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Influence of habitat edges on spatial and spatio-temporal occurrence patterns of mesocarnivores in landscapes dominated by *Eucalyptus* plantations

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A B S T R A C T

Human population growth leads to drastic changes in landscape structure that often result in fragmentation. Fragmentation modifies the landscape and divides it into smaller habitat patches, creating habitat edges. These can affect the distribution and abundance of species and influence interspecific interactions. By comparing edges with habitat interiors, we intend to study how or if habitat edges influence mesocarnivores': i) activity patterns, ii) co-occurrence in time, and iii) occupancy. We used camera-trapping to monitor the mesocarnivore community in two *Eucalyptus* plantations interspersed with patches of natural habitats, producing a landscape rich in habitat edges. 18 camera traps were placed in each study site, half on habitat edges and half in the interior habitat. We found a higher overlap of the mesocarnivores activity patterns in interior habitat than in habitat edges and a consistent positive effect for edge density on occupancy at both species and community-level. This study demonstrates that habitat edges shape mesocarnivores' spatial and temporal behaviour. While spatially all species are positively affected by edges, as these can provide alternative or higher availability of resources, or act as travel corridors, to minimize interspecific interactions in edges, species activity overlap is greater within interior habitats than in edge habitats. Our findings support the design of better management measures in human-altered ecosystems, such as agricultural areas and forestry plantations, to guarantee the conservation of biodiversity while maintaining economic profitability.

1. Introduction

Understanding how landscape structure (i.e. the number, size, shape and arrangement of land use types; Walz, 2011) shapes biodiversity, and the patterns of species occurrence and interaction, is essential to delineate and implement efficient wildlife management and conservation strategies (Moreira-Arce et al., 2016; Pita et al., 2009). It influences several important ecological processes, such as the composition of wildlife assemblages and its species abundance (e.g., Gray et al., 2004), the individuals home-range size and configuration (e.g., Quinn et al., 2013) and movement patterns (e.g., Kanagaraj et al., 2013), the prevalence of diseases (e.g., Gras et al., 2018), seed dispersal patterns (e.g., Herrera et al., 2016) and the flow of materials and nutrients (e.g., Murcia, 1995). The increased influence of humans in the landscape dynamics led to rapid and drastic changes in landscape structure. Often this process results in habitat fragmentation, mainly by dividing the existing habitats into patches, reducing their size, increasing patch isolation, and creating wider and more contrasting habitat edges (Laurance and Yensen, 1991; Regolin et al., 2017; Šálek et al., 2010; Svobodová et al., 2011), which induce changes on how animals use the different landscape elements.

Habitat edges can be identified as discontinuities or boundaries separating two or more distinct adjacent patches with different biotic and abiotic characteristics (Lidicker, 1999; Lidicker and Peterson, 1999). These can correspond to different land uses, plant communities, or vegetation successional or development stages (Ries and Sisk, 2004; Yahner, 1988). Habitat edges can either be an obvious and well-defined boundary (sharp, high-contrast), often separated by empty corridors, or

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a transition zone (soft, low-contrast) where the two habitats gradually change from one type to the other (Lidicker, 1999; Lidicker and Peterson, 1999; Yahner, 1988), with soft edges tending to originate weaker responses than sharp ones (Ries et al., 2004). It can also be natural or induced (Fagan et al., 1999; Yahner, 1988), with the former resulting from variation of different abiotic factors, such as climate or topography, and the later from anthropogenic disturbances and modification of the naturally occurring patches (e.g. agriculture or forestry activities; Yahner, 1988). Although the presence of edges can be often identifiable by field observation, its limits (i.e., were two contiguous patches end and the edge begins) might be hard to define (Fagan et al., 1999).

Habitat edges can expose organisms to different abiotic conditions, such as different temperature, wind intensity and solar incidence, for example, creating variable microclimatic conditions (Murcia, 1995). As such, edges can alter species' movement patterns (Cantrell et al., 2002; Fletcher et al., 2007; Maciel and Lutscher, 2013). While they can act as a barrier to the movement of some species (Fagan et al., 1999; Ries et al., 2004; Yahner, 1988), others take advantage of them and use them as travel corridors to facilitate movement (Heske, 1995; Maciel and Lutscher, 2013; Šálek et al., 2010). Thus, edges can affect species' diversity, distribution and abundance, which in turn will influence the interaction among species and may induce cascading effects into the entire communities (Cantrell et al., 2002; Regolin et al., 2017; Ries et al., 2004). Inversely, habitat edges can also act as a unique habitat and facilitate the interaction between species that would not be possible otherwise (Fletcher et al., 2007). Collectively, these processes are commonly referred to as "edge effects" (Ries et al., 2004).

Habitat edges can have positive (increase in abundance on or near edges due to complementarity of resource availability between contiguous habitats; Lidicker, 1999; Svobodová et al., 2011), negative (avoidance, due to increased disturbance or undesirable environmental conditions; Lidicker, 1999; Ries and Sisk, 2004; Svobodová et al., 2011; Wimp et al., 2019) or neutral effects on species (Heske, 1995; Wimp et al., 2019). Habitat edges can also act as an alternative habitat, when it has resources that are absent or are rare in both the adjacent patches, resulting in an increased use of these zones (Ries and Sisk, 2004).

Mediterranean Europe is a region where important biodiversity hotspots (Myers et al., 2000; Pascual et al., 2011) coexist with agriculture and forestry lands, shaped by centuries of human activities and settlements (Blondel, 2006). In the second half of the 20th century, the increased demand for pulp and paper products led to a growth of forestry monocultures, especially in Western Mediterranean regions (NW Spain and Portugal) (Tomé et al., 2021). In some regions (e.g., centre of Portugal) this expansion of forestry monocultures led to native habitat fragmentation, patch size reduction (and consequent increase edge effects) and isolation, and to a landscape matrix composed of anthropic land uses, such as pine or eucalyptus plantations (García-Ruiz et al., 2013; Geri et al., 2010).

Despite these changes in the landscape, Portugal still hosts 13 native mammalian carnivores (Bencatel et al., 2018), representing c.a. 55 % of all native European terrestrial carnivores (IUCN, 2021), in only less than 1 % of Europe's area (Rosalino et al., 2023). These species occupy higher levels of the trophic network and play a crucial role in ecosystems' functioning and dynamics (e.g., prey regulation, seed dispersion, energy transference within ecosystems and direct and indirect ecosystem engineers; Bencatel et al., 2018; Rosalino et al., 2010; Prugh et al., 2009) and are affected by cascading effects that act at different trophic levels. Thus, they are good study models to assess the edge effects on Mediterranean communities.

