UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS
DEPARTAMENTO DE BIOLOGIA ANIMAL

Ecological plasticity facilitates Mediterranean mesocarnivore spatio-temporal co-existence in an agroforestry ecosystem

Margarida Rodrigues Melo e Pinto Marques

Mestrado em Biologia da Conservação

Dissertação orientada por:
Professora Doutora Margarida Santos-Reis

2020

Este estudo foi realizado no contexto do plano de atividades do(a):

a) Protocolo de investigação estabelecido desde 2007 entre a Companhia das Lezírias, S.A. (CL) e o Centro de Ecologia, Evolução e Alterações Ambientais (cE3c), unidade de I&D da Faculdade de Ciências da Universidade de Lisboa (FCUL).
b) Plataforma LTsER Montado (http://www.ltsermontado.pt/), dedicada à investigação sócio ecológica de longo prazo do sistema Montado.

Index

Figures index

Tables index

Agradecimentos

À Professora Margarida Santos-Reis, deixo o meu primeiro agradecimento pelo apoio e orientação. Pelo acompanhamento e ajuda nas voltas que esta tese foi dando até chegar ao trabalho final.

À Sandra, por toda a ajuda e por me ter recibo de braços-abertos. Por desde o início ter vivido o trabalho de campo com o mesmo entusiasmo como se fosse a sua tese, e por ter sido a minha salvação e da fotoarmadilhagem nestes estranhos tempos pandémicos.

À Maria, pela companhia e ajuda no trabalho de campo. À Ana Luísa, por ter levado o material para a quinta pedagógica e pela ajuda que me deu mais tarde.

À Companhia das Lezírias e ao Engenheiro Rui Alves por me terem recebido e por terem permitido a realização deste projecto. E ainda, a todos os Guardas-florestais com quem nos fomos cruzando que sempre se mostraram disponíveis para ajudar, incluindo por nos terem ido salvar da pedra no disco do pneu.

Por último, deixo os agradecimentos mais especiais. Ao meu pai e ao André, pela longa viagem para levar as caixas até à Companhia das Lezírias. Aos meus pais e aos meus irmãos, pelo apoio incondicional que sempre me deram para atingir os meus objectivos. Espero que sintam orgulho no que alcancei (alcançámos). Ao André, pela incansável companhia nas idas para o campo, e pelo incentivo para passar este desafio e sonhar com o que se avizinha. Muito muito obrigado, a conclusão desta etapa deve-se a vocês e é também para vocês!

Resumo

O estudo de relações interespecíficas entre predadores, enquanto modeladores da estrutura e funcionamento do ecossistema, é um tópico de relevância em biologia da conservação, especialmente no contexto de sistemas geridos ou perturbados, dada a alarmante perda de habitat e espécies em vários ecossistemas. Os efeitos da perturbação, principalmente com origem antropogénica, inerentes a habitats mediterrânicos, têm intensificado a coexistência interespecífica, e consequente competição, o que se traduz na crescente importância do estudo dos mecanismos de simpatria e comportamentos de adaptação adotados por estes predadores. Para garantir a coexistência de espécies potencialmente competidoras e a persistência de comunidades resilientes, estas devem segregar, pelo menos parcialmente, ao longo de um ou mais eixos do seu nicho ecológico. No entanto, as espécies apenas têm a capacidade de adotar estratégias de coexistência dentro do que seus limites biológicos permitem, no sentido em que estes mecanismos são inerentemente mediados por características morfológicas e comportamentais específicas de cada espécie. Estas mesmas estratégias adquirem uma crescente complexidade em sistemas alvo de impactos antropogénicos, em que a disponibilidade de recursos varia consideravelmente relativamente a meios naturais, e as estratégias dinâmicas de adaptação por parte das espécies são um requisito para a respetiva sobrevivência e coexistência.

Para abordar esta temática, o presente estudo foi realizado num ecossistema agroflorestal ativamente gerido - a Companhia das Lezírias, S.A. -, cuja paisagem é dominada por Montado de sobro, um sistema agro-silvo-pastoral maioritariamente representado por uma matriz de sobreiro com subcoberto de variadas densidades, intercalada por plantações de outras espécies de árvores, culturas e manchas de vegetação natural, contribuindo para a heterogeneidade da paisagem. Esta paisagem caracteriza-se por um elevado dinamismo espaço-temporal devido às medidas de gestão e às condições climáticas da região, resultando numa resposta complexa por parte das comunidades bióticas. O conhecimento mais aprofundado acerca desta resposta, concretamente do seu efeito nas interações interespecíficas, é fulcral para o estabelecimento de medidas de gestão mais adequadas ao alinhamento dos objetivos de produção com os esforços de conservação.

Enquadrado na teoria do nicho ecológico, e no seu conceito de nicho multidimensional, este estudo pretendeu investigar as interações entre pares de mesocarnívoros, considerando a partição de nicho a três níveis distintos, de forma a representar adequadamente a complexidade destas interações. Primeiramente, avaliando a dimensão temporal, estudou-se a sobreposição dos padrões de atividade de cada par de espécies, esperando-se uma elevada sobreposição noturna, complementada por uma segregação parcial do tempo (H1). Segundo, procurou-se investigar as relações interespecíficas espaciais com recurso a modelos de ocupação de duas espécies, estação única. Para este objetivo, propõe-se como hipótese a agregação espacial entre pares de espécies, no entanto, espera-se também uma segregação espacial a escala fina, potenciada pela resposta heterogénea, de caracter específico, a fatores ambientais (H2). Por último, pretendeu-se ainda estudar as interações associadas ao uso simultâneo do espaço e do tempo, avaliando o tempo entre encontros de pares de espécies com recurso a um procedimento de permutação multiresposta. A este nível, espera-se que a coexistência interespecífica seja facilitada através da partição espaço-temporal do nicho (H3).

Para o efeito, estabeleceu-se uma rede de 25 estações de amostragem, distribuídas equitativamente ao longo da área de estudo para representar de forma adequada a heterogeneidade do sistema, sendo que em cada estação se procedeu à instalação de uma câmara fotográfica e à amostragem de vários fatores ambientais. Com recurso a 5 meses de armadilhagem fotográfica, realizou-se a monitorização da comunidade local de mesocarnívoros com foco em 5 espécies: raposa (*Vulpes vulpes*), fuinha (*Martes foina*), texugo europeu (*Meles meles*), geneta (*Genetta*

genetta) e sacarrabos (*Herpestes ichneumon*). Com base no conhecimento prévio acerca da ecologia dos mesocarnívoros mediterrânicos, para efeitos de análise foram selecionados fatores ambientais que se prevê serem determinantes para a utilização do espaço por parte das espécies em estudo. Estes fatores ambientais foram categorizados consoante a sua relevância ecológica em variáveis de habitat, fonte de alimento ou perturbação, e amostrados num buffer de 350 metros em redor de cada estação de amostragem.

O esforço de amostragem consistiu em 3104 dias efetivos de armadilhagem fotográfica, e resultou num total de 724 registos independentes das espécies alvo. A espécie mais detetada foi a raposa, com 245 registos independentes, seguida pelo sacarrabos, com 181 registos independentes, e o texugo, com 136. Esta última espécie apresentou a ocupação *naïve* mais elevada, sendo detetada em 18 das 25 estações de amostragem. Contrariamente, a fuinha, com o menor número de registos independentes, foi também a espécie com menor ocupação *naïve*, sendo detetada em apenas 52% das estações de amostragem.

