus and pine stands, and some riparian vegetation stretches. However, estates differ in the type and intensity of management. Seven mesocarnivore species occur in both areas, five (red fox, European badger, stone marten, Egyptian mongoose, and common genet) being more common and two (Eurasian otter and least weasel) occurring in low density.

In both areas, we implemented a mammalian carnivore survey using camera traps. This non-invasive field method is commonly used to survey and monitor cryptic carnivores and data obtained allows studying species spatio-temporal patterns. In CL, camera traps were deployed at 60 locations, ~1km apart, for two months (October-December 2021). At SG, camera-traps were deployed at 55 locations, ~1km apart, between January-March 2022. At both locations, camera traps were model Browning Dark Ops HD Pro x, and were set to take 3 photographs

per trigger, with a 5 second delay between consecutive triggers. Cameras were placed on trees, up to 30 cm from the ground (Kelly, 2008), without bait. Roads and trails were not preferentially targeted, but selected when available (Kolowski & Forrester, 2017).

During the camera-trapping surveys, we collected carnivore scats to analyse species diet and assess the trophic niche overlap. Scats were collected opportunistically, along transects near the camera trap locations and other random transects in the study areas. Although carnivore scats can be identified using morphological criteria, this can be rather challenging and error prone (Monterroso et al., 2013). Therefore, we used molecular methods (genetic markers) to identify the carnivore species (Monterroso et al., 2019; Morin et al., 2016).

#### *DNA extraction from scats and PCR*

Following the approach from Fernandes et al. (2008), we implemented a two-step method, using a system of species-specific primers. This approach is based on the species-specific PCR amplification of short ( $\leq 250$  bp) DNA sequences of the mitochondrial cytochrome b gene. The first step concerned the extraction of DNA from the scats collected, using the EZNA V-spin Stool DNA isolation kit, by following the manufacturer's instructions. Contamination was monitored by including an extraction blank in every extraction round. The DNA samples were then stored at  $-20^{\circ}\text{C}$  until needed for the PCR assays. Amplifications were undertaken in  $15\ \mu\text{L}$  reactions with  $0.5\ \mu\text{M}$  of each primer (Table 1),  $0.75\ \text{U}$  of Multiplex NZYtaq,  $1.2\ \mu\text{L}$  H<sub>2</sub>O and  $6\ \mu\text{L}$  of DNA extract. PCRs were run with an initial incubation at  $95^{\circ}\text{C}$  for 5 minutes, followed by 55 cycles of 30 seconds at  $94^{\circ}\text{C}$ , 30 seconds at  $50^{\circ}\text{C}$  and 30s at  $72^{\circ}\text{C}$ . The final extension was 10 min at  $72^{\circ}\text{C}$ . Blank controls were used for each species PCR reaction. Amplification products were run in 1.5% agarose/TBE gels containing  $2.8\ \mu\text{L}$  of RedSafe Nucleic Acid Staining Solution.

As advised in Fernandes et al. (2008), the field collected scats were initially screened with only the primer pair (forward and reverse) of the species identified in the field by the collector. PCR products showing a single band of the expected size were considered identified as the target species. If no positive result was obtained, we screened for the next likely species until identification was made.

*Table 1 – Primers for PCR identification of non-invasive samples from target Iberian carnivores at the study areas*

Primer name	Target species	Sequence (5'-3') with M13 and PIG-tail	bp w/tail
Hichneumon F2		AGGGTTTTCCAGTCACGACGTTATGCTTGTAGCACTCATG	254

<b>Hichneumon R2</b>	<i>Herpestes ichneumon</i>	GTTTCTTATATGGAGTAGTGGTACG	
<b>Ggenetta F2</b>	<i>Genetta genetta</i>	AGGGTTTTCCCAGTCACGACGTTCCGTGATTACAAACCTCT	246
<b>Ggenetta R2</b>		GTTTCTTCTGAGTCAGATATTACGC	
<b>Vvulpes F2</b>	<i>Vulpes vulpes</i>	AGGGTTTTCCCAGTCACGACGTTATAATCCTAGCCCTAGTG	257
<b>Vvulpes R2</b>		GTTTCTTGCGGTCAATAAGATAGCA	
<b>Mmeles F1</b>		AGGGTTTTCCCAGTCACGACGTTTCGCCTAATAYTAATGCTC	222
<b>Mmeles R1</b>	<i>Meles meles</i>	GTTTCTTAGGAAGATTAGGGCTAAC	
<b>Mfoina F2b</b>	<i>Martes foina</i>	AGGGTTTTCCCAGTCACGACGTTATATTAGAACCAGCCTCG	272
<b>Mfoina R2b</b>		GTTTCTTCAGAAGTAGGGCACCTAA	
<b>Fsilvestris F2</b>	<i>Felis silvestris</i>	AGGGTTTTCCCAGTCACGACGTTATTATGGCTCCTACACCT	211
<b>Fsilvestris R2</b>	<i>(Felis catus)</i>	GTTTCTTCGTTCTACTAGTTCAGTC	
<b>Clupus F1</b>	<i>Canis lupus</i>	AGGGTTTTCCCAGTCACGACGTTCCCACTAGCCAAAATTGT	282
<b>Clupus R1</b>	<i>(Canis lupus familiaris)</i>	GTTTCTTATGAAGAATATGGAAGCG	
<b>Mnivalis F1</b>	<i>Mustela nivalis</i>	AGGGTTTTCCCAGTCACGACGTTTAGTCCGCTATTCCGTAT	212
<b>Mnivalis R1</b>		GTTTCTTTATGAGGGGTTGTTAGAC	

#### *Species diet analysis*

Scats were dried in an oven at 50°C, washed in a 1x1 mm fine-meshed sieve, and prey items were separated and classified in the following broad categories: mammals, birds, amphibians, reptiles, insects, fruits, and other plant material. Each food item was then dried and weighed. For each category, the volume in terms of proportion to other food categories in the scat, was visually assessed.

Each food category was quantified in terms of frequency of occurrence (FO) as the proportion of samples where a given prey category was identified. Also, we calculated each species' niche breadth using Levins' standardized equation, which is calculated as:

$$B_A = \frac{[\left(\frac{1}{\sum p_i^2}\right) - 1]}{n-1}$$

, where  $p_i$  is the proportion of occurrence of each prey category in the species diet and  $n$  is the number of prey categories in the species diet. Values range from 0 (specialist) to 1 (generalist). We also assessed the trophic niche overlap (O) between species pairs using Pianka's index, which is calculated as:

$$O = \frac{\sum p_{ij} \times p_{ik}}{\sqrt{\sum p_{ij}^2 \times \sum p_{ik}^2}}$$

, where  $p_{ij}$  and  $p_{ik}$  are the proportions prey class  $i$  comprised of the diets of species  $j$  and  $k$ . Values range from 0 (no overlap) to 1 (complete overlap) (Bakaloudis et al., 2012; Santos et al., 2007).