Several studies conducted in the Mediterranean evaluated edge effects targeting lichens (Belinchón et al., 2007; Brunialti et al., 2013) and plants, such as flowers or trees (Concepción et al., 2012; González-Moreno et al., 2013; Torras et al., 2008), invertebrates (Holway and Suarez, 2006; Peyras et al., 2013) and even birds and nest predation (Herrando and Brotons, 2002; Santos and Tellería, 1992). However, studies assessing the edge effects on mammals inhabiting the Mediterranean region are scarce and often use small mammals as models (Rodríguez-Pastor et al., 2016; Torre and Díaz, 2004). Thus, there is a major knowledge gap regarding how carnivores ecological patterns may be influenced by landscape edges, especially those created by anthropic landscapes, as *Eucalyptus* exotic plantations in SW Europe. Based on this scenario, the main goal of this study is to understand if and how habitat edges influence the spatial-temporal patterns of mesocarnivores in a Mediterranean humanised landscape. To address this goal, we analysed mesocarnivores' temporal and spatio-temporal patterns in edges and habitat interiors. We predict that edges can have a positive effect on carnivores' ecology as they can facilitate prey access, since predators can find different prey from both contiguous habitats than from edges (Červinka et al., 2011; Svobodová et al., 2011), and prey might be more exposed in edges and therefore more easily predated (Wirsing et al., 2010). Such effect can overrule the negative effect of an increased disturbance commonly linked to edges (Brodie et al., 2015).

2. Methods

2.1. Study area

Our study was conducted in two forestry farmsteads (Caniceira and Zambujo) located in Central Portugal (Fig. 1), characterized by a matrix of *Eucalyptus globulus* forestry plantations, but where Mediterranean vegetation (e.g., cork oak, sclerophyllous vegetation and mixed forests; Rocha et al., 2023) is also present. Both are managed by a forestry company (The Navigator Company), but the Caniceira farmstead presents a higher anthropogenic disturbance (e.g., buildings, forestry activities), and intensive management, with *Eucalyptus* trees lines well-defined, with some isolated patches of native vegetation, more humid climate and a permanent stream (Ribeira Alcolobre) bordering the western limit of the farm. Zambujo farmstead is characterized by a low intensity management (i.e., less human activities and higher understory vegetation), and a higher cover of oak trees (Tomé et al., 2013); it is characterized by a drier climate, with some temporary streams and stepper slopes, and a permanent river (Erges) located in the easter border of the farmstead.

In both study sites, the mesocarnviore community is mostly composed of generalist and common species, such as the red fox (*Vulpes vulpes*), the common genet (*Genetta genetta*), the stone marten (*Martes foina*), the European badger (*Meles meles*), and the Egyptian mongoose (*Herpestes ichneumon*) (Bencatel et al., 2017).

2.2. Study design

We considered edges as the line or area, identifiable in the field, that separates two adjacent habitats (Fig. A1). In both study sites, we set nine camera-traps in interior habitat locations (Fig. A2) (i.e., three cameras placed in the interior of each of the available habitats: native (oak) forest, *Eucalyptus* plantation and riparian vegetation patches), and nine cameras in edges (three per edge type). In Zambujo, edges between all those habitats were monitored (i.e. oak:eucalyptus, oak:riparian and eucalyptus:riparian). In Caniceira, due to the area's landscape structure no cameras were placed in the edge oak forest - riparian vegetation, since there was no contact between these habitats. Instead, we monitored the edge between a plantation of *Eucalyptus* and a plantation of pine trees (*Pinus pinea*) included in the native forest category (Fig. 1). Thus, in Caniceira we also monitored three areas of each of the available edges: oak:eucalyptus, eucalyptus:riparian and eucalyptus:pine. Cameras sites were selected to cover each of the defined habitat interior and type of edges and maintain a 500 m interval between each other to assure spatial independence of the data (e.g., Andrade-Ponce et al., 2022).

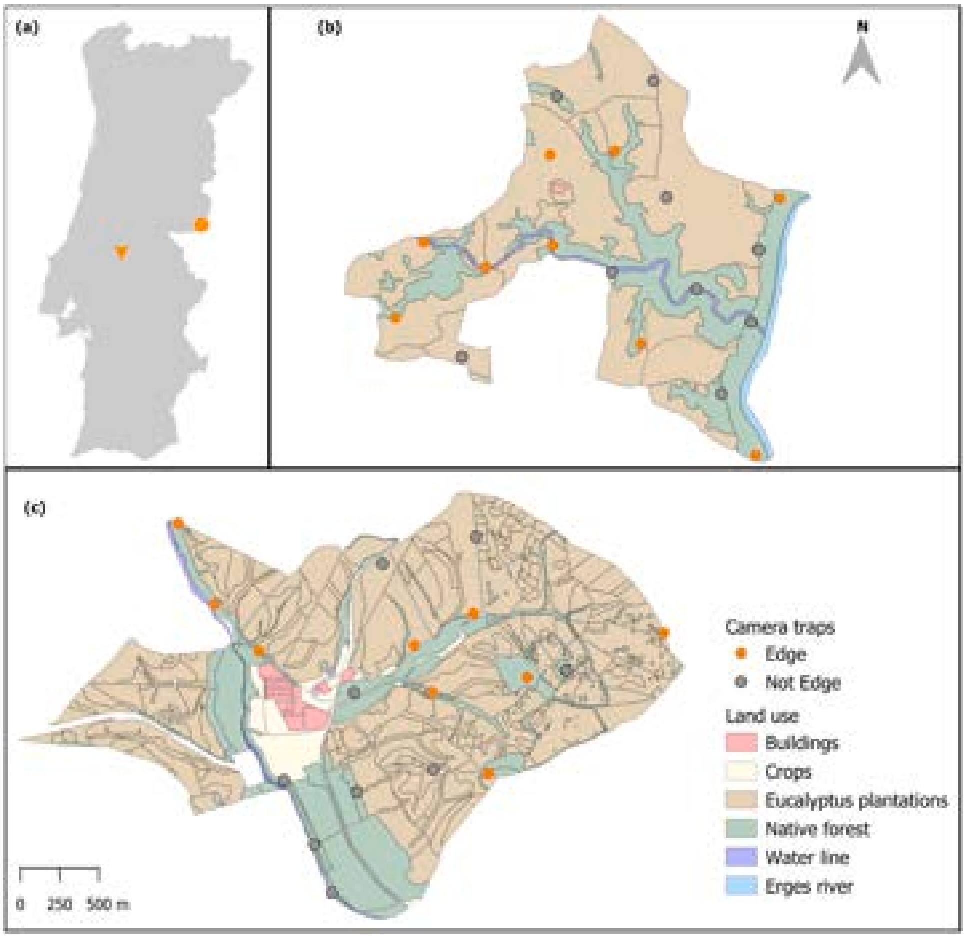

Fig. 1. (a) Location of the two farmsteads in Central Portugal, Caniceira represented by a black triangle, and Zambujo by a circle; (b) Camera trap locations within the studied land covers in the Zambujo farmstead; (c) Camera trap locations within the studied land covers in the Caniceira farmstead. Camera traps placed in edges are represented with orange circles and camera traps placed in habitat interiors (not edge) are represented with grey circles.

2.3. Carnivore survey

Between July 2020 and January 2021, we deployed 36 camera-traps (Cuddeback H-1453 and Browning BTC-7E; every habitat interior and edge type were monitored by at least one camera of each type, randomly assigned), 18 trap sites in each farmstead (Fig. 1). The average minimum distance between cameras was 435 m. Cameras were unbaited, placed on tree trunks, 30–50 cm above ground, and remained active throughout the monitoring period, which spanned 5345 active trap-nights, with 13.7 % of malfunctioning instances (i.e., nights in which cameras-traps didn’t work). Cameras were set to take three consecutive photos per trigger, with a delay of 15 s between triggering events, recording the date and time of each event, and checked every 25–30 days to replace batteries and SD cards.