Ao nível da dimensão temporal, observou-se uma elevada sobreposição entre os pares de espécies durante o período noturno, tal como esperado, sendo que a exceção foi a única espécie estritamente diurna – o sacarrabos. Adicionalmente, também se verificou uma segregação parcial temporal devido ao uso dessincronizado das horas de noite através do desfasamento dos principais picos de atividade. Pensa-se que esta estratégia contribui para evitar encontros agonísticos, favorecendo assim a coexistência interespecífica.

Relativamente ao uso do espaço, dois pares de espécies (raposa – sacarrabos, geneta – fuinha) demonstraram agregação espacial, enquanto que os restantes pares coocorreram de forma independente; não obstante, a detetabilidade da maioria das espécies revelou-se condicional à presença do par. Apesar de não se ter observado um efeito evidente das variáveis ambientais na ocupação dos mesocarnívoros, a segregação espacial a uma escala fina parece contribuir para um cenário de coexistência, graças à resposta heterogénea, específica de cada *taxa*, a fatores de habitat, alimento e perturbação. Com base no conhecimento prévio acerca da comunidade de mesocarnívoros mediterrânicos, pensa-se que este padrão espacial de facilitação da coexistência interespecífica poderá ocorrer na área de estudo.

A nível espaço-temporal, observaram-se padrões de alteração do comportamento no sentido da agregação, indicando que o tempo entre encontros dos pares de espécies é menor do que o estatisticamente esperado. Como tal, sugere-se que as espécies devem segregar ao longo do nicho trófico para permitir esta sobreposição. Considerando os hábitos alimentares generalistas dos mesocarnívoros mediterrânicos, pensa-se que a variedade de recursos utilizada, incluindo fontes vegetais, é um dos principais catalisadores de cenários de coexistência.

O presente estudo contribui para demonstrar a plasticidade ecológica como fator determinante para promover a coexistência de mesocarnívoros mediterrânicos através da: i) dessincronização dos padrões diários, e portanto fazendo uso da partição parcial de tempo; ii) resposta heterogénea a fatores ambientais, originando cenários segregação espacial a escala fina; e iii) segregação de hábitos alimentares, facilitando a coexistência espaço-temporal. O conhecimento adquirido assume um papel crucial na melhoria das medidas de gestão em ambientes onde se verifica a influência antropogénica com fins de exploração, permitindo o alinhamento dos objectivos de produção com os esforços de conservação. Adicionalmente, a utilização de modelos de ocupação de duas espécies, estação única, que permitem conclusões mais robustas acerca das interações interespecíficas espaciais do que métodos utilizados anteriormente, bem como a inclusão da análise da partição de nicho a nível espaço-temporal, contribuíram para complementar o conhecimento já existente na área de estudo. No entanto, recomenda-se que futura investigação inclua estudos a longo prazo e de estação múltipla, permitindo corroborar as presentes conclusões, e ainda incorporar os efeitos da sazonalidade e da dinâmica das características ambientais e ecológicas de áreas mediterrânicas geridas com objetivos de exploração e produção.

Palavras-chave: Carnivora; uso do espaço e do tempo; nicho ecológico; foto-armadilhagem; interações interespecíficas, modelos de ocupação.

Abstract

The study of interspecific interactions among predators is a topic of scientific relevance in conservation biology, especially in the context of production systems given the alarming habitat and biodiversity loss that has been occurring across all kinds of ecosystems. The disturbance effects upon habitats, inherent to most Mediterranean habitats mainly due to anthropogenic causes, are increasing the overlap between species, and consequent competition, becoming increasingly important to study the species coexistence mechanisms and adaptative behaviours. To achieve a resilient community favouring species coexistence, competing species must segregate, at least partially, along one or more axes of the ecological niche. However, species can only adopt coexistence strategies within the limits of their biology, giving these mechanisms are inherently mediated by specific morphological and behavioural traits. These same strategies become increasingly complex in man-shaped ecosystems, where the environmental factors vary significantly, and species assume a dynamic response accordingly.

To address this subject, the present study was conducted at an actively managed agroforestry ecosystem, Companhia das Lezírias, S.A., where a rich mesocarnivore community inhabits, represented by the red fox (*Vulpes vulpes*), the stone marten (*Martes foina*), the European badger (*Meles meles*), the common genet (*Genetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*). Based on a 5-month camera trapping approach with 25 sampling stations, we aim to give a better understanding on the underlying mechanisms that allow the Iberian mesocarnivore community to coexist in an intensively exploited Mediterranean ecosystem. Framed by the ecological niche theory, and its concept of the multidimensional niche, we investigated the pairwise mesocarnivore interactions considering the temporal, spatial and spatio-temporal ecological niche partitioning, to properly reflect the ecological complexity of mesocarnivores interactions.

The sampling effort resulted in 3104 effective trapping days, with a total of 724 independent records of the target species. The species most detected was the red fox, with 245 independent records, followed by the Egyptian mongoose and the European badger. This last species showed the highest *naïve* occupancy, being detected in 18 of the 25 sampling stations. Contrarily, the stone marten, with the lowest number of independent records, also presented the lowest *naïve* occupancy, being detected in 52% of the sampling stations.

On a temporal dimension, we studied the activity patterns and the degree of overlap in the diel cycle use. As expected, with the exception of the Egyptian mongoose, a high nocturnal overlap was observed for the other species but with partial time segregation through the asynchrony on the diel cycle use. This strategy is thought to contribute to avoid agonistic encounters, therefore favouring coexistence. Regarding space use, two species pairs (red fox – Egyptian mongoose, common genet – stone marten) showed spatial aggregation, while the remaining co-occurred independently; nevertheless, most species detectability was conditional on the species pair presence. Despite the observed weak effect of environmental covariates in mesocarnivores' occupancy, a fine-scale spatial segregation facilitates coexistence, due to a heterogenous response to habitat, food and disturbance factors. When considering time and space simultaneously, a behaviour displacement towards aggregation was observed, suggesting that species must segregate along the trophic niche to coexist. Given the generalist dietary patterns of most Mediterranean mesocarnivores, we assume the differential use of a variety of food resources, including vegetable materials, as a major niche contributor to species coexistence and a resilient community.

This study shows the ability of Mediterranean mesocarnivores to take advantage of their ecological plasticity in order to coexist, i) by desynchronizing their diel cycle use, and therefore partitioning time use; ii) by segregating in space at a fine-scale; iii) by segregating in their dietary patterns, to facilitate spatio-temporal coexistence. This knowledge can be useful to improve the current management decisions in man-shaped ecosystems, aligning exploitation aims and conservation efforts. We would, however, recommend further research to be based on long-term data considering a multi-season approach, to corroborate the reliability of our conclusions, and ultimately to properly address the seasonality and dynamics of Mediterranean areas' environmental and ecological features.

Keywords: Carnivora; time and space use; ecological niche; camera-trapping surveys; pair-wise interactions; occupancy modelling.