## Occupancy analysis

Occupancy models make use of spatial-temporal replicated data to generate a likelihood-based estimate using probabilistic arguments that account for false absences (MacKenzie et al., 2002). However, failure to account for interspecific interactions may lead to biased inferences when modelling habitat associations. The multispecies occupancy model proposed by Rota et al. (2016) generalizes MacKenzie et al.'s (2002) single-species model to two or more species. Therefore, the basic sampling protocol and assumptions are identical to the single-species case (MacKenzie et al., 2017). Basically, a set of  $n$  sites are surveyed  $J$  times. During each survey, detection/non-detection of  $S$  focal species is recorded. Therefore, a detection history is constructed for each site and species; for example, if a site is surveyed three times ( $t=3$ ), then one possible detection history of species  $s$  at location  $i$  would be  $y_{sit} = 010$ , where the species was only detected on the second survey.

For species  $s$  at site  $i$  during replicate survey  $t$ , detection is modeled as a Bernoulli random variable, conditional on the presence of species  $s$  ( $z_{si} = 1$ ):

$$y_{sit} | z_{si} \sim \text{Bernoulli}(z_{si} p_{sit}),$$

where  $p_{sit}$  is the probability of detecting species  $s$  during replicate survey  $t$ , if the species is present at site  $i$ . The latent occupancy state of all species at site  $i$  is modelled as a multivariate Bernoulli random variable:

$$Z_i \sim \text{MVB}(\Psi_i),$$

where  $Z_i = \{z_{1i}, z_{2i}, \dots, z_{Si}\}$  is an  $S$ -dimensional vector of ones and zeros denoting the latent occupancy state of all  $S$  species and  $\Psi_i$  is a  $2^S$ -dimensional vector denoting the probability of all possible sequences of ones and zeros  $Z_i$  can attain (Rota et al., 2016). Covariate information can be included by modelling the natural parameters as linear functions, using the multinomial logit link. An advantage of the multivariate Bernoulli model is that it allows the influence of environmental variables on one species to differ in the presence and absence of another species.

Here, we defined occupancy as the probability of a species using the area sampled by a camera trap (site) during the survey period, since the mesocarnivores' home range can encompass several sites (Cavallini & Lovari, 1994; Palomares, 1994; Rosalino et al., 2005; Santos-Reis et al., 2005). At each site, species observations were recorded during the survey

period, and we considered two events of the same species to be independent when they occurred more than 30 minutes apart. Species events were collapsed into 13 5-day occasions, recording a species either as present (1) or absent (0) on that 5-day period.

Occupancy and detection parameters were modelled by covariates. Species-specific detection probability was modelled using camera-trapping effort (*Effort*) as an observation covariate, accounting for the number of days the camera was functioning at each occasion; as site-specific covariates we used: *Shrubs* related to the visually estimated percentage of shrub cover in a 50m radius buffer around the camera site, *Feature* as a categorical covariate indicating if the camera was positioned at a dirt road, animal trail or none, and *Alterations* indicating if the vegetation in front of the camera was cleared or not to reduce false triggers. Species-specific site occupancy probability was modelled as a function of covariates measured for a 500 m radius buffer around the camera trap site, namely: *DenseFor* related to the proportion of dense tree cover; *PernVeg* related to the proportion of perennial vegetation cover, calculated as the ratio of September/April NDVI; *NDVlstdev* calculated as the mean standard deviation of NDVI calculated for each 10m pixel in the buffer, as a proxy of vegetation cover diversity; *Slope* calculated as the average slope in the buffer, calculated from a DEM layer with 25m spatial resolution; *Graz* as a disturbance covariate related to the grazing pressure by cattle, calculated as the number of livestock units in a plot for a given area and number of days; and *ForInt* also as a disturbance covariate related to the proportion of area where forestry work (e.g., shrub clearing, pruning, logging) was conducted. These last two covariates were only available for the CL study area.

Models were fit for each study area, testing hypothesis regarding each species habitat preferences and potential interspecific interactions. For model ranking, we used the Akaike Information Criterion corrected for small sample size (AICc). This approach assumes that, within the candidate set, models with  $\Delta AICc \leq 2$  comparatively to the best model are strongly supported and their covariates are good predictors of the dependent variable (Burnham & Anderson, 2002). However, the use of an apparently arbitrary cut-off value has been previously criticized, and other values of  $\Delta AICc$  of 4, 6 or even 8 may also include relevant models. Therefore, we resorted to the Akaike's weight (AICw), which indicates the weight of the evidence in favour of a certain model being the most parsimonious in the set. According to Burnham & Anderson (2002), unless a single model has a AICw >0.9, then other models are likely to be relevant and therefore should be considered for inference. We estimated 95% confidence intervals for occupancy and detection probability estimates, but also to ascertain

the effect of covariates on these estimates. Occupancy analysis was conducted in R software (Team, 2022) using package unmarked (Chandler et al., 2021).

#### *Temporal activity analysis*

Each species independent record was regarded as a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken within any particular interval of the day (Ridout & Linkie, 2009). The probability density function of this distribution was estimated nonparametrically using kernel density (Ridout & Linkie, 2009) only for samples with more than  $\geq 10$  detections. First, time stamps were converted to solar time, since clock times can generate substantial errors compared with real time events, given by the position of the sun in the sky (Nouvellet et al., 2012). To ascertain the potential temporal interspecific interactions, we implemented pairwise comparisons between species and study areas by estimating the coefficient of overlap. For small samples ( $\leq 50$ ), we used the  $\hat{\Delta}_1$  coefficient, otherwise we used the  $\hat{\Delta}_4$  coefficient (Ridout & Linkie, 2009). The coefficients range from zero (no overlap) to 1 (complete overlap). The precision of this estimator was obtained by computing the 95% confidence interval from 10000 bootstrap samples. However, these coefficients are purely descriptive and their interpretation extremely subjective in terms of classifying the degree of overlap between two activity patterns (Monterroso et al., 2014). Therefore, we used the Mardia-Watson-Wheeler test (MWW test hereafter; Batschelet (1981)) to compare the distribution of detections across the diel cycle for all species pairs. Any significant difference between the diel cycle of each species will lead to the rejection of the null hypothesis of identical distributions between species. All analyses were conducted in the R software (Team, 2022) using the packages overlap (Ridout & Linkie, 2009) and circular (Agostinelli & Lund, 2022).

### 2.3. Resultados obtenidos (cumplimiento de objetivos)

#### *Trophic niche*

During the winter surveys, 150 scats were collected, 74 at CL and 76 at Grândola. Of these, 143 scats were genetically identified for the carnivore species which produced it (see Table 2) and processed in terms of diet components. At CL, most scats were from red fox, while at Grândola, only the red fox and the stone marten had a majority of scats collected (Table 2).



Table 2 – For each study area, column *N* indicates the number of scats analyzed and column  $B_A$  indicates the value for the Levins standardized equation of niche breadth, for each species. Niche breadth values range from 0 (specialist) to 1 (generalist).