We used CamtrapR (Niedballa et al., 2016) to process all the camera-trap images. A detection record was considered an independent event if a record of the same species in the same camera had a minimum time interval of 30 min to the next one (Azevedo et al., 2018). Carnivore detection histories were generated using occasions of 24 hr only for days when the cameras were operational.

2.4. Data Analysis

2.4.1. Activity pattern

We estimated the mesocarnivores’ activity pattern using the nonparametric kernel density estimator (Ridout and Linkie, 2009). Using the “solaR” package (Perpiñán, 2012), time records were converted to solar time to standardize the temporal data, accounting for variation due to study areas location and time zone and seasons (Foster et al., 2013). Time was converted into a 0–1 range and then transformed into radians (time*2π). To visualize the daily activity patterns of the mesocarnivores, we generated probability density function plots to uncover pattern variation between edge and interior habitat, using the “overlap” package (Meredith and Ridout, 2018). Density plot was calculated between edge and interior habitat for two subsets of data: i) for each mesocarnivore species, and ii) for each mesocarniore species pair. The comparison between activity patterns estimates was made by calculating the coefficient of overlap Δ1 (Ridout and Linkie, 2009; Vilella et al., 2020), which is the most accurate metric for small sample sizes (Ridout and Linkie, 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap). The precision of this estimator was accomplished by computing a standard deviation from 999 bootstrap samples (Foster et al., 2013; Ridout and Linkie, 2009). The Mardia-Watson-Wheller’s test (W) (Tasdan and Cetin, 2014) was used to compare the differences between the diel activity for all the previous combinations of mesocarnivore data, using the “circular package” (Jammalamadaka and Sengupta, 2001). We excluded the Egyptian mongoose from the analysis of the data subset, since this species presents a diurnal diel activity, and therefore not comparable with the remaining mesocarnivores that are nocturnal. All the activity pattern analyses were conducted using R Statistical Software (R Core Team, 2020).

2.4.2. Spatio-temporal analysis

We assessed the spatiotemporal relationship (i.e. segregation, neutral or aggregation) between mesocarnivores in our study sites, by using a time-to-encounter analysis approach, following Karanth and collaborators (2017). First, we established the dominant and subordinate species of a pair, using the body mass as a threshold (Monterroso et al., 2020). We considered the European badger as the dominant species in every pair (Macdonald et al., 2004), while red foxes assumed a dominant role in the presence of stone martens and common genets (Pereira et al., 2012). Finally, genets were considered dominant in relation to stone martens (López-Martín, 2006; Santos-Reis et al., 2005). We created a dataset comprising the species captures intervals, in days, between interspecific pairs. Next, we generated the expected statistical distribution of capture intervals by performing 1000 simulations where encounter times were randomly assigned to sampling stations (i.e., camera trap locations). Finally, we compared the observed median capture interval with the randomly simulated and tested for differences between the observed time-to-encounter and the randomly generated detection intervals.

We consider the existence of segregation between two species if the observed time-to-encounter period was larger than expected (i.e. larger than the median random simulated values, and assuming species independence), whereas smaller observed time-to-encounter periods indicated aggregation (Karanth et al., 2017). In the time-to-encounter plots, the vertical line corresponds to the mean observed time-to-encounter between the two species and the line represents the randomly simulated times-to-encounter density per period of days. The same procedure was followed for species detections in the habitat interior and edges.

2.4.3. *Community occupancy model*

We applied hierarchical community occupancy models to estimate species-specific occupancy probability, while accounting for imperfect detection (Dorazio and Royle, 2005). Specifically, in this framework, the model estimates the occupancy of species I at a site j, z_{ij}, as a Bernoulli random variable governed by occupancy probability ψ_{ij}. We defined occupancy as the probability of a species using the area sampled by a camera-trap (site) during our survey period. Sites have k occasions (active days of camera-trap) and records y_{ijk} are assumed to be Bernoulli distributed with detection probability p_{ijk}, conditional on the latent true occupancy z_{ij}. These two parameters can be modelled as a logit-linear function of site covariates. Species-specific parameters are random effects coming from a common underlying distribution governed by hyperparameters that are shared by the community. Hyperparameters specify the mean occupancy response and variation among species to a covariate. This model structure can improve parameter estimates for species with sparse data and simultaneously allows for inference on the community and species level (Kéry and Royle, 2020). To determine differences in baseline occupancy across edges and habitat interior among species, we estimated species-specific occupancy probabilities as random effects with edge- habitat interior-specific intercept ($\beta_{0,\ i,\ \text{edge-habitat interior}[j]}$). Moreover, we were interested in testing the influence of fine-scale environmental effects on species occupancy, namely, habitat structure and prey availability. Species-specific occupancy was modelled as a function of: i) the distance of each station to the nearest water line (D_Water); ii) the edge density within a 200-m radius buffer around each camera station (Edge_D); iii) *Eucalyptus* cover (Portugal Land Use Map, https://snig.dgterritorio.gov.pt) estimated as the proportion of *Eucalyptus* cover within a 200-m radius buffer around each camera (Euca_C); and iv) prey relative abundance in each study site, estimated using an adaptation of Pounds relative abundance index (Pounds, 1981) from small mammals live capture (Prey; see Appendix A). We selected a 200 m radius as it corresponds roughly to the core area of the largest mesocarnivore species present in each area – the red fox (0.15 km^2; Alexandre et al., 2020). The variation in detection probability was modelled as a function of site-level (camera) covariates, namely, the camera placement on or off animal/human trail (Trail, binary), and vegetation height in the vicinity (20 m), of each site (Veg_H). The 20 m radius was defined to allow us to visually estimate this variable with accuracy. Prior to analysis, we standardized all covariates with z-scores, to have a mean of 0 and standard deviation of 1, with exception of trail.

We fitted a single global model, considering the strong a priori justification for the covariates used (Curveira-Santos et al., 2017, Castro et al., 2022). We implemented the model using Bayesian Markov chain Monte Carlo (MCMC) simulation in JAGS (version 3.4.0), using R2Jags package (Su and Yajima, 2015). We ran three MCMC chains of 150 000 iterations each, with a 30 000 as burn-in, and thinned by 10 iterations. We assessed convergence using the Gelman-Rubin statistic (values < 1.1 indicate convergence; Gelman et al., 2013). We considered covariate effects significant when 95 % Bayesian Credible Intervals (BCI) did not overlap 0.

3. Results

Across the two study sites we detected five mesocarnivores with a total of 472 records in 5345 effective trap nights (Appendix A, Table A1): red fox (*Vulpes vulpes*), stone marten (*Martes foina*), European badger (*Meles meles*), common genet (*Genetta genetta*) and Egyptian mongoose (*Herpestes ichneumon*). Sites located on interior habitat had overall higher mesocarnivores records ($n = 258$) then habitat edges ($n = 214$). Red fox was the most detected mesocarnivore ($n = 161$), whereas the Egyptian mongoose was the species with the lowest number of detections ($n = 45$) (See full data description in supplementary material).