1. Introduction

1.1.1 *Species interactions in a competition context*

Species interactions occur along the full array of biotic and abiotic conditions where organisms survive and reproduce, being determined as the fundamental ecological niche (Elton, 2001). These interactions can emerge at several levels and vary in intensity, but competition has been broadly recognized as one of the primary drivers for defining community structure (Schoener, 1983; Tilman., 2004; Hunter & Caro, 2008; Mpakairi et al., 2017). Competition is defined as a biotic interaction resulting in negative effects on one organism upon the consumption, or control of access to, a limited resource by another organism (Keddy, 1989).

The strength of interactions among species in a community tends to be highly asymmetric, with species organized in competitive dominance hierarchies where dominant species may outcompete subordinates. This asymmetry is predicted to be mediated by density (Křivan & Schmitz, 2004), morphological adaptations (Donadio & Buskirk, 2006) and relative body size (Palomares & Caro, 1999; Monterroso et al. 2020) or to be contingent with behavioural traits (Hunter & Caro, 2008). The dominant species distribution is expected to be influenced mainly by resources availability, while the subordinate species must find a balanced trade-off between the most profitable resources and its safety (Heithaus, 2001).

Depending on the mechanisms that potentiate the species interaction, two categories were identified: exploitation competition (Schoener, 1983) and interference competition (Case & Gilpin, 1974). In the former category, the use of resources by one species deprives its use by a competitor, which can limit its fitness (Schoener, 1983). This indirect form of competition can occur when there are asymmetric competitive abilities to use limited resources, and the most apt species outcompetes the other. The interference competition, also described as direct competition, occurs when one individual is aggressive towards another, hindering the access to the shared resource (Case & Gilpin, 1974). An example of this interaction is intraguild predation, when killing and sometimes consumption occurs among competitors, resulting in two advantageous outcomes for the dominant species: energetic gain and potential competition decrease (Polis et al., 1989). This form of competition has been recognized to influence species abundance and distribution (Fedriani et al., 2000), although highly mediated by habitat structure (Janssen et al., 2007).

The concept of competition has been extended to the competitive exclusion principle (Hardin, 1960), establishing that “complete competitors cannot coexist”. In communities of sympatric non-interbreeding populations, if relying on the same ecological niche in Elton’s sense[1], the population with the faster growth rate will eventually outcompete the other, leading to its extinction. Realising the reality of coexistence among competitors should be more complex, the limiting similarity theory (MacArthur & Levins, 1967) proposed an improvement on the former principle. This hypothesis stated that, to preserve a sustainable coexistence, competing organisms or populations must segregate, at least partially, along one or more axes of the ecological niche. Therefore, species are compelled to exploit alternative resources, segregating along one or more of the following axes: trophic, temporal and spatial (Schoener, 1974).

Regarding the trophic dimension, food resources are vital for any organism. It heavily affects the use of space and time, for example by directly shaping the individual home range, to

---

[1] an organism’s “place in the biotic environment, its relations to food and enemies” (Elton, 2001). The concept is based on invariances in the communities; therefore, “place” does not stand for a geographical position, but rather the organism role in the community. Similar sized species with similar feeding habits were assumed to share the ecological niche.

answer its metabolic needs (Gittleman & Harvey, 1982; Kelt & Van Vuren, 2001), or by adapting its activity patterns according to its prey rhythms (Monterroso et al., 2013).

Interspecific interactions are highly mediated by trophic requirements, and it is predicted that competitors sharing food resources segregate: i) *spatially*, if food is widely distributed, ii) *temporally*, if food distribution is spatially restricted and there is a need to avoid agonistic encounters, or, ideally, through iii) *trophic niche segregation*, if at least one of the species is not a food specialist. Therefore, the tropic niche must be analysed considering the other two niche axes, temporal and spatial.

Along the temporal dimension of the ecological niche, each species activity pattern is endogenously regulated and dependent on specific ecological traits (Kronfeld-Schor & Dayan, 2003). However, time-related species interactions are determined not only by species-specific traits, but also by abiotic and external biotic factors, as for example human disturbance (Moll et al., 2018), prey's activity patterns (Monterroso et al., 2013) or the presence of competitors (Cozzi et al., 2012). Time partitioning becomes a highly important coexistence mechanism when species overlap on other dimensions, as the disparity in the diel cycle use facilitates sharing a preferred habitat or a profitable prey, while avoiding agonistic encounters.

On the spatial axe of species ecological niche, space use is determined by species-related (morphological and/or behavioural) and environmental features. Species' physical and physiological adaptations and habitat preferences, availability of food resources, refugee opportunities and the risk of predation influence spatial patterns (Jones & Barmuta, 2000; Mortelliti & Boitani, 2008; Schuette et al., 2013). As these factors determine species-specific space use, they will consequently reflect on species interactions as well. The community dynamics along the spatial dimension remains as a very important determinant of interspecific competition, as it can constrain the access to profitable food resources or to the most adequate habitat (Fedriani et al., 2000), and therefore affect species fitness. Spatial competition can reflect the asymmetrical relationship by leading the subordinate species to change its space use at the landscape level or, at finer-scales, for example by restricting its activities to less optimal habitat patches (Pereira et al., 2012). Spatial partitioning strategies, such as differential habitat selection, have been reported to successfully mediate interactions promoting competitors' coexistence (Pereira et al., 2012; Schuette et al., 2013; Soto & Palomares, 2015; Torretta et al., 2016; Monterroso et al., 2020).

Given their high spatial and food requirements, interspecific competition can occur severely among top predators (Fedriani et al., 2000), and the underlying mechanisms have been widely studied in carnivores due to their cultural value, wide distribution ranges and great variety of morphologic and behavioural features (Dayan & Simberloff, 2005). The partial niche partitioning processes mentioned above, represented by character or behavioural displacement, are inherently mediated by morphological features and behavioural mechanisms. Characteristics like dentition (Davies et al., 2007) or body-size (Monterroso et al., 2020), and strategies such as space partitioning (Soto & Palomares, 2015), temporal activity desynchrony (Vilella et al., 2020) and segregation of dietary patterns (Carvalho & Gomes, 2004) have been documented as a mechanism facilitating the coexistence of sympatric carnivores.

The inherent complexity of carnivores' interactions requires, therefore, a multidimensional analysis, where spatio-temporal patterns should also be accounted. Studies considering only one of the axes of the ecological niche might not properly represent the community structure if species apport the space and time simultaneously. To date only a limited number of studies have addressed the multidimension context of competition (Karanth et al., 2017; Moll et al., 2018; Farris et al., 2020), and further research is still needed in order to give a deeper understanding on communities' dynamics and improve conservation management accordingly.