Species	CL		Grândola	
	<i>N</i>	$B_A$	<i>N</i>	$B_A$
<i>Common genet</i>	7	-	3	-
<i>Egyptian mongoose</i>	14	0.73	5	-
<i>Stone marten</i>	11	0.75	23	0.65
<i>European badger</i>	13	0.52	2	-
<i>Red fox</i>	28	0.67	37	0.66
<i>Total</i>	73	-	70	-

In terms of frequency of occurrence, there was a predominance (> 70% of scats) of fruit in the diet of all carnivores, except the mongoose and the genet, in both study areas. The insect category was also predominant, occurring in more than 70% of scats for all species, except the stone marten in CL and the genet in Grândola. Mammals occurred in 57% of mongoose's scats and 71% of genet's scats at CL, and in 62% of red fox's scats at Grândola (Figure 1). However, it is worth noting the disparity in terms of sample size for some of the carnivore species (e.g., three genet scats from Grândola). Nonetheless, for species with a larger sample size we can compare between study areas; the red fox has a much higher proportion of scats with mammals at Grândola (62% of  $N=37$ ) than at CL (36% of  $N=28$ ); also, at Grândola there was a higher proportion of red fox's scats with fruits (92%) and insects (95%). For the stone marten, 91% of the scats collected at CL ( $N=11$ ) had fruits, while that value was slightly lower at Grândola (78% of  $N=23$ ). However, the proportion of scats with insects was much higher at Grândola (87% of  $N=23$ ) than at CL (36% of  $N=11$ ). For both study areas, the proportion of stone marten's scats with mammals was low (13% of  $N=23$  at Grândola; 27% of  $N=11$  at CL) (Figure 1). In terms of niche breadth, we only calculated the index for species with 10 or more scats analysed. At CL, species are mostly characterized as generalists, given the index values are closer to 1 (Table 2), although the values for badger and fox are lower than the other two species, showing some specialization particularly in fruits and insects. For Grândola, the index values are also intermediate for fox and stone marten, thus these species are not completely generalists, as fruits and insects are extremely preponderant in their diets.

To calculate the diet niche overlap between species pairs, we applied the Pianka's index only to pairs for which species had 10 or more scats analysed. The index was applied to the estimated volume of each prey category in the scat. For CL, this allowed estimating the



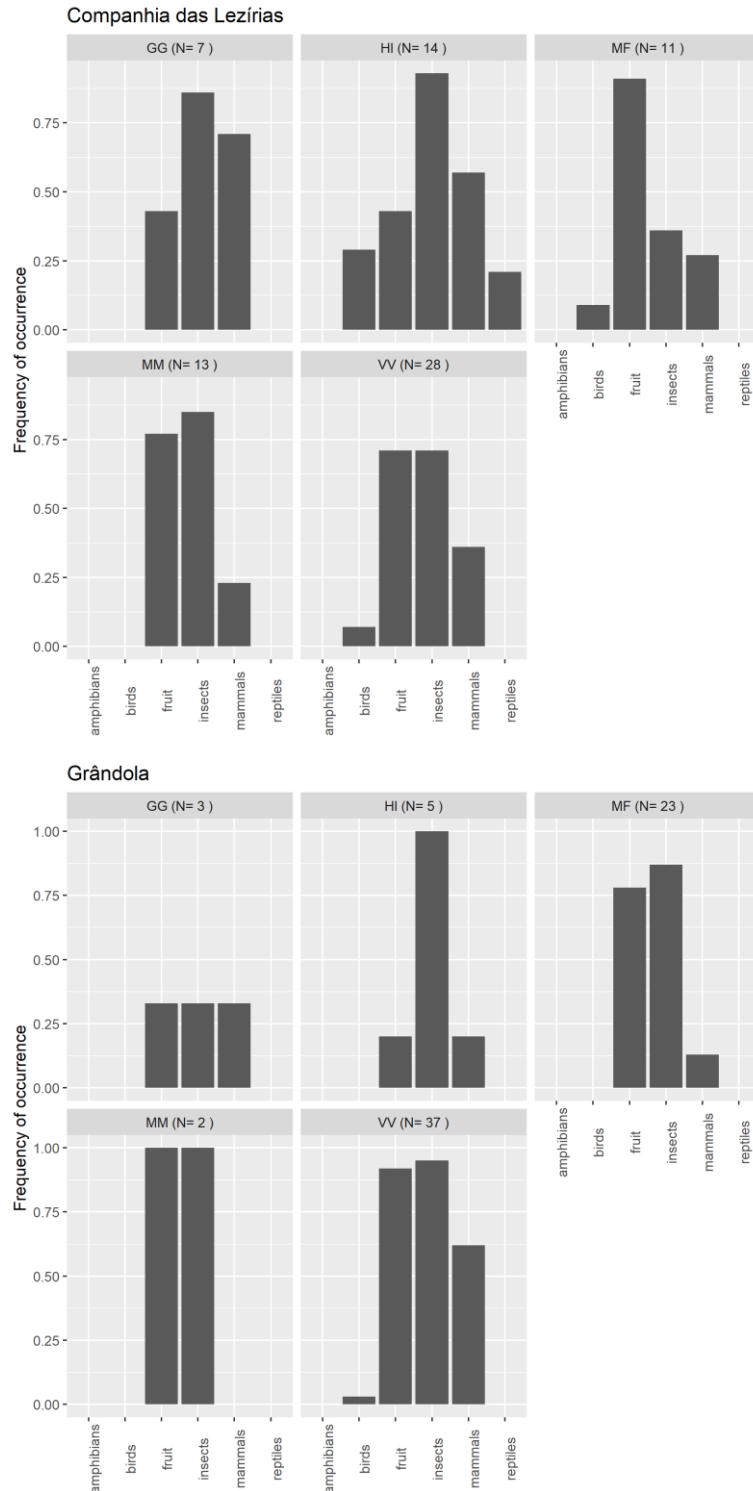


Figure 1 - Frequency of occurrence of each food category in the diet, analysed from scats of the five carnivore species genetically identified. Results are presented for each study area. Species codes: common genet – GG –, Egyptian mongoose – HI –, stone marten – MF –, European badger – MM –, red fox – VV.

overlap between the diet of all species pairs, except with the genet. The highest overlap was between badger and fox's diet (0.96) and the lowest between mongoose and stone marten (0.32). The high overlap between badger and fox's diet is due to the high volume of insects and

fruits. The trophic niche overlap was also high between mongoose and badger (0.88), mainly because of the high volume of insects in their diet; and between mongoose and fox (0.82), because of the preponderance of insects, but also a similar consumption of mammals; and