3.1. *Mesocarnivores activity and spatio-temporal pattern*

Despite a slight variation in the activity patterns estimated for edges and habitats interior, all species exhibited a high coefficient of overlap (Δ_1) in habitat edges and interior (Fig. 2), revealing no statistical differences between activity in edges and habitats interior. The European badger and the Egyptian mongoose revealed the most similar activity patterns in edges and interior habitats ($\Delta_1 = 0.81$ and $\Delta_1 = 0.86$, respectively).

The majority of mesocarnivores present in our study sites exhibited an overall bimodal nocturnal activity pattern, with higher activity near sunset and sunrise. Overall, in both areas the activity peaks were less pronounced in the habitat interiors when compared to the edges (Fig. 2). The European badger did not follow such a pattern, as they presented a unimodal nocturnal activity in the habitat interior. In habitat edges badgers revealed two main activity peaks, one near dusk and another near dawn, similarly to what was observed for red fox and stone martens. The Egyptian mongoose also did not follow this pattern, as this species presented a strictly diurnal diel activity, showing only one activity peak in habitat edges at the middle of the day and resting during the night, and two less pronounced activity peaks in habitat interiors, one near midday and the other at sunset. Common genet presented three activity peaks in edges, although the one closer to dawn was less pronounced. Moreover, our results indicate that the red fox, badger, genet activity occurs slightly later in the habitat interior, as highlighted by the mismatch delay in the two main first activity peaks in all species (Fig. 2).

The comparison between the different mesocarnivore activity patterns in the two study sites showed that species temporally overlap more in interior habitats than in habitats edges (Fig. 3). However, there isn't strong evidence to suggest a significant difference between the overlapping coefficients of species pairs in both habitat types based on confidence intervals (Table A2).

Overlap indices between red fox and badger were significantly different in both landscape contexts (Fig. 3). Additionally, badger, genet, and stone marten overlap indices revealed a significantly difference in edge and habitat interior, respectively (Fig. 3). Red fox and genet were the species pair with the most similar temporal pattern.

The spatio-temporal analysis revealed an overall unclear behaviour (higher p-values of 0.83–0.99), both for the habitat interior and edges (Table A3). Only red foxes and genets, and only in edge environments,

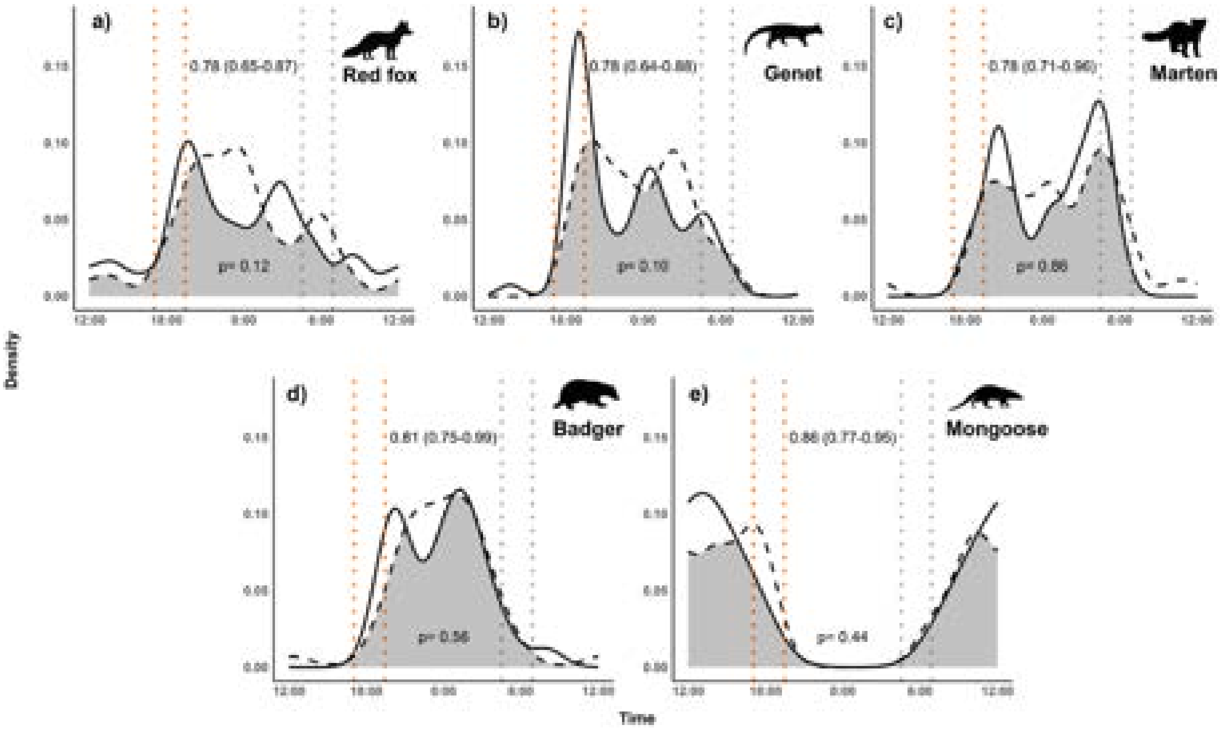

Fig. 2. Overall mesocarnivore diel activity patterns in habitat edges (black line) and habitat interior (black dashed line). Orange and grey dotted vertical lines represent the sunset and sunrise period, respectively. Shaded area represents the activity overlap. p indicates the Mardia-Watson-Wheller's test p-value. (a) Red fox, (b) Common genet, (c) Stone marten, (d) European badger and (e) Egyptian mongoose.