1.2 The rise of mesocarnivores

Carnivores play a crucial role in the ecosystem functioning, structure and dynamics (Jiménez et al., 2017). Although their abundance can be relatively sparse across landscapes, working as ecosystem engineers they can impact on several ecological services, by directly or indirectly influencing the availability of resources for other species (Vandermeer & Perfecto, 2007; Ritchie et al., 2012). Mammalian predators contribute to ecosystem resilience against introduced species (Carlsson et al., 2010) or, in some cases, as seed dispersers (Rosalino & Santos-Reis, 2009), and yet the ecological function that has cascading effects over the entire ecosystem is top-down regulation (Ripple et al., 2014). As predators, carnivores can directly influence their prey density, and consequently shape the trophic levels below, impacting on a demographic level (Estes, 1996). This phenomenon could possibly result in the thriving of weaker competitors, if the density of their dominant competitor, the carnivore's prey, is reduced (Estes et al., 2001). On a behavioural level, carnivores can indirectly influence their prey or subordinate species habits to make itself less vulnerable to predation, affecting its distribution, foraging strategies, group size and activity patterns (Miller et al., 2001) - which therefore reflects deeply on the ecosystem dynamics and biodiversity, for example by promoting coexistence of sympatric competitors.

The survival and persistence of a carnivore population can be severely affected by anthropogenic impacts. Human disturbance has been, disgraceful on a world scale, directly or indirectly impacting ecosystems through habitat fragmentation and disruption of ecological processes (Crooks, 2002; Baker & Leberg, 2018; Sévêque et al., 2020). These impacts, along with direct persecution (Ripple et al., 2014), resulted in an overall decline of top predators' populations, a phenomenon determined as trophic downgrade (Estes et al., 2011), and a consequent narrowing of their distribution due to regional extinctions (Michalski & Peres, 2005).

The extinction of apex predators has caused the population growth of species at the food web intermediate levels (Verdade et al., 2011), such as mesocarnivores, that are now released from the former suppression effect (Ritchie & Johnson, 2009). A mesocarnivore has been defined based on body weight, representing a mammalian carnivore with mean proportions of 1-15 kilograms (Roemer et al., 2009). Later, Prugh et al. (2009) proposed that it should be defined as a mammalian predator with a midrank position in the food web, despite its size. Today's reality of apex predators' extinction allowed the mid proportion carnivores to rise from their intermediate food web levels to top positions. Therefore, a midsize carnivore, here after mesocarnivore, can perform as an apex predator in environments where larger carnivores are absent, while still acting as a mesopredator in different geographical contexts (Roemer et al., 2009).

The mesocarnivores fitness is highly favoured by the decreased interference and exploitative competition that resulted from apex carnivores' extinction, leading these to be responsible for top-down effects in many places (Prugh et al., 2009). The decline in intraguild predation and consequent mortality rate, and the increase in resources availability and subsequent natality rate, both contribute to mesocarnivores' higher abundance (Prugh et al., 2009; Verdade et al., 2011). This phenomenon is described under the mesopredator release hypothesis (Ritchie & Johnson, 2009), and can have aggressive impacts in ecosystems structure and dynamics (Prugh et al., 2009). The species now performing the role of top predators fundamentally differ from these species, diverging in their biological traits and ecological requirements (Cove et al., 2012).

The release deriving from the suppression effect and the decreased predation risk, leads mesocarnivore communities to be regulated by the increased intraguild competition over the same space and resources (Roemer et al., 2009). As mentioned previously, to sustainably coexist, species adopt different strategies within their multidimensional ecological niche. These strategies, along with the resulting impact on the ecosystem structure, has been subject of study due to its relevance for appropriate conservation management (Ripple et al., 2013). Nonetheless, this matter should remain as major concern considering species can adopt different strategies along their distribution range, hence, the interspecific interactions and the coexistence mechanisms are local-specific (Kneitel & Chase, 2004; Grant & Grant, 2006).

1.3 The human-shaped Mediterranean landscape and its effects on carnivores

One of the most important biodiversity hotspots in Europe is the Iberian Peninsula, situated at the western Mediterranean basin (Myers et al., 2000). Here the landscape is a combination of human-shaped areas deeply connected with natural areas (Blondel et al., 2006). Over time, native habitats have been replaced by agricultural or forestry areas, strongly influencing ecosystem structure and community composition and dynamics.

In southern Portugal, today's landscape is predominantly represented by the Montado ecosystem, an agro-sylvo-pastoral system mainly composed by a matrix of cork (*Quercus suber*) or holm (*Quercus ilex*) oak woodland interspersed by patches of other tree species and shrubby understory of varied density. This ecosystem resulted from centuries of resource exploitation progressively converting the original landscape in a man-shaped one (Pinto-Correia, 2000). Depending on the local conditions and the anthropogenic activities and management options that occur, the Montado landscape may potentiate a high habitat heterogeneity that favours a diverse animal community (Rosalino et al., 2009). Consequently, despite the human disturbance, the Portuguese Mediterranean landscape is still inhabited by a rich carnivore community (Bencantel et al., 2019)

A heterogenous landscape may benefit species resource use, as the variety of habitat patches potentiates the use of different primary resources (landscape complementation) and supplements the alternative resources intake (landscape supplementation) (Dunning et al., 1992). The complementation and supplementation between the cork oak woodland matrix and other habitats, such as the riparian vegetation or the orchard yards, provide a variety of resources allowing different ecological responses from the carnivore guild (Rosalino et al., 2009). Riparian habitats are especially important in semi-arid ecosystems (Gonçalves et al., 2011; Grilo et al., 2016; Santos et al., 2016), providing water, food, shelter and anti-predator cover (Rosalino et al., 2009). The orchard yards become particularly significant as food resource, given the importance of fruits and other vegetable materials in Mediterranean carnivores' diet (Rosalino & Santos-Reis, 2009).

It has been therefore suggested that this man-shaped heterogenous landscape of cork oak woodland interspersed with other habitats may benefit mesocarnivores communities, given the higher resource abundance and easier accessibility than in natural systems (Pita et al., 2009; Rosalino et al., 2009; Verdade et al., 2011). Nonetheless, these features only seem to favour generalist species, more apt to take advantage of a wide spectrum of habitats and the characteristic seasonality of Mediterranean environments. Contrarily, specialists may face local extinction, or a severe population decrease if lacking the habitat where their main resources were available (Carvalho et al., 2011).

If the anthropogenic activities and management options surpass the moderate threshold, instead of benefiting from habitat heterogeneity, the mesocarnivore community, and the overall ecosystem, may suffer severe impacts. High cattle grazing pressure and direct human interference are major drivers of ecosystem disruption, mainly because both are associated with understory destruction or removal (Gonçalves et al., 2011). Shrubs can be removed either as a result of management options (e.g. for fire prevention - Mangas et al., 2008), or as a consequence of direct consumption from cattle and other large herbivores (Dotta & Verdade, 2007). However, the conservation of shrub cover in Mediterranean habitats should be of conservation concern, as it is essential to minimize predation risk, provide food sources and serve as shelter (Lozano et al. 2003; Mangas et al., 2008). The destruction of such a habitat feature that represents an essential ecological requirement for many species, can affect the mesocarnivore community. This management option, and other highly disturbing practices, may therefore contribute to loss of habitat connectivity, affecting the resource use along all axes of the species ecological niche (Sévêque et al., 2020).

Previous studies have documented the niche partitioning among carnivores communities in natural systems (Fedriani et al., 2000; Monterroso et al., 2013; Monterroso et al., 2020; Tsunoda et al., 2020). However, due to the high complexity of mesocarnivores' response to the anthropogenic disturbance factors previously mentioned, and the need to improve management practices, further efforts must be carried in order to conciliate production and conservation aims, preventing an irreversible scenario of agricultural intensification and habitat loss.