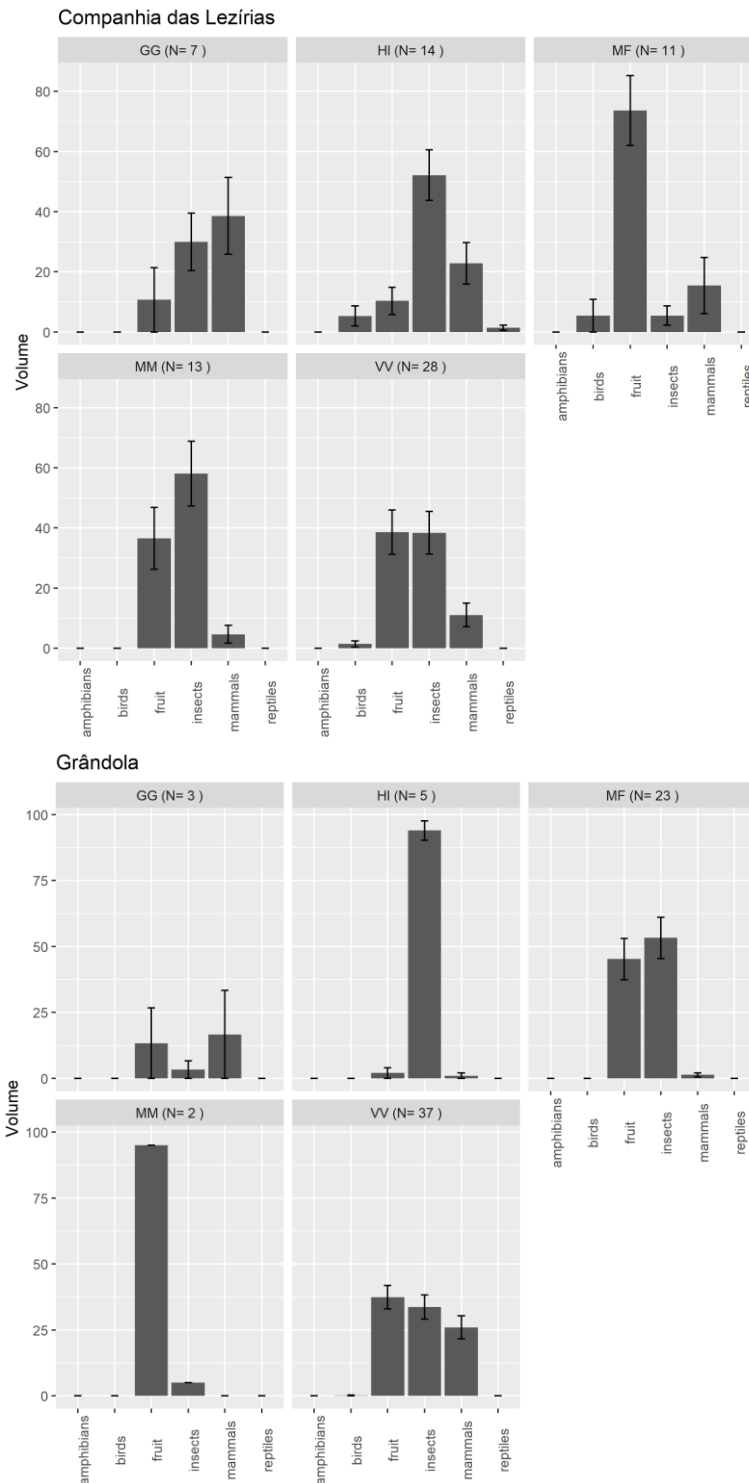


Figure 2 – Percentage of volume of each food category in the diet, analysed from scats of the five carnivore species genetically identified. Results are presented for each study area: Companhia das Lezírias (CL) and Serra de Grândola. Species codes: common genet – GG –, Egyptian mongoose – HI –, stone marten – MF –, European badger – MM –, red fox – VV.

finally between stone marten and fox (0.76), due to the similar consumption of mammals, and high volume of fruits, although much higher for the stone marten ( $74 \pm 12\%$ ) than the fox ( $39 \pm 7\%$ ). The low trophic niche overlap between mongoose and stone marten is due to a very low consumption of fruits (10% volume), but high volume of insects (52%) in the mongoose's diet, which is the exact opposite of the stone marten's diet (Figure 2). At Grândola, the index could only be estimated for the stone marten-fox pair. As in CL, the trophic niche overlap was high (0.89), mainly due to the high volume of fruits and insects in both species diet. However, the red fox had a much higher volume of mammal prey in its diet (26%) than the stone marten (1%) (Figure 2).

We also estimated the trophic niche overlap between study areas, for a given species. This was only possible for the stone marten and the red fox, with a higher overlap for the latter (0.94) than the former (0.69). Therefore, the fox's diet was more similar between study areas than the stone marten's diet. The main difference in the stone marten's diet between areas is the consumption of insects, which was much higher at Grândola than at CL (53% and 5% volume, respectively). Conversely, fruits had a much higher volume in the species diet at CL (74% volume), as did mammal preys (15%) (Figure 2). Although the low sample size did not allow estimating the diet overlap index between study areas for other species, we acknowledge some key differences, namely: an overwhelming predominance of fruits in the badger's diet at Grândola, but a higher consumption of insects at CL. For mongoose, the diet at Grândola was dominated by insects, while at CL, we also saw a high consumption of mammals. The genet had a higher volume of mammals and insects in the diet at CL than at Grândola (Figure 2).

#### *Spatial niche*

From model selection of the CL multi-species occupancy models, the highest-ranking model accounts for the effect of *Features* on each species detection probability, and the co-occurrence of genet with mongoose, genet with badger and mongoose with badger. For the detection probability, the type of feature had a significant positive effect on fox, mongoose and badger detection, with detection being higher on dirt roads, and also on animal trails for mongoose. In terms of occupancy, for the mentioned species pairs, the two species co-occurred more often than expected by chance (Figure 3). This difference was quite striking for

genet and badger, where the 95% confidence intervals of the two occupancy estimates (either badger present or not) do not overlap.

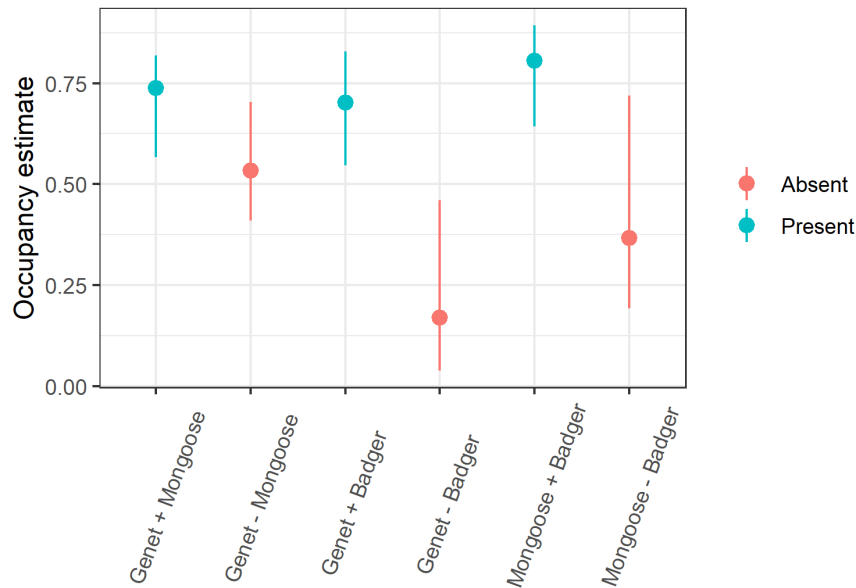


Figure 3- Occupancy estimate conditional (Present) or not (Absent) on the other species presence, for the three species pairs accounted for in the highest-ranking multi-species occupancy model for CL's carnivore community. In the x axis labels, (+) indicates the other species is present, while (-) indicates it is absent.

However, three other models should also be considered, since, along with the highest-ranking model, they account for more than 0.9 of the AICc weight. These other three models only account for the co-occurrence of genet and mongoose. For one of them, species co-occurrence is modelled by the proportion of perennial vegetation in a 500m buffer (*PernVeg*), while for the other, co-occurrence is modeled by the proportion of dense tree cover (*DenseFor*). Both covariates had a positive effect on genet and mongoose co-occurrence (Figure 4).