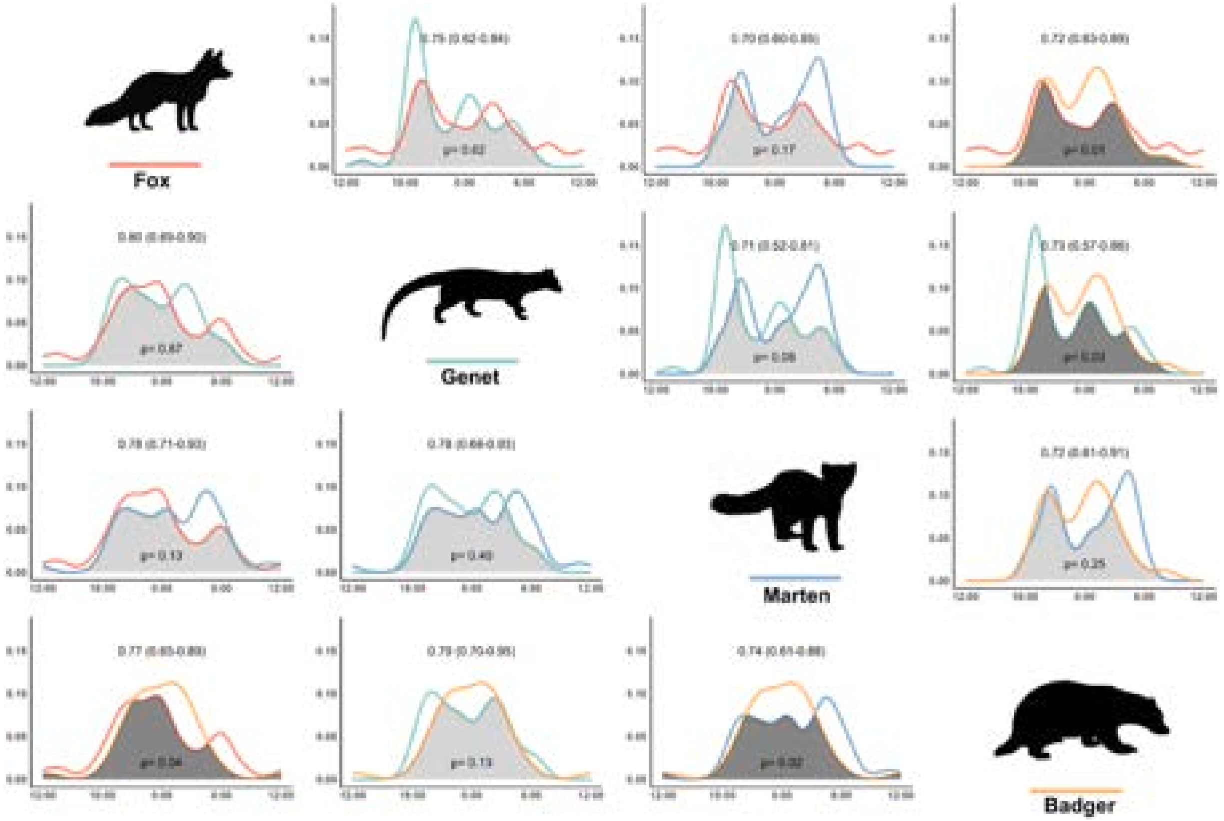

Fig. 3. Comparisons between mesocarnivore diel activity patterns on edge (right side) and habitat interior (left side). Activity patterns are showed according with species colours (under silhuette). Each graph presents: Dhat 1 indices with 95 % CI (top), and the p-value of the overlap index (bottom; Mardia-Watson-Wheele's test p-value). Darker shaded area corresponds to a significant statistical difference in activity overlap between species.

exhibited a clear segregation behaviour, since the randomly generated detection interval between both species is significantly smaller than the observed one ($p = 0.02$; Fig. 4; the remaining results are presented in the Appendix Table A3).

3.2. *Mesocarnivores occupancy pattern*

Comparing species-specific occupancy probability between sites located on the habitat edge and habitat interior, occupancy tends to have similar values (Fig. A3, Table A4). However, there is an 89.7 % probability that the stone marten's occupancy likelihood is statistically higher in interior habitat than the edge (Fig. 5).

Mesocarnivores exhibited strong associations with the site-scale variables that may influence occupancy probability, with observed responses consistent among species (i.e., BCIs not overlapping zero; Fig. 6a). Red fox occupancy was positively related to prey abundance ($\beta = 1.45$, 0.23–3.65), being this canid the only species whose occupancy showed to be promoted by prey abundance (Fig. 6a). Inversely, distance to water had a negative effect on all species: European badger ($\beta = -1.02$, -1.95 to -0.12), Egyptian mongoose ($\beta = -1.38$, -2.66 to -0.45) and common genet ($\beta = -1.04$, -1.99 to -0.15) occupancy (Fig. 6a). This pattern holds for the entire community as site-scale covariate had a community-level negative effect on occupancy ($\beta = -1.5$, -1.99 to -0.13), revealing that mesocarnivores occupancy increase near water sources (Fig. 6a). Additionally, we found a consistent occupancy species and community-level positive effect for edge density ($\beta = 1.56$, 0.46–2.83), with sites with higher edge density showing higher mesocarnivores occupancy probability (Fig. 6a). No effect of the *Eucalyptus* cover was detected in any species. Overall, species had higher detection probabilities in sites located on human/animal trail with low vegetation (Fig. 6b).

4. Discussion

Habitat fragmentation is one of the most important anthropogenic disturbances of natural ecosystems worldwide, yet our understanding of its impacts on space-demand species such as mesocarnivores remains limited. Our results suggest that the presence of habitat edges had an effect in the Mediterranean mesocarnivores' ecology, although its scale varied between the temporal and spatial dimensions and species, with implications in interspecific relationships.

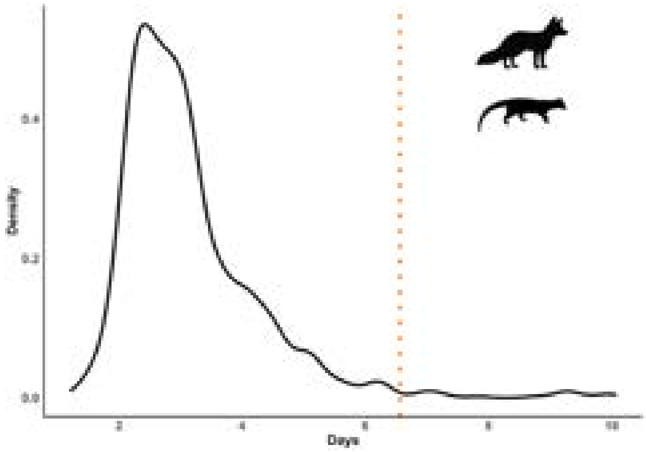

Fig. 4. Expected randomly simulated times-to-encounter density per period of days generated from a multiresponse permutation procedure for red fox and common genet for edge habitat (black line). Vertical line represents the median observed detection interval between the two species. The randomly generated detection interval (black line) is significantly smaller than the observed one (doted red line).

4.1. *Edge effects on activity patterns*

Not unexpectedly, mesocarnivores overall activity patterns showed two pronounced peaks (at dusk and dawn), a common pattern in Mediterranean Europe (e.g., Monterroso et al., 2014; Vilella et al., 2020), although less pronounced in habitat interiors. Furthermore, animals use of habitat edges occurs earlier in the night (i.e. dusk). This higher concentration of activity in shorter periods (i.e., sharper peaks) in edges might be linked to edges structural features. They are a transition zone between habitats with different structural characteristics and, in areas dominated by forestry plantations, as our study areas, edges are often more open (sometime overlapping with plantations' dirt roads), linear and an easier travel path (Kalcounis-Rueppell et al., 2013). Such characteristics may enhance the risk of encountering humans or competitors'. Therefore, edges might be used by mesocarnivores predominantly as travel corridors between resource rich patches (e.g., Barding and Nelson, 2008), with animals spending less time in these areas. Mesocarnivores might leave the habitat where they found refuge during day resting and use the edges as a faster lane to reach different habitats with complementary food resources (ecotonal effect – Lidicker, 1999; Svobodová et al., 2011), justifying the observed earlier activity peak at dusk in edges, compared to habitat interiors. At dawn, however, no such clear pattern is observed when they return to the daily resting sites in habitat interior, to use less disturbed places, such as dense bushes and tree hollows for the common genet and the stone marten (Carvalho et al., 2014; Santos-Reis et al., 2005) or dens for the European badger and the red fox (Mori et al., 2015; Silva et al., 2021). No clear increase in activity was observed in edges, which might suggest that these landscape features are not so important in their return to resting sites. Within habitat interiors species might feel less vulnerable to disturbance and thus have a more homogeneous activity during the night period.