1.4 Study aims

The ultimate goal of this study is to contribute to a better understanding of the underlying mechanisms that allow the coexistence of a rich mesocarnivore community in an intensively exploited Mediterranean agroforestry system.

Framed by the ecological niche theory, and its concept of the multidimensional niche, the specific aim of this study was to investigate pairwise mesocarnivore interactions considering the temporal, spatial and spatio-temporal ecological niche partitioning, to properly reflect the ecological complexity of mesocarnivore interactions. Using this approach, we addressed 4 hypotheses.

(H1) High nocturnal overlap in activity patterns but with a partial time segregation.

(H2) Spatial aggregation between species but with fine-scale space segregation.

(H3) Species coexistence facilitated through the spatio-temporal niche partitioning.

To address H1 we investigated the activity pattern of the coexisting mesocarnivores and the degree of overlap in their diel cycle use. Considering previous studies documenting mesocarnivores' behavioural traits in natural and semi-natural Mediterranean environments (Monterroso et al., 2013; Almeida, 2016; Vilella et al., 2020) and, in particular, a study conducted in our study area (Curveira-Santos et al., 2017), we hypothesize a high nocturnal overlap in the activity patterns of the studied species but with partial time segregation (H1), as this behaviour has been documented to facilitate coexistence among sympatric carnivores (Monterroso et al., 2014; Torretta et al., 2016; Vilella et al., 2020).

As for H2, we studied the occupancy patterns of the local mesocarnivore community and the environmental and ecological drivers of the observed spatial interactions. We assessed competitors' coexistence on an asymmetrical pairwise analysis and hypothesize that, given the characteristics of this Montado ecosystem, species pairs spatially aggregate within the limits of their biology, while also spatially segregating at a fine-scale. The fine-scale segregation pattern is expected to be a consequence of the heterogeneous spatial response to habitat features and food resources, given the diversity of species-specific ecological requirements and the complexity of the studied ecosystem. Predictions also include an impact of cattle grazing, as it has been shown to interfere with mesocarnivores habitat use (Gonçalves et al., 2011; Curveira-Santos et al., 2017).

To address H3 we study the spatio-temporal interactions, assessing scenarios of fine-scale behaviour displacement through the time between encounters of species pairs. We hypothesize species facilitate coexistence through partial niche differentiation, potentiated by the man-shaped ecosystem characteristics, by adopting spatio-temporal segregation patterns.

2. Study Area

The study was conducted at Charneca do Infantado, which is part of Companhia das Lezírias, S.A. (CL), an agroforestry farmstead located in the Lezíria do Tejo (Ribatejo province), northeast of Lisbon (Figure 2.1). The Charneca occupies an extension of 8,853 hectares and is a multi-use landscape[2].

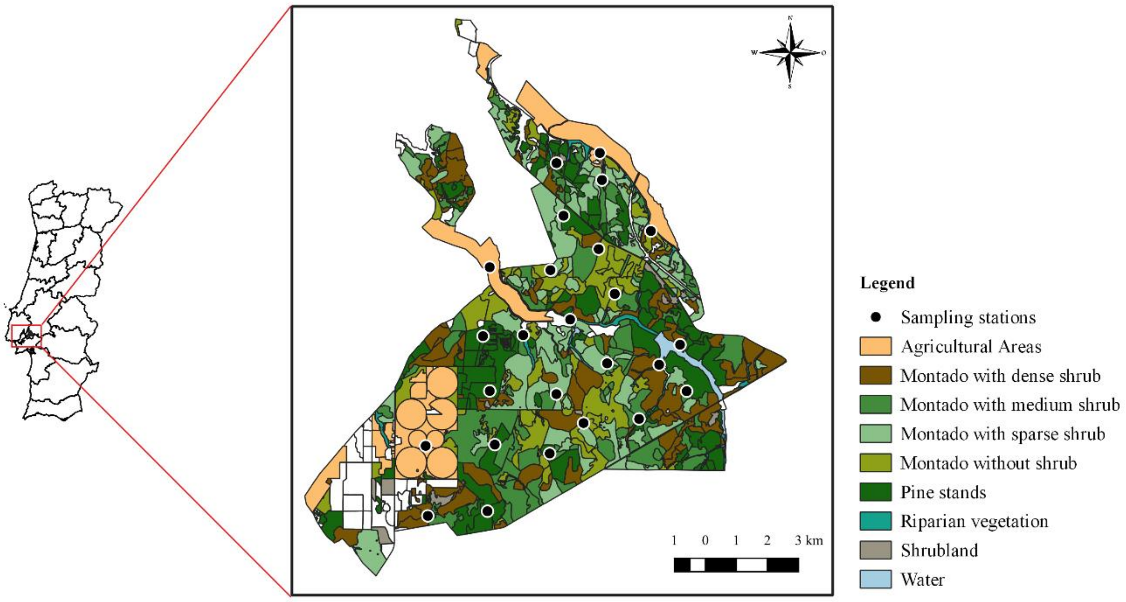


Figure 2.1 - Study area location, land-cover types and camera-trap stations in the Charneca do Infantado (Companhia das Lezírias, S.A.).

The anthropogenic influence on Charneca do Infantado has led to a heterogenous forested landscape. This area has been intensively managed for silvicultural and agricultural purposes, resulting in a complex mosaic of different habitats. The Charneca management focuses on forestry exploitation, mainly for cork extraction, and biological cattle raising, mostly dedicated to bovine production, but several other activities occur in the area, such as agricultural productions (e.g., rice plantations, vineyards and olives groves, and other cultivated at a minor scale). Occasionally, recreational and touristic activities, and regulated game hunting events also occur[3].

Despite its agricultural and silvicultural vocation, CL has a long tradition of pioneering and innovation in the agroforestry sector having supported several research projects over the years to monitor and preserve this complex landscape and its biodiversity, whose results are contributing to the sustainability of its forest management, certified by an international standard (FSC) since 2010.

Typical of Mediterranean region, the habitat matrix of Charneca is mainly composed by Montado, a cork oak (*Quercus suber*) system, pure or interspersed by patches or stands of other tree species, and with different densities of shrubby understory (Gonçalves et al., 2011). This system resulted of years of human influence through shrubs clearing and thinning in the dense evergreen oak forest in order to maximize land use on unfavourable climate conditions and poor soils (Pinto-Correia et al., 2011). Nowadays, Montado's value and uniqueness is acknowledged internationally due to its distinct landscape, biodiversity, aesthetic and cultural importance (Surová et al., 2011; Pinto-Correia et al., 2011). Other forested areas in Charneca do Infantado are occupied by maritime pine (*Pinus pinaster*), umbrella pine (*Pinus pinea*) and eucalyptus

---

[2] https://www.cl.pt/en/activity-areas/sustainable-forest-management

[3] https://www.cl.pt/storage/user/pdf/relatoriocontas2018br.pdf

(*Eucalyptus globulus*) stands, comprehending different ages and understory structures (Gonçalves et al., 2011). The understory, mainly shrublands, is represented by halimium (*Halimium* sp.), gorse (*Ulex* spp.), false olive (*Phillyrea* spp.), rock rose (*Cistus* spp.) and common heather (*Calluna vulgaris*). Riparian areas are composed by developed arboreal and shrubby vegetation strata including willows (*Salix alba*), alders (*Alnus glutinosa*), ashes (*Fraxinus angustifolia*), and hawthorns (*Crataegus monogyna*) (Ferreira & Aguiar, 2006; Gonçalves et al., 2011).