Table 3 – Model ranking of the multi-species occupancy models for the CL, with a cumulative AICc weight > 0.9. The model description indicates the covariates and species interactions accounted for to model species occupancy and detection probabilities.

Model	K	AICc	ΔAICc	AICc weight
$\Psi(\sim\text{Genet:Mongoose}, \sim\text{Genet:Badger}, \sim\text{Mongoose:Badger}),$ p(Features)	23	2874.29	0	0.5
$\Psi(\sim\text{Genet:Mongoose:PernVeg}),$ p(Features)	24	2875.82	1.52	0.23
$\Psi(\sim\text{Genet:Mongoose}),$ p(Features)	21	2876.33	2.03	0.18
$\Psi(\sim\text{Genet:Mongoose:DenseFor}),$ p(Features)	24	2878.13	3.84	0.07

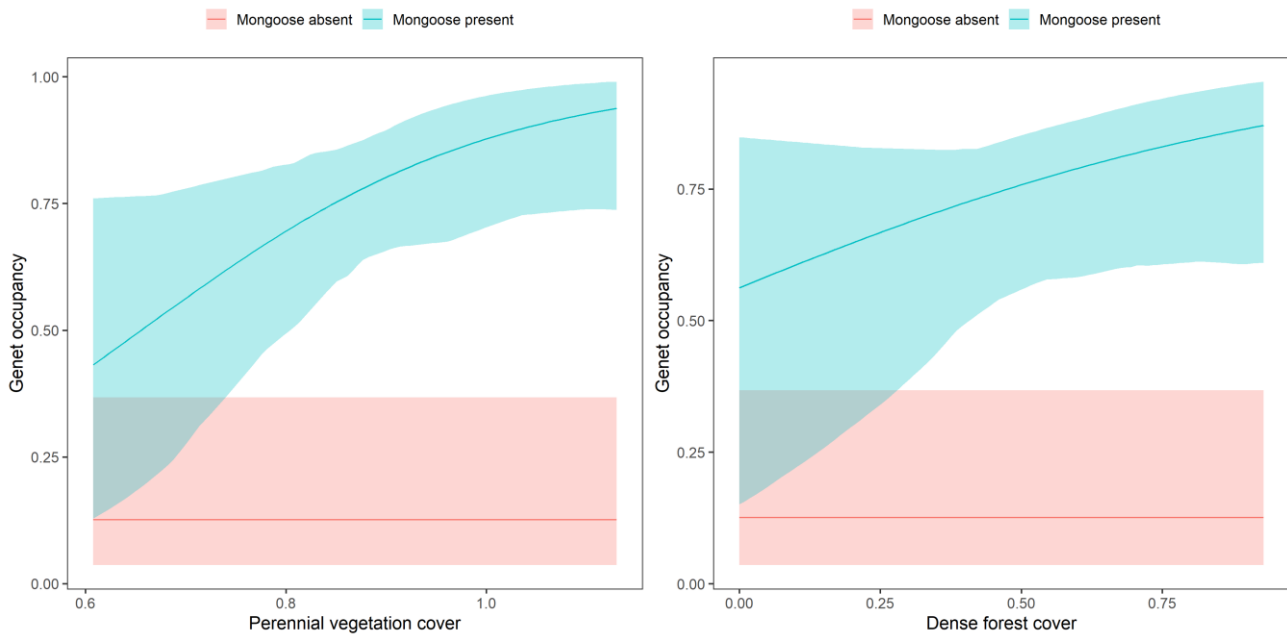


Figure 4- Genet and mongoose co-occurrence at CL, modelled by the proportion of perennial vegetation (on the left) and proportion of dense tree cover (on the right) in a 500m radius buffer around the camera site. In blue the occupancy of genet when mongoose is present, and in red when mongoose is absent, for increasing values of the covariates. Shaded area represents the 95% confidence interval.

For the Grândola mesocarnivore community, the best ranking model accounts for the effect of camera-trapping effort (*Effort*) on species detection probability, and the co-occurrence of fox with badger, mongoose with marten, marten with genet and mongoose with badger. In terms of species detection, *Effort* had a significant positive effect on stone marten's detection. For all species pairs considered, the two species were more likely to co-occur. This was especially true for mongoose and stone marten, and mongoose and badger's co-occurrences, since the 95% confidence intervals for the occupancy estimates, conditional or not on the other species presence, did not overlap (Figure 5). However, two other models should also be considered since, with the highest-ranking model, they account for 0.99 of the AICc weight (Table 4). Both account for the species co-occurrences previously identified, but in one model, stone marten and genet's co-occurrence is modeled by the proportion of dense tree cover (*DenseFor*), and in the other fox and badger's co-occurrence is modeled by vegetation cover diversity (*NDVIstdv*). The effect of *NDVIstdv* had a positive effect on fox's co-occurrence with badger, while *DenseFor* had a negative effect on stone marten's co-occurrence with genet. In both cases, the overlap between the 95% confidence intervals was extremely high, and thus there is a lack of support for a significant effect of these covariates (Figure 6).

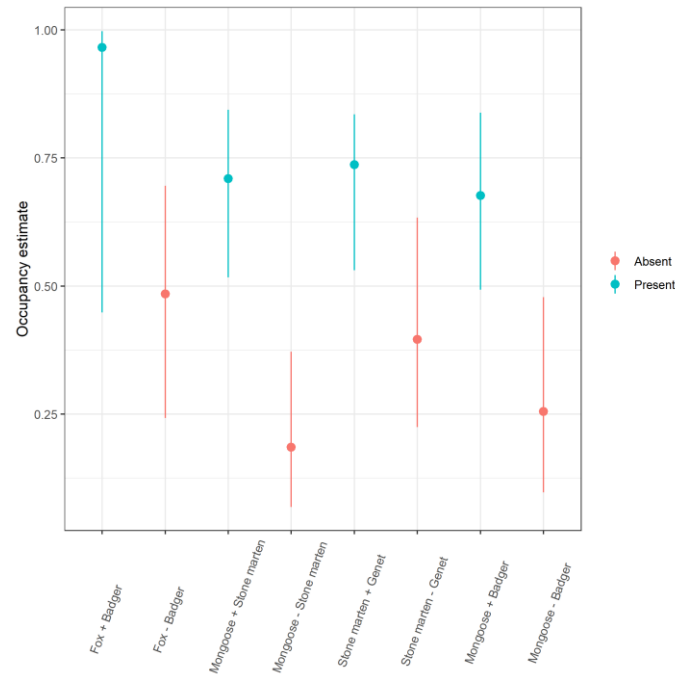


Figure 5 - Occupancy estimate conditional (Present) or not (Absent) on the other species presence, for the four species pairs accounted for in the highest-ranking multi-species occupancy model for Grândola's carnivore community. In the x axis labels, (+) indicates the other species is present, while (-) indicates it is absent.