The exceptions to the above referred pattern are badgers and mongooses. Both species show a higher activity overlap coefficient between habitat edges and interior, and only one activity peak. They differ however where the activity peak occurs: in habitat interior for the badger (a typical pattern for the species; Vilella et al., 2020) and on habitat edges in mongooses (where they may find one of their main preys in Iberia; wild rabbits *Oryctolagus cuniculus*; Palomares and Delibes, 1990). This implies that the edge effect on badgers' and mongooses' activity is less important than for the other mesocarnivores, as the pattern changes less between the two habitat contexts. In the badger's, this can be due to two different factors. First, the European badger is the largest mesocarnivore in our study area (Bencatel et al., 2018) and, as such, is the dominant species within the guild, and the one that is most likely to come out winner in case of an interaction with other species, as described in Macdonald et al., (2004). Hence, badgers might not feel the need to change its activity to avoid possible interactions with the other mesocarnivores in the study area. Second, badgers are generalist in terms of its habitat and diet (Hipólito et al., 2016; Soto and Palomares, 2015). While it might benefit from more open areas to dig in search for invertebrates, it can also use areas with a higher tree cover, where it can find insects under the tree bark (Marassi and Biancardi, 2002) or fruits that fall from trees (e.g. acorns - Rosalino et al., 2005). In Mediterranean Portugal, badgers' diet is dominated by fruits (45 % of biomass consumed) or adult or larvae insects (44 % of biomass) (Rosalino and Santos-Reis, 2009). Badgers can also predate small mammals, abundant in areas with more shrubs (Carrilho et al., 2017), and commonly detected in our camera-traps with 278 independent records (Table A1). Regarding the Egyptian mongoose, its uniqueness as the single species with a diurnal diel activity (Palomares and Delibes, 1992) may lead to an absence of need to alter the activity pattern to avoid possible interaction with other mesocarnivores which will be resting during the day, minimizing the probability of such encounters.

Mesocarnivores temporally overlap more in interior habitats than in habitats edges, indicating that the activity patterns between the species is more similar in habitat interior. In our study area, habitat interiors

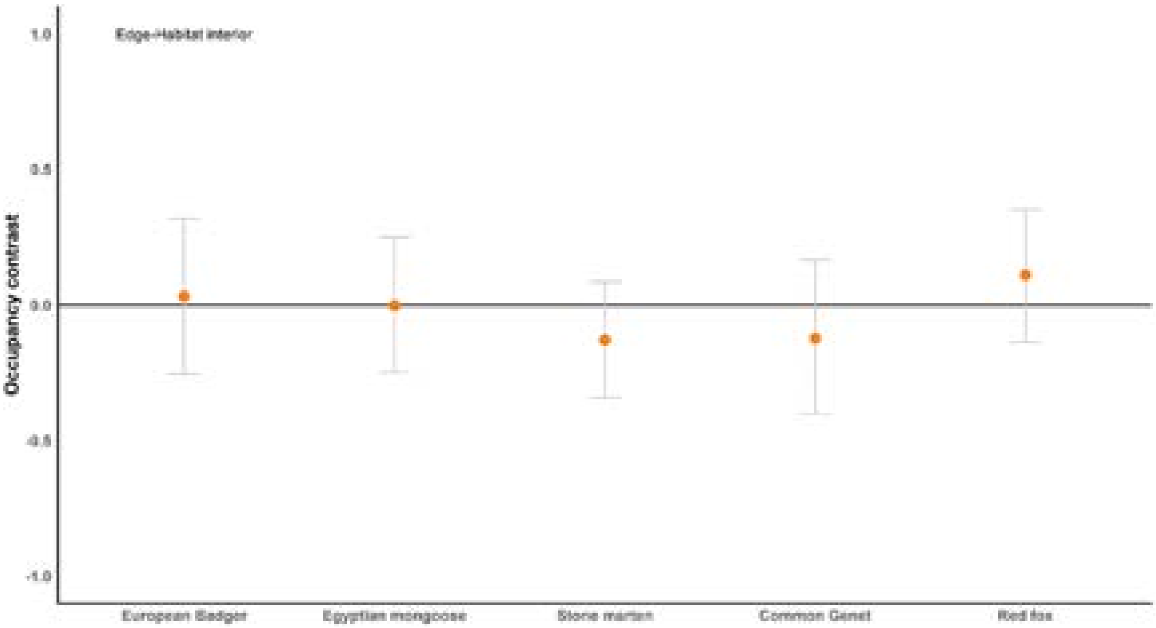

Fig. 5. Species-specific occupancy contrasts between the edges and habitat interior. Points above the horizontal bar indicate higher species occupancy in edges. Bars represent the 95 % Confidence Interval.