The study area is part of the Long-Term Ecological Research (LTER) Network[4], as a site that proved to be very relevant for long-term socio-ecological research of the Montado ecosystem. Within this framework, research projects are conducted with the aim to monitor the ecosystem dynamics and its biodiversity, investigate the effects of management options, and enhance a preserved habitat network where refugee and feeding areas are connected to important biodiversity sectors along the matrix. These goals are achieved by monitoring the fauna and flora, rehabilitating water lines, protecting important vegetation patches, and by implementing and monitoring an ecological corridor. Today, Companhia das Lezírias is nationally recognised as one of the most important state-owned areas where agriculture and biodiversity conservation coexist (Gonçalves et al., 2013). Further, some sectors of Companhia das Lezírias are protected as part of the Natura 2000 Network, being included in the Tejo Estuary Special Area of Conservation (SAC) and classified as a Site of Community Importance (SCI) (von Essen et al., 2019).

Charneca do Infantado heterogenous landscape, where naturalized or managed habitats are intermingled with remnants of natural habitats with different abiotic and biotic characteristics, promotes a variety of animal responses and, consequently, results in a community ecologically more complex (Rosalino et al., 2009). Therefore, despite the anthropogenic influence, the mesocarnivore community in the study area is diverse, including the following 8 species: red fox (*Vulpes vulpes*), least weasel (*Mustela nivalis*), European polecat (*Mustela putorius*), stone marten (*Martes foina*), European badger (*Meles meles*), Eurasian otter (*Lutra lutra*), common genet (*Genetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*) (Gonçalves et al., 2013). Mesocarnivores in Companhia das Lezírias are not classified as Endangered, even though the European polecat is suspected to be so and currently considered Data Deficient in the Portuguese Vertebrates Red Data Book (Cabral et al., 2005).

---

[4] http://www.ltsermontado.pt/

3. Methods

3.1.1 Target community

We focused on 5 species known to be present in Companhia das Lezírias, S.A.: red fox, stone marten, European badger, common genet and the Egyptian mongoose. Following the pairwise analysis framework, we formed species pairs according to their ecological features and a dominance-subordination hierarchy. We assumed the red fox would interact with the remaining target species, given its generalist habits (Alexandre et al., 2020) and expected wide distribution (Curveira-Santos et al., 2017). We considered the fox would be the dominant species in all pairs except for the European badger, as this mustelid dominance over the canid has been previously documented (Macdonald, Buesching, et al., 2004). The interaction between the stone marten and the common genet was also studied, due to their morphological and ecological similarities (Santos-Reis et al., 2005), and based on body size, the common genet was considered dominant. Accordingly, we determined 5 pairs (dominant – subordinate): European badger – red fox; red fox – Egyptian mongoose, red fox – common genet, red fox – stone marten; common genet – stone marten.

3.2 Sampling Design and Data Collection

Camera-trapping was the survey method used to evaluate the community structure and occupancy patterns of Charneca's mesocarnivores. Camera-trapping is the most widely used method to study wild carnivores, due to its adequateness to survey species with elusive habitats and/or low-density populations (Ferreras et al., 2017). It is also non-invasive, has low requirements in human resources and allows to survey large spatial scales (Karanth et al., 2017).

The selected sampling design included a network of 25 sampling stations, pre-determined by superimposing a 2x2 km grid over the Charneca limits and selecting the centroid of each grid cell using QGIS version 3.4.8 with GRASS 7.6.1 software. This design allowed an approximately even distribution across the landscape covering the main land-cover types and assuring a good representativeness of habitat heterogeneity. Each selected sampling station was visited before the start of the survey, and the camera-trap final position was adjusted within a buffer of 200 meters radius around the grid cell centroid, according to the purpose of this study and habits of the target community. Whenever possible, the cameras faced animal trails to increase species detectability (Kolowski & Forrester, 2017) and no bait was used. The average distance between sampling stations was 1783.51 meters (SD=246.89, min=1503.09, max=2085.53) - calculated considering the three nearest stations -, with purpose of maximizing total area covered while minimizing spatial autocorrelation (MacKenzie & Nichols, 2004; Ferreras et al., 2017; Monterroso et al., 2020).

Each camera trap station consisted of one Browning Dark OPS camera placed on a tree or artificial stake, 20 – 30 cm above the ground. Cameras were programmed to operate for 24h per day and to take 3 sequential photographs when triggered, with an interval of 1 second between each burst. Sampling stations were visited every 15 days to monitor the battery status and replace the memory cards. The cameras remained active for 5 months (February to July of 2020).

For image analysis and data extraction, the package "CamtrapR" for R software version 3.6.0 was employed. A 30-minute interval between two consecutive records of the same species was the minimum time considered to assume these as independent records, reducing the chances of considering the same wandering individual multiple times (Ferreras et al., 2018).

3.2.1 *Data analysis*

3.2.2 *Temporal analysis*

For temporal analysis, independent records capture times were converted to solar time as it potentiates an adequate ecological interpretation of species activity patterns (Foster et al., 2013). Thus, we considered four diel periods relevant to mesocarnivores activity patterns: day, night, dawn (one hour before and after sunrise) and dusk (one hour before and after sunset). Records were considered random samples of an underlying distribution, which represented the record probability as function of time of the day (Linkie & Ridout, 2011). The species activity pattern is represented by the probability density function of this distribution (Ridout & Linkie, 2009).

To quantify the temporal co-occurrence, we estimated the overlap coefficient (Δ), using the estimator Δ_1 as it is the most advisable for small sample sizes (Ridout & Linkie, 2009). The coefficient ranges from 0, indicating no overlap, to 1, for a complete overlap. Following the classification proposed by Monterroso et al. (2014), based on a pairwise comparison between Iberian mesocarnivores species activity patterns across different study areas and seasons, we considered three overlap categories: low ($\Delta < 0.66$), moderate ($0.66 \leq \Delta \leq 0.76$), and high ($\Delta > 0.76$) overlap.

The activity patterns and the overlap coefficients were estimated through a nonparametric kernel density function, using the package “overlap” for R software version 3.5 (Meredith & Ridout, 2014). For these estimates, we generated confidence intervals using empirical bootstrapping.

3.2.3 *Spatial analysis*

To understand space-use patterns of mesocarnivores, single-season occupancy modelling was employed, applying a likelihood approach to estimate detection (ρ) and occupancy (Ψ) using probabilistic arguments that correct false-negative situations, thus accounting for imperfect detection (Mackenzie et al., 2002) - which makes this analysis adequate for elusive species like carnivores. To estimate these parameters, site and survey covariates are incorporated via a logit link function (Mackenzie et al., 2018). However, it is important to have in consideration that, even though the term “occupancy” is broadly employed, the estimates provided in this study are better described as probability of site use during the study period than true occupancy, as the analysis is based on camera trap data of carnivores with large home ranges, whose movement may lead to temporary absence of the sampling area (Mackenzie & Royle, 2005). By assuming the study of site-use, we relax the occupancy modelling assumptions that require for sampling site independence and for occupancy status to remain constant across sites during the survey (Mackenzie et al., 2018).