Table 4 -Model ranking of the multi-species occupancy models for Grândola, with a cumulative AICc weight > 0.9. The model description indicates the covariates and species interactions accounted for to model species occupancy and detection probabilities. K indicates

Model	K	AICc	ΔAICc	AICc weight
$\Psi(\sim\text{Fox}:\text{Badger}, \sim\text{Mongoose}:\text{StoneMarten},$ $\sim\text{StoneMarten}:\text{Genet}, \sim\text{Mongoose}:\text{Badger}), p(\text{Effort})$	19	2423.92	0	0.79
$\Psi(\sim\text{Fox}:\text{Badger}, \sim\text{Mongoose}:\text{StoneMarten},$ $\sim\text{StoneMarten}:\text{Genet}:\text{DenseFor}, \sim\text{Mongoose}:\text{Badger}), p(\text{Effort})$	20	2428.03	4.11	0.1
$\Psi(\sim\text{Fox}:\text{Badger}:\text{NDVIstdv}, \sim\text{Mongoose}:\text{StoneMarten},$ $\sim\text{StoneMarten}:\text{Genet}, \sim\text{Mongoose}:\text{Badger}), p(\text{Effort})$	21	2428.15	4.23	0.1

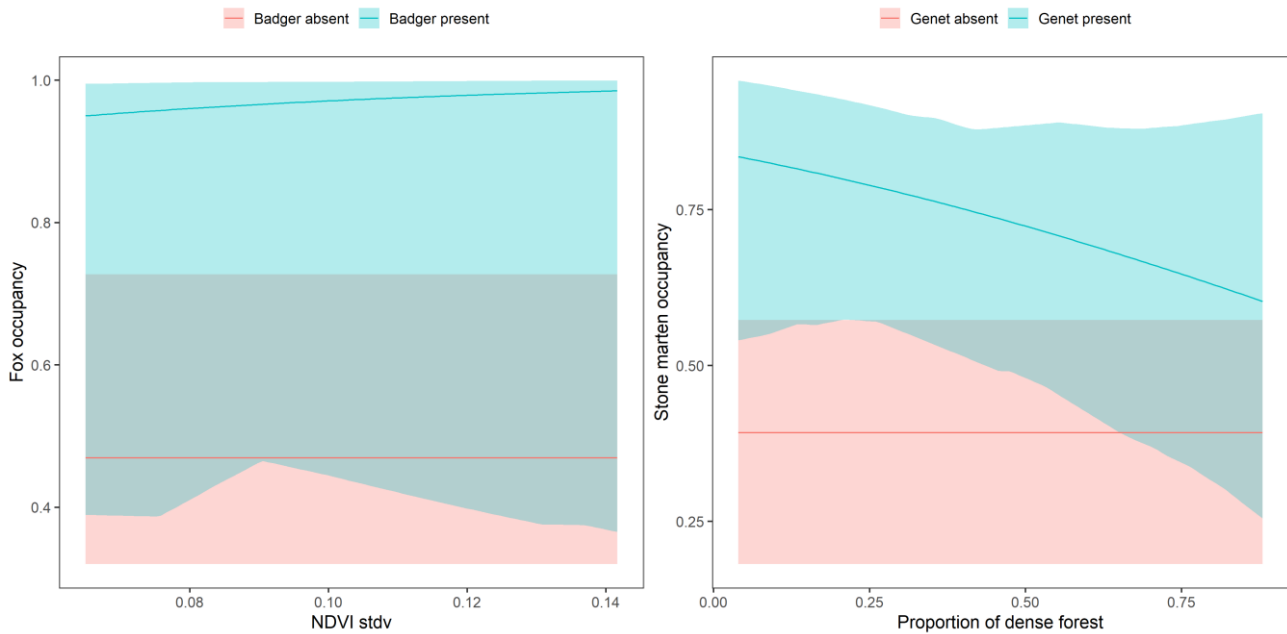


Figure 6 – Fox and badger co-occurrence at Grândola, modelled by the NDVI standard deviation as a proxy of vegetation cover diversity (on the left); and stone marten and genet co-occurrence at Grândola, modelled by the proportion of dense tree cover (on the right) for a 500m radius buffer around the camera site. In blue the occupancy of a species when the other is present, and in red when it is absent, for increasing values of the covariates. Shaded area represents the 95% confidence interval.

### Temporal niche

Table 5 - Coefficient of overlap calculated for each species, comparing the winter activity pattern between study areas.  $\hat{\Delta}_1$  was used when either sample size was <50, and  $\hat{\Delta}_4$  otherwise.

Species	$\hat{\Delta}_1$ or $\hat{\Delta}_4$ (CI)
Fox	0.94 (0.92-0.96)
Badger	0.95 (0.9-0.98)
Stone marten	0.89 (0.8-0.95)
Genet	0.89 (0.82-0.95)
Mongoose	0.86 (0.78-0.92)

The species' winter activity pattern was homogeneous between study areas (Table 5). As expected, all species had the lowest activity overlap with the Egyptian mongoose, given this is the only diurnal carnivore of the assemblage. Furthermore, for both study areas, the following species' pairs had a low activity overlap and statistically significant MWW test indicating lack of homogeneity: fox-badger, fox-stone marten and fox-genet (Table 6). This is due to the fox's activity pattern peaking just after sunset and decreasing along the night-time, while the other carnivores have a more constant nocturnal activity (Figures 7 and 8), except the genet at CL, which also has a more pronounced activity peak after sunset (Figure 7). Also, for the CL, badger and genet had significantly different activity patterns (Table 6), mainly



because the genet has a bimodal activity pattern, with a peak after sunset and another one around 3am, while the badger has a more constant nocturnal activity (Figure 7).

Table 6 - Coefficient of overlap calculated for each pairwise comparison between species, for Companhia das Lezírias and Serra de Grândola.  $\hat{\Delta}_1$  was used when either sample size was <50, and  $\hat{\Delta}_4$  otherwise.

Species pairs	$\hat{\Delta}_1$ or $\hat{\Delta}_4$ (CI)	
	CL	Grândola
Fox-Badger	0.75 (0.7-0.79)**	0.75 (0.65-0.84)**
Fox-Stone marten	0.81 (0.73-0.87)*	0.82 (0.75-0.88)**
Fox-Genet	0.87 (0.82-0.91)*	0.82 (0.73-0.89)*
Fox-Mongoose	0.24 (0.2-0.28)**	0.13 (0.09-0.18)**
Badger- Stone marten	0.89 (0.81-0.95)	0.89 (0.8-0.95)
Badger-Genet	0.85 (0.78-0.91)**	0.9 (0.8-0.95)
Badger-Mongoose	0.12 (0.1-0.15)**	0.06 (0.04-0.1)**
Stone marten – Genet	0.91 (0.85-0.96)	0.95 (0.91-0.98)
Stone marten-Mongoose	0.14 (0.11-0.18)**	0.03 (0.02-0.05)**
Genet-Mongoose	0.18 (0.15-0.22)**	0.07 (0.04-0.11)**