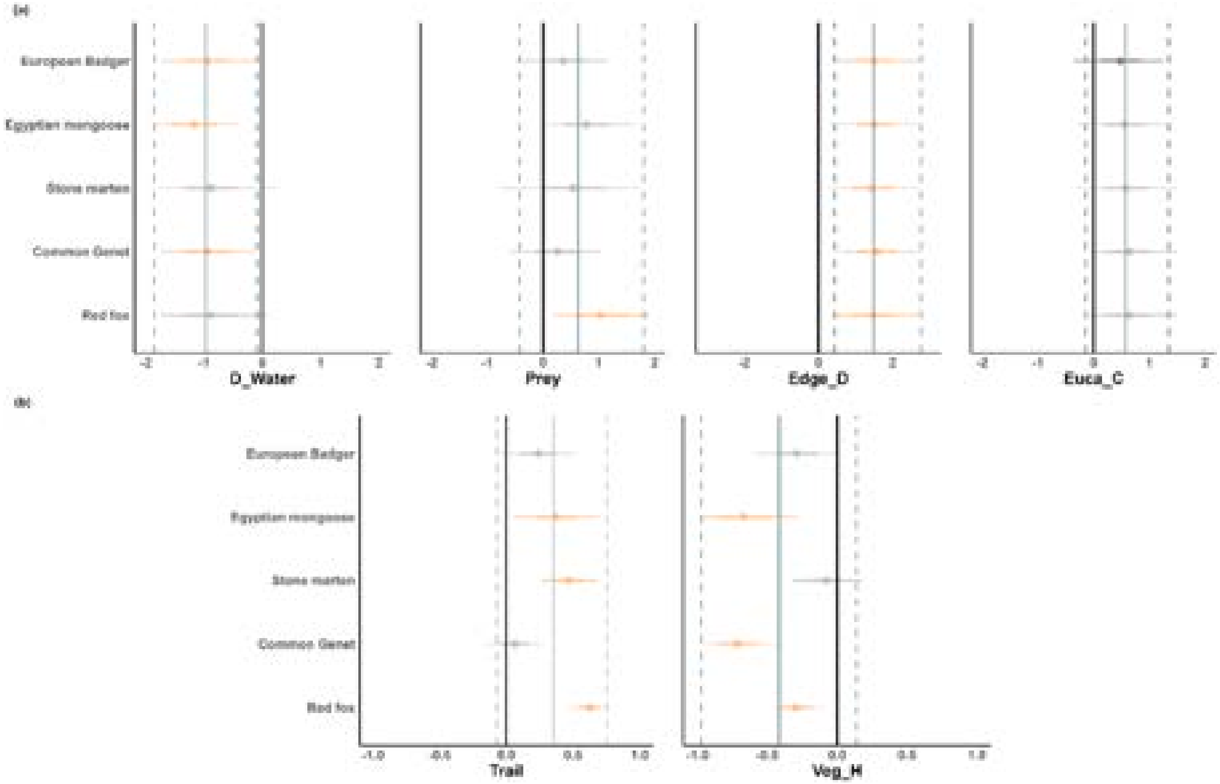

Fig. 6. Effect size of site-scale covariates on (a) occupancy and (b) detection probabilities of carnivores, from the community hierarchical occupancy model. Points are posterior distribution means and error bars represent 95 % Bayesian credible intervals (BCIs). Well-supported effects, i.e.95 % BCIs do not overlap zero are highlighted in orange. Vertical grey lines indicate community mean effects.

have a higher arboreal and shrub cover, which increases the number of possible shelters and enables species with arboreal habits to use the trees to move inside the habitat and hide under the shrubs or in tree hollows (Carvalho et al., 2014; Santos and Santos-Reis, 2010; Soto and Palomares, 2015). It further decreases the probability of encounters and consequent confront between the different species, allowing them to use the same space without the need to segregate temporarily. But there are some exceptions. Badgers showed a significant mismatch in activity with foxes in both landscape context (i.e. interior habitats and in edges), which can be related to the fact that they have more similar body sizes and habits, becoming more probable competitors (Macdonald et al., 2004) and thus coexistence may be facilitated by diverging their activity patterns.

A significantly different activity was also detected between badgers and genets, in edges, and stone martens, in habitat interiors. Santos and Santos-Reis (2010) showed that, in Portugal, stone martens forage preferably in areas far from roads and in large and complex patches of cork oak woodlands, i.e., in habitat interiors (as corroborated by the higher occupancy probability we detect for habitat interiors). Since badgers also show a similar pattern (Rosalino et al., 2004), this temporal mismatch (already detected in other Iberian areas; Vilella et al., 2020) in interior habitats may be a mechanism to facilitate coexistence (Monterroso et al., 2014), and the mentioned higher refuge provided by habitat interior (mentioned before) may not be enough to overcome this spatial interference.

The temporal mismatch between badgers and genets in edges might be shaped by the detected spatial-temporal segregation between genets and foxes in edges. The only way genets can use edges without facing higher competitors (i.e., foxes and badgers) is to avoid spatial and/or temporally these bigger predators, i.e., adopting a segregation behaviour. Since foxes and badgers may have changed their activity in edges to promote coexistence, and genets showed a spatial-temporal avoidance of foxes in edges (i.e., they avoid being active in the same place at the same time but can be active at the same time in different places) they have to temporally avoid badgers in edges to minimize contact risks. The habitat edges in our study area are a small-scale landscape unit, with less available space, being also a more open area, often with less shrub coverage. Thus, the probability of encounters between the two species and consequent interference is considerably higher in such patches. The common genet's ability to use trees and shrubs to move and take refuge could contribute to reduce the probability of encounters in habitat interiors (Pereira et al., 2012). One could be moving and feeding in the trees, while the other moves and feeds on the ground, without interacting (Pereira et al., 2012). But such avoidance mechanism is not possible on habitat edges, due to its structural characteristics and, therefore, the detected segregation behaviour could be a strategy to allow and promote the coexistence between these two mesocarnivores.

4.2. *Edge effects on spatial patterns*

Edge density was one of the drivers promoting occupancy at the species and community levels. Edges can induce higher disturbance or undesirable environmental conditions, and act as barriers to movements (Cantrell et al., 2002; Lidicker, 1999; Ries and Sisk, 2004; Svobodová et al., 2011; Wimp et al., 2019) which may affect wildlife. But they can also provide alternative or higher availability of resources, such as food, due to complementarity of environmental conditions in contiguous landscape components (Lidicker, 1999; Svobodová et al., 2011), or act as travel corridors within the landscape (Heske, 1995; Maciel and Lutscher, 2013; Šálek et al., 2010). These benefits seem to overrule the disadvantages for the mesocarnivores guild on central Portugal, in an area dominated by exotic *Eucalyptus* plantations, usually recognised as a resource poor environment (da Silva et al., 2019). This guild is composed by mostly generalist species that commonly feed on mammals, invertebrates, or fruits (Verdade et al., 2011), although with some species-related variations. For example, while the red fox is considered a generalist opportunist feeder (Soto and Palomares, 2015) that predates on small mammals whenever they are available (Papakosta et al., 2010), the common genet is considered to be at an intermediate stage between generalists and specialist (Soto and Palomares, 2015), as it feeds mainly on small mammals but will consume intensively other food resources – e.g., fruits and invertebrates – when available (Rosalino and Santos-Reis, 2002; Santos et al., 2007). Therefore, they can use whatever food resources edges can provide, especially if the alternative is, among other things, searching for food in *Eucalyptus* plantations, an anthropic system that usually support less biodiversity, and consequently, less food resources for carnivores (da Silva et al., 2019). Furthermore, species can use these components as movement lanes or scent marking sites (e.g., O'Brien et al., 2016.; Bischof et al., 2019).

The proximity to water sources (riparian areas) seems also a crucial factor promoting the occupancy of badgers, mongooses, and genets. Matos et al., (2009) already showed that Iberian riparian habitats (i.e., those where water is available) are important for mesocarnivores, with genets and mongooses reaching higher abundances in those environments when compared to areas further away from water sources. A similar pattern was detected for Iberian badgers (Molina-Vacas et al., 2009; Rosalino et al., 2004). In Mediterranean Europe these environments assume a higher importance for wildlife, especially during the xeric period where water scarcity is higher. Climate in the Iberian Peninsula is in a change pace, leading to an increase of aridity in many regions (Andrade et al., 2021), which enhance the importance of habitats that can still provide some humidity or water to wildlife. Associated to water sources are often food resources (e.g., fruits, invertebrates and small mammals) and refuge providing patches that can act as traveling corridors (Rosalino et al., 2009; Matos et al., 2009; Virgós, 2001; Santos et al., 2011), factors that may enhance their attractability by mesocarnivores.