Occupancy models use data on temporally replicated surveys at a given site or sites, thus a species-specific binary detection history was built for each sampling station, where 0 represents non-detection and 1 means detection. Considering that most Mediterranean mesocarnivores exhibit crepuscular or nocturnal behaviour, including those inhabiting the Charneca (Curveira-Santos et al., 2017), a trap-day consisted of a 24-h period starting on midday and until the midday of the following day. The detection histories were constructed considering each sampling occasion was a set of 14 consecutive trap nights.

In order to analyse carnivores’ interactions, we used single-season two-species occupancy models (Mackenzie et al., 2004) following the conditional parameterization presented by Richmond et al. (2010) (see Table 3.1 for parameterization description). This methodology allows the estimates of a subordinate species’ (B) occupancy and detection to be conditional on the presence of a dominant species (A) (Richmond et al., 2010). Thus, we considered the following species pairs: European badger (A) – red fox (B); red fox (A) – Egyptian mongoose (B); red fox (A) – common genet (B); red fox (A) – stone marten (B); common genet (A) – stone marten (B).

We assessed if the dominant species' presence influenced the subordinate species detection by testing for scenarios of conditional and independent detection, as it could reflect behaviour displacement upon the dominant species presence. We were also interested in determining if species B occupancy is conditional on species A presence or if the two species occurred independently. To study the dominant species' influence on the subordinate species spatial patterns, the previous scenarios were combined formulating 4 types of model as presented in table 3.1.

Table 3.1 – Hypotheses tested for studying dominant and subordinate species co-occurrence using two-species occupancy models (Mackenzie et al., 2004) following the conditional parameterization determined by Richmond et al. (2010). ρA represents the probability of detection for species A given species B is absent, rA is the probability of detecting species A given both species are present, ρB describes detection probability of species B knowing species A is absent, rBA is defined as detection probability of species B given both species are present and species A is detected, rBa is the detection probability of species B given both species are present but species A is not detected, ΨA refers to occupancy probability of species A, ΨBA represents occupancy probability of species B given species A is present, ΨBa characterizes occupancy probability of species B given species A is absent.

Hypothesis	**Model**	**Parameterization**
Subordinate's species occupancy and detection are independent of dominant species' presence.	ρ(independent) Ψ(independent)	$\rho A = rA$ $\rho B = rBA = rBa$ ΨA ΨBA = ΨBa
Subordinate's species detection is conditional on dominant species' presence, but they occur independently.	ρ(conditional) Ψ(independent)	$\rho A = rA$ $\rho B \neq rBA = rBa$ ΨA ΨBA = ΨBa
Subordinate's species detection is independent of dominant species' presence, but its occupancy is conditional.	ρ(independent) Ψ(conditional)	$\rho A = rA$ $\rho B = rBA = rBa$ ΨA ΨBA ≠ ΨBa
Subordinate species' occupancy and detection are conditional on dominant species' presence.	ρ(conditional) Ψ(conditional)	$\rho A = rA$ $\rho B \neq rBA = rBa$ ΨA ΨBA ≠ ΨBa

When the subordinate species detection probability was considered conditional on the dominant species presence, we calculated the ratio between the probability of detecting species B when species A is present (rBA) and when it is absent (ρB) (Richmond et al., 2010). Otherwise, in a scenario of independent detection, the ratio is 1.

In the event the subordinate species' occupancy proved to be conditional on the dominant species' presence, we derived the species interaction factor (SIF) – determined as φ according to Richmond et al. (2010) parameterization-, which characterizes the likelihood of both species co-occurring at the same site compared to the expected under the assumption of independence (Mackenzie et al., 2004). It is defined by the following:

1. $\varphi = \frac{\Psi A * \Psi BA}{\Psi A\,(\Psi A * \Psi BA + (1 - \Psi A) * \Psi Ba)}$,

ΨA refers to occupancy probability of species A, ΨBA represents occupancy probability of species B given species A is present, ΨBa characterizes occupancy probability of species B given species A is absent.

In a scenario of independent co-occurrence φ=1, whereas φ<1 indicates that species B is less likely to co-occur with A, representing a situation of avoidance, and φ>1 is assumed as a scenario of aggregation.

Providing spatial co-occurrence was not independent, an attempt was made in order to determine if co-occurrence relationships are mediated by environmental factors. We intended to understand if species co-occur, either positively or negatively, regardless of environmental factors (ΨBA(.) ≠ ΨBa(.)), or if their interactions changed across environmental conditions (ΨBA(environmental covariates) ≠ ΨBa(environmental covariates)).

3.2.3.1 Covariates

Based on published literature on the Mediterranean mesocarnivore community ecology in the study area (Gonçalves et al., 2011; Gonçalves et al. 2013; Grilo et al., 2016; Hipólito et al., 2016a; Curveira-Santos et al., 2017), a set of relevant predictor variables was selected. It resulted in three main categories, according to its ecological relevance: habitat, food sources and disturbance (Table 3.2).

Table 3.2 - Covariates selected to analyse the mesocarnivores community occupancy and detection at Charneca do Infantado (Companhia das Lezírias, S.A.).

Covariate	Code	Parameter	Description	Units
Habitat				
Distance to water courses	Water _dist	ρ, Ψ	The linear distance between the camera-trap location and the nearest water source.	meters
Landscape Diversity	LD	Ψ	Simpson's Landscape Diversity Index representing patch diversity, considering a buffer of 350m for each station. 0≥SLDI≤1, where higher results indicate greater diversity, composed by higher numbers of different patch types occupying the buffer area or a greater proportional distribution. When SLDI=0, the buffer area occupies only one patch type.	[0,1]
Montado with dense shrub	MDS	ρ, Ψ	Cork oak stands, with dense (>70% cover) and high to intermediate understory dominated by *Halimium* sp., *Ulex* sp. and *Cistus salvifolius*.	% buffer cover
Montado with medium shrub	MMS	ρ, Ψ	Cork oak stands with understory of medium density (30% - 70%), mainly composed by *Halimium* sp., *Ulex* sp. and *Cistus salvifolius*.	% buffer cover