\* MWW test: p-value <0.05

\*\* p-value <<0.001

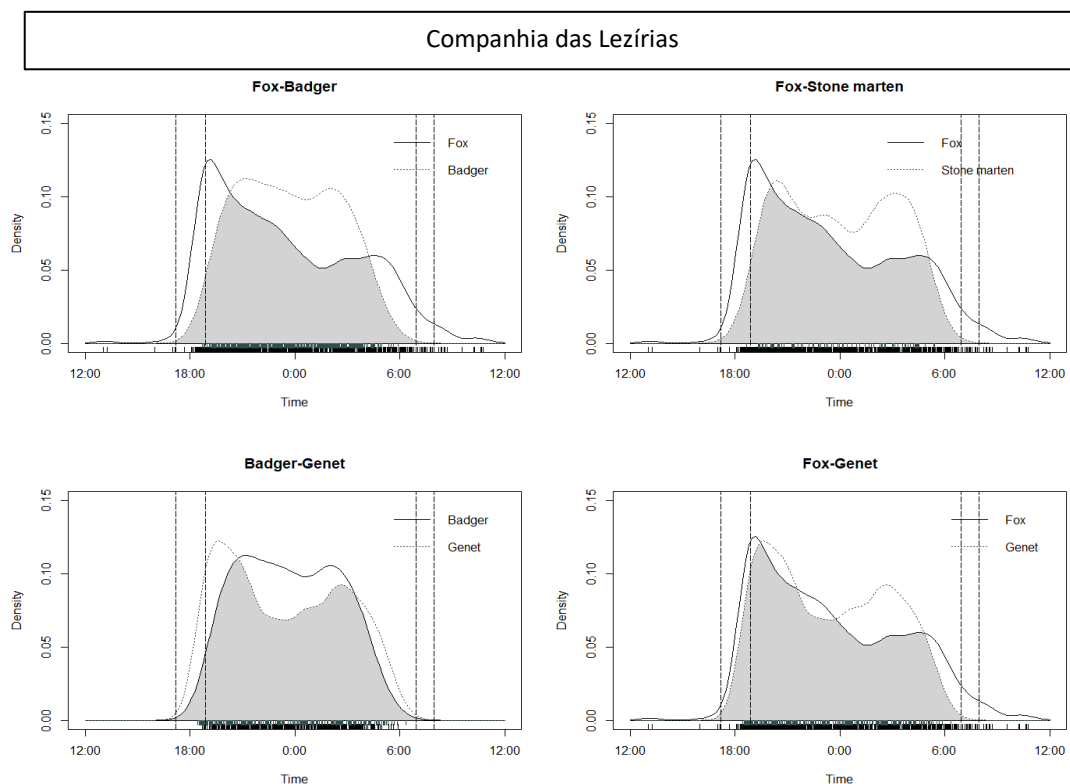


Figure 7 – Activity pattern overlap for nocturnal species pairs, from CL, for which the MWW < 0.05. The overlap is represented by the grey shaded area. The dashed vertical lines represent the sunset and sunrise periods.

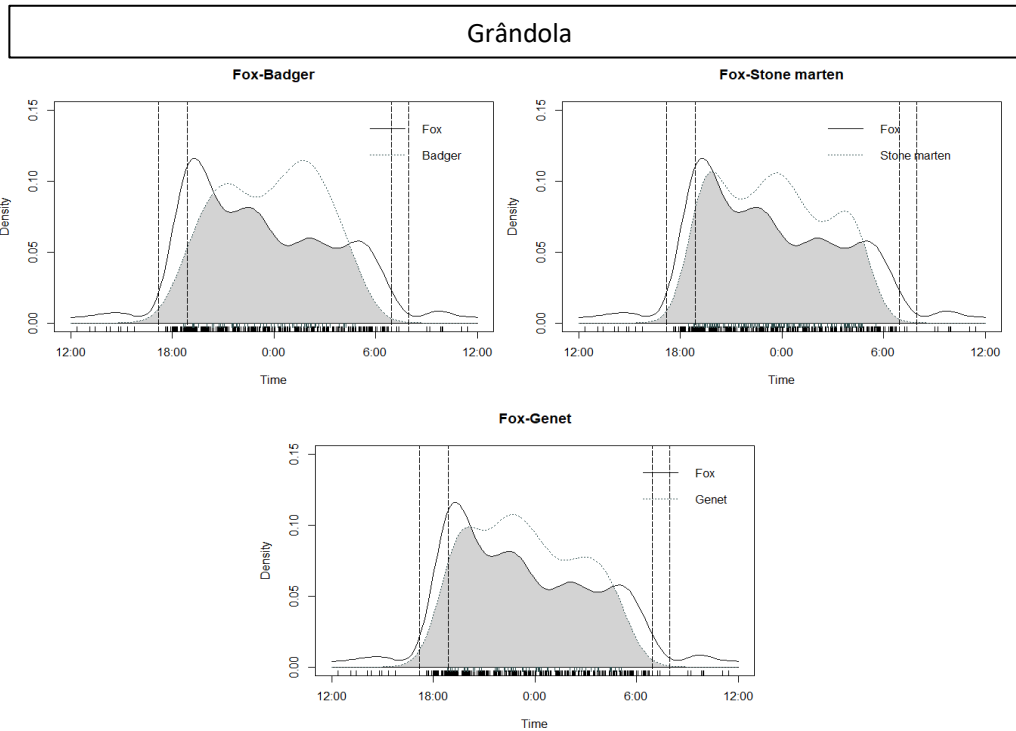


Figure 8 - Activity pattern overlap for nocturnal species pairs, from Grândola, for which the MWW < 0.05. The overlap is represented by the grey shaded area. The dashed vertical lines represent the sunset and sunrise periods.

## 2.4. Conclusiones y valoración de la ejecución

Mesocarnivore species in the Iberian Peninsula are mostly generalists (Curveira-Santos et al., 2017; Pita et al., 2009), which makes it difficult to disentangle the mechanisms that allow a stable coexistence. However, understanding such mechanisms is essential to ensure a

Table 7 - Summary of the results obtained for each species pair of the mesocarnivore community at CL, in terms of trophic niche and diel activity overlap, and spatial co-occurrence. In the upper half of the table, the results are depicted as either overlapping (=) or not ( $\neq$ ), and spatial co-occurrence is indicated as either avoidance (-), co-occurrence (+) or independent (0). The symbol (x) indicates the pairs of species for which a specific analysis could not be conducted. The lower half of the table translates the same information in a color code: green for overlapping trophic niche, diel activity, and spatial co-occurrence; red for low overlap of trophic niche, activity, and spatial avoidance.
















Companhia das Lezírias															
	VV			MM			MF			GG			HI		
VV				=	$\neq$	0	=	$\neq$	0	x	$\neq$	0	=	$\neq$	0
MM							$\neq$	=	0	x	$\neq$	+	=	$\neq$	+
MF										x	=	0	$\neq$	$\neq$	0
GG													x	$\neq$	+
HI															

healthy ecosystem, particularly in managed landscapes where human activities can disturb that balance. Although previous studies have investigated such potential interactions (Ferreiro-Arias et al., 2020; Sévêque et al., 2020; Soto & Palomares, 2015), failing to simultaneously account for all the components of a species ecological niche might hinder conclusions on pathways for coexistence between these generalist carnivores.