Only foxes' occurrence patterns seem to be driven by prey availability, namely small mammal abundance. According to the review of fox's diet in Iberia (Díaz-Ruiz et al., 2013), this canid diet changes regionally, with lagomorphs and invertebrates composing the bulk of the diet in southern areas and small mammals and fruits consumption increasing towards northern regions (while lagomorphs loose importance). Our study area is located in Central Portugal, where rabbits and hares are rare (Mathias et al., 2023). Thus, we hypothesise that in the absence of lagomorphs, foxes may focus in small mammals and fruits. In such context, foxes may adapt their spatial behaviour to use areas where small mammals are present in higher abundances, to optimize food acquisition.

5. Conclusion

Habitats edges seem to affect the spatial and temporal dimensions of Mediterranean mesocarnivores ecological niche, but the effect on temporal and spatio-temporal patterns is species specific, with some species appearing to be more resilient than others to habitat fragmentation. Spatially, all individual species, and the community as a whole, are positively affected by edges, a pattern supporting our initial hypotheses. In central Portugal, the landscape context (heterogeneous environment where exotic *Eucalyptus* plantations dominate) shapes the effect of edges, and their role to support wildlife populations, a result that should be considered when managing forestry landscapes (Hatfield et al., 2020). The effect of edges in the temporal niche dimension was less clear, with some species showing a change in behaviour in edge environments when compared to habitat interiors, but no overall pattern emerged. However, the presence of edges might be a factor facilitating coexistence in heterogeneous environments, as mesocarnivores are able to use the available resources in the different landscape components by shaping their temporal behaviour to minimize interspecific encounters. These data contribute to more informed management decisions that can account for the edge effects to improve management aiming to create condition to allow plantations to maximize their ability to host native biodiversity and contribute to an effective biodiversity conservation.

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CRediT authorship contribution statement

Luis Miguel Rosalino: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation. **Margarida Santos-Reis:** Writing – review & editing, Supervision, Conceptualization. **Gonçalo Matias:** Methodology, Investigation, Formal analysis. **Rita Pereira:** Writing – original draft, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A

Fig. A1. Example of an habitat edge in the Caniceira farmstead: oak forest on the right and *Eucalyptus* plantation on the left.

Fig. A2. Example of habitat interior in the Zambujo farmstead. In this case, a habitat interior corresponding to an oak woodland.

Table A1

Number of independent records for each species detected during the survey period at each habitat and edge type.

	Species							
Farmstead	**Habitat / Edge**	**Red fox**	**Stone Marten**	**European Badger**	**Common Genet**	**Egyptian mongoose**	**Small mammals***	**Sub-total**
Caniceira	*Eucalyptus*	46	25	4	4	0	5	84
	Waterline	17	5	18	34	16	8	98
	Montado	7	4	1	3	1	18	34
	Eucalyptus – Pine Trees	10	8	0	0	3	7	28
	Eucalyptus – Waterline	19	12	6	26	23	5	91
	Eucalyptus – Montado	11	2	0	1	0	100	114
Zambujo	*Eucalyptus*	6	2	0	3	0	19	30
	Waterline	6	13	4	3	0	12	38
	Montado	15	5	11	4	1	43	79
	Eucalyptus – Waterline	5	4	4	3	1	46	63
	Eucalyptus – Montado	16	8	4	9	0	1	38
	Montado – Waterline	3	3	14	19	0	14	53
	Total	161	91	66	109	45	278	

* Unable to identify at a species level

Table A2

95 % confidence intervals (CI 95 %) of the activity overlap coefficients (Δ1) between each species pair in the edges habitat interior environments.

	CI 95 % for each Δ1	
Species pair	**Edge**	**Habitat Interior**
Red fox – Common genet	0.62–0.84	0.69–0.90
Red fox – Stone marten	0.60–0.85	0.71–0.93
European badger – Red fox	0.63–0.89	0.65–0.89
Common genet – Stone marten	0.52–0.81	0.68–0.93
European badger – Common genet	0.57–0.86	0.70–0.95
European badger – Stone marten	0.61–0.91	0.61–0.88

Table A3

Median observed time-to-encounter (days) for each species pair and the p-values of the test that indicates if the proportion of randomly generated times-to-encounter is greater than the observed. Values for each species pair and for edge and habitat interior (Statistical differences are highlighted in bold).

	Edge		Habitat interior	
Species pair	**Days**	**p-value**	**Days**	**p-value**
Red fox – Common genet	**6.56**	**0.02**	12.48	0.93
Red fox – Stone marten	27.17	0.83	6.83	0.96
European badger – Red fox	5.57	0.99	2.98	0.98
Common genet – Stone marten	22.14	0.97	9.76	0.98
European badger – Common genet	14.73	0.91	2.26	0.98
European badger – Stone marten	18.19	0.99	11.42	0.97

Table A4

Species-habitat context-specific mean realized occupancy probability estimates, standard deviation (SD) and 95 % Bayesian credible intervals (95 % BCI) from the community hierarchical occupancy model.

	Edge		
Species	**mean**	**SD**	**95 %BCI**
Red fox	0.81	0.08	0.63–0.94
Common genet	0.56	0.11	0.35–0.77
Stone marten	0.79	0.09	0.60–0.95
Egyptian mongoose	0.27	0.09	0.12–0.47
European badger	0.37	0.10	0.20–0.59
	Habitat interior		
Species	**mean**	**SD**	**95 %BCI**
Red fox	0.70	0.88	0.09–0.51
Common genet	0.67	0.85	0.09–0.47
Stone marten	0.93	0.99	0.07–0.76
Egyptian mongoose	0.27	0.47	0.09–0.11
European badger	0.34	0.58	0.11–0.15

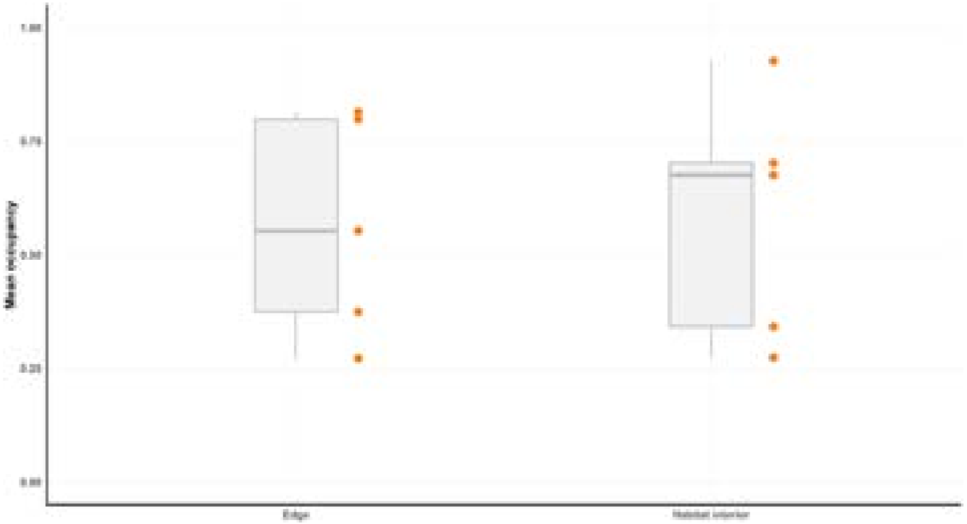

Fig. A3. Average species-specific occupancy on edges and habitat interiors from the community hierarchical occupancy model

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