Montado with sparse shrub	MSS	ρ, Ψ	Semi-disturbed cork oak patches, generally with moderate grazing pressure levels, with sparse understory (10–30% cover) dominated by *Ulex* sp. - which could be aggregated to trees.	% buffer cover
Montado without shrub	MNS	ρ, Ψ	Highly disturbed cork oak stands with reduced or absent understory (<10% cover), mostly natural or permanent biodiverse pastures. This habitat is a result of intense grazing pressure or forestry intervention activities.	% buffer cover
Pine stands	P	ρ, Ψ	*Pinus pinaster* or *Pinus pinea* stands of varying age with well-developed understory structure of mixed composition.	% buffer cover
Shrubland	S	ρ, Ψ	Tall shrubs (>1 m) of *Cistus ladanifer* and *Cistus monspeliensis*, with null or sparse arboreal cover of *Quercus suber* and/or *Pinus pinaster*.	% buffer cover
Riparian areas	RIP	ρ, Ψ	Linear segments of dense vegetation adjacent to waterlines, mainly formed by patches of willows (*Salix alba*), ashes (*Fraxinus angustifolia*), alders (*Alnus glutinosa*), hawthorns (*Crataegus monogyna*) and Blackberries (*Rubus fruticosus*).	% buffer cover
Agricultural areas	AGRI	ρ, Ψ	Agricultural areas mainly composed by croplands of rice or irrigated fields.	% buffer cover
Food sources				
Lagomorphs	LAGO	Ψ	Lagomorphs encounter rate calculated as the number of independent records per 100 trapping days.	
Small mammals	SM	Ψ	Small mammals encounter rate calculated as the number of independent records per 100 trapping days.	
Artificial feeding structures	Alim	Ψ	The linear distance from the trapping stations to the nearest artificial feeding structure.	meters
Disturbance				
Cattle Grazing Intensity	Cattle	ρ, Ψ	Cattle grazing intensity index calculated within a buffer of 350 meters (radius) of the sampling station, considering the number of livestock units (LSU) grazing in a plot of a known area (ha) during a known number of days (n_days).	

Distance to cattle excluded areas	Cattle _Exc	ρ, Ψ	The linear distance from the trapping stations to the nearest cattle excluded area.	meters
Forest intervention	Forest _interv	ρ, Ψ	Disturbance caused by forest intervention categorized according to its level of perturbation, from 0 (non-disturbed) to 4 (highly disturbed).	(0 - 4)
Wild boar	SS	ρ, Ψ	Wild boar encounter rate calculated as the number of independent records per 100 trapping days.	
Wild boar with juveniles	SS_ juv	ρ, Ψ	Encounter rate of wild boars accompanied by its litter calculated as the number of independent records per 100 trapping days.	

3.2.3.1.1 Habitat Covariates

The habitat covariates represent the patch type and land cover characteristics, which were collected based on a GIS database (Gonçalves et al., 2011) updated during this study (Table 3.2). These variables were measured within a 350 meters radius buffer around each camera-trap station, a buffer that was determined considering the smallest core-area of the mesocarnivore species present in Charneca, the common-genet core-area of 0,34 square kilometres (Santos-Reis et al., 2005).

Furthermore, to estimate landscape diversity, the Simpson's Landscape Diversity Index was calculated:

2. $SLDI = 1 - \sum_{i=1}^{m} p_i^2$,

p_i represents the proportion of the landscape occupied by patch type i.

It characterizes habitat heterogeneity, where higher results indicate greater diversity, composed by larger numbers or greater proportional distribution of different patch types occupying the landscape, and when $SLDI = 0$ it is represented by only one patch type (Nagendra, 2002).

3.2.3.1.2 Food sources covariates

Previous studies showed that small mammals and lagomorphs, mostly European rabbit, are an important component of mesocarnivores diet in Mediterranean Portugal (e.g., Santos et al., 2007; Loureiro et al., 2009; Grilo et al., 2016; Bandeira et al., 2018; Monterroso et al., 2020), although in some cases hare was also reported as a food resource (Reynolds & Aebischer, 1991; Knauer et al., 2010; Remonti et al., 2012; Lanszki et al., 2019). Thus, assessing these preys' availability might be relevant when studying the target community structure and occupancy.

In this study, to analyse prey availability regarding lagomorphs, we considered camera trap independent records (accounting for a minimum of 30-minute interval between consecutive records, as mentioned above for mesocarnivores). We calculated an index of prey encounter rate considering the site-specific lagomorphs detection rate per 100 trapping days. Even though this index does not measure the lagomorphs' true abundance, it represents a robust proxy for a prey site use frequency, which could influence a predator's use of the same site (Parsons et al., 2019).

Therefore, this covariate was interpreted as the likelihood of carnivore-prey encounters at each sampling point.

To analyse small mammals' availability, we used Mostela camera-traps (Mos & Hofmeester, 2020), a monitoring device developed by the Dutch Small Mustelid Foundation to monitor small mustelids, and calculated the index of prey encounter rate as well. Mostela device compromises a Browning Dark OPS camera inside a wood box placed at the ground-level. The box has an opening where an 8 cm diameter PVC tunnel is positioned to allow the camera to record any movement inside the tube. For a full description of the design see Mos and Hofmeester (2020). At each sampling location, one Mostela device was placed at 2 – 6 m distance from the camera-trap station and, when possible, on its field of view (with the exception of one point where the distance between the Mostela and the camera was 67 meters).

A previous study by Hipólito et al. (2016a) proved that artificial feeding structures, a game management option adopted in Companhia das Lezírias, are an important food source for European badger. Given carnivores ecological plasticity to adapt to the resources' availability and the greater diversity of mesocarnivores' diet in Mediterranean regions, which includes more plant material (Rosalino & Santos-Reis, 2009), the distance from the camera-trap stations to these feeding structures was also included in the covariate set.

3.2.3.1.3 Disturbance covariates

Human activities can have an impact on mammals' community ecology and dynamics depending on the pressure intensity it represents. Even though some management options kin to an agro-sylvo-pastoral system, can result in increased mammal richness due to a more complex landscape (Rosalino et al., 2009), high grazing intensities may have a negative effect as it results in shrub clearance and larger areas of permanent pastures, decreasing habitat heterogeneity (Gonçalves et al., 2011). This phenomenon affects not only carnivores but also its prey, resulting in a bottom-up effect. Therefore, cattle grazing intensity was calculated for each station within a buffer of 350 meters, following Gonçalves et al. (2011) equation:

3. $\mathrm{GI} = \frac{LSU}{ha * n\_days}$,

considering the number of livestock units (LSU) grazing in a plot of a known area (ha) during a known number of days (n_days).

As a management option to preserve patches of natural habitats and landscape heterogeneity, Companhia das Lezírias excludes cattle from certain areas through fencing. Given these are undisturbed areas, they might represent important refugee and food source locations or reflect an avoidance behaviour of carnivores to cattle presence. Therefore, we included the distance from each sampling station to the nearest cattle excluded area as a covariate.

Forestry-related practices are an important part of the management approach adopted in Charneca, not only to extract cork and wood, the main economic assets of Companhia das Lezírias, but also to control the spread of pathogens and prevent fire through tree pruning and shrub clearing, for example. The forestry management activities that occurred during the survey period were quantitatively classified, considering its negative effect on the mesocarnivores community, within a buffer of 350 meters, using a score that represented the level of disturbance, from 0 (non-disturbed) to 4 (highly disturbed).

Wild boar (*Sus scrofa*), a species with increasing numbers at the Charneca do Infantado, foraging activities may also represent a disturbance factor. Its rooting behaviour, by breaking up and loosening the surface and near-surface layers of the soil column, leaving them bare of vegetation (Cuevas et al., 2012), could result in a damaged landscape which will negatively impact carnivores' habitat structure and its food availability (Mangas & Rodríguez-Estival, 2010).

Hence, an index of encounter rate representing site-specific wild boar detection rate on camera-traps per 100 trapping days was calculated.

Triggered by a maternal care behaviour, female wild boars can become aggressive and intensify their antipredator response (D'Eath & Turner, 2009), which may