With this funding, we were able to investigate each mesocarnivore species' ecological niche and disentangle the potential pathways of species interaction, through avoidance or co-occurrence at the spatial, temporal and/or trophic levels. In these mesocarnivore communities, the main mechanism for coexistence appears to be at the activity level (Tables 7 and 8). In fact, in both study areas, a disjoint activity pattern seems to be the main mechanism of segregation between species pairs. Nevertheless, there are some exceptions. At CL, the badger and the stone marten have a similar activity pattern, however, their diets appear to differ in terms of the consumption of fruits and mammals. Although fruits can be quite an abundant resource, small mammals are not quite as abundant, and thus consuming these resources in different proportions could allow coexistence (Table 7). At Grândola, the stone marten and the genet seem to co-occur spatially, but also temporally with a similar activity pattern (Table 8). This was not expected, as the two species have similar habitat preferences, and thus for coexistence should partition at another level of their niche. This could either be at the trophic level, which due to the small sample size could not be assessed, or spatial segregation occurs at the vertical level as both species are able to climb trees and are known

*Table 8- Summary of the results obtained for each species pair of the mesocarnivore community at Grândola, in terms of trophic niche and diel activity overlap, and spatial co-occurrence. In the upper half of the table, the results are depicted as either overlapping (=) or not (≠), and spatial co-occurrence is indicated as either avoidance (-), co-occurrence (+) or independent (0). The symbol (x) indicates the pairs of species for which a specific analysis could not be conducted. The lower half of the table translates the same information in a color code: green for overlapping trophic niche, diel activity, or spatial co-occurrence; red for low overlap of trophic niche, activity, or spatial avoidance.*

to rest there (Santos-Reis et al., 2005; Sarmiento et al., 2010). The broad confidence intervals

Grândola															
	VV			MM			MF			GG			HI		
															
VV				x	≠	+	=	≠	0	x	≠	0	x	≠	0
MM							x	=	0	x	=	0	x	≠	+
MF										x	=	+	x	≠	+
GG													x	≠	0
HI															

when estimating the influence of dense tree cover on species co-occurrence hinders interpretations on the effect of this covariate. However, it does show a dependence on these dense forest patches by both species, since when the availability is low the species are more likely to co-occur, but as the availability increases, they tend to occur independently (Santos-Reis et al., 2005).

At the spatial level, we found most species pairs tend to co-occur. This does not mean that species interact directly, but that they do tend to use the same space. At CL, the badger appears to co-occur more often with the genet and the mongoose, however their activity patterns are different, and thus are active at different hours of the day (Table 7). The genet also co-occurs more often with mongoose, and this spatial pattern seems to be better explained by the proportion of dense tree cover and perennial vegetation. Co-occurrence is higher as the availability of these resources increases. As stated before, the genet is an arboreal species and thus can exploit the vertical dimension of the forest. Thus, although they spatially co-occur, not only is there a mismatch in the activity pattern because the mongoose is a diurnal species, but also, they are able to explore different dimensions of the landscape. At Grândola, badger's occupancy is higher when fox and mongoose are present, but their activity patterns are different, which means coexistence might be mediated by temporal partitioning of their diel activity. Stone marten's occupancy is also higher when mongoose is present, but once again, their temporal overlap is very low (Table 8).

Although this approach has given us a more comprehensive look into the mesocarnivore community structure, there are some limitations. The multi-species occupancy models, although a powerful tool, are very data hungry and thus building this dataset further will likely give us new insights into co-occurrence patterns. Furthermore, as stated before, co-occurrence or avoidance does not directly translate into species interactions, and that is a shortcoming of all non-experimental studies (Tobler et al., 2019). We also intend to explore new statistical methods that either account simultaneously for the spatial and temporal patterns (Kellner et al., 2022) or that include an abundance component (Amir et al., 2022; Zhao et al., 2022) to disentangle these spatial patterns. Furthermore, we intend to increase the number of scat samples for the trophic niche analysis, as some species are very underrepresented and could not be included in the analysis. The funding from AEET was essential to start this process but continuing to build the dataset will surely uncover more on these community dynamics.



This funding allowed an integrated analysis of the mesocarnivore community structure, and it was essential to fulfill the goals outlined in my PhD. Going forward, as we explore other potential analysis, we hope to disentangle more of the community patterns to be able to inform on sustainable management practices in these human-altered landscapes.

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## 2.6. Publicaciones resultantes

So far, the dataset generated from AEET funding and subsequent results presented in this report have not been published. However, besides my PhD, this funding is allowing a master student to develop his own thesis on the trophic niche of mammalian mesocarnivores in agro-forestry landscapes. All subsequent publications from either work will acknowledge this AEET funding.

**3. Informe de gastos del proyecto.** Relación de partidas de gastos y sus importes. Se deberán aportar justificantes originales de los pagos realizados (tickets, recibos o facturas).

Budget category	Description	Supplier	Invoice Nr	Date	Value
Materials	MultiplexPCR NZYTaQ	nzytech	18/453	07/02/2022	337.02
	DNA Primer 25nmol	Alfagene	2022/2220222	16/02/2022	100.96
	Scat collection tubes	VReis	284330	09/03/2022	44.28
	Scat collection tubes	VReis	284624	18/05/2022	151.79
	MultiplexPCR NZYTaQ	nzytech	18/3614	12/07/2022	337.02
	MultiplexPCR NZYTaQ	nzytech	12/278	14/10/2022	584.4
Missions	Gas - Lisbon to Grândola	Prio	7918	24/01/2022	43.37
	Gas - Grândola to Lisbon	Prio	8134	25/01/2022	28.57
	Toll - Lisbon to Grândola	Brisa	FS 02161022202/0003804	24/01/2022	14.6
	Toll - Grândola to Lisbon	Brisa	FS 12131152202/0002790	25/01/2022	14.6
	Gas - Lisbon to Grândola	Prio	385	08/02/2022	39.79
	Gas - Grândola to Lisbon	Prio	FS 925121002/039222	09/02/2022	20
	Toll - Lisbon to Grândola	Brisa	FS 02161012202/0002969	08/02/2022	14.2
	Toll - Grândola to Lisbon	Brisa	FS 12131152202/0004531	09/02/2022	14.6
	Toll - Grândola to Lisbon	Lusoponte	7210902221757000	09/02/2022	6.55
	Gas - Lisbon to Grândola	Prio	4560	02/03/2022	46.98
	Gas - Grândola to Lisbon	Prio	4836	03/03/2022	31.19
	Toll - Lisbon to Grândola	Brisa	FS 02161022202/0010917	02/03/2022	14.2
	Toll - Grândola to Lisbon	Brisa	FS 12131112202/0013919	03/03/2022	14.6
	Toll - Grândola to Lisbon	Lusoponte	8210303221753000	03/03/2022	6.55
	Gas - Lisbon to Grândola	Prio	7639	16/03/2022	55.89
	Gas - Grândola to Lisbon	Prio	7836	17/03/2022	34.72
	Toll - Lisbon to Grândola	Brisa	FS 02161022202/0013275	16/03/2022	14.2
	Toll - Grândola to Lisbon	Brisa	FS 12131102202/0012020	17/03/2022	14.6
	Toll - Grândola to Lisbon	Lusoponte	8211703221842000	17/03/2022	6.55
				TOTAL	1991.23

Fdo: Ana Luisa Barros

en Lisboa, a 16 de enero de 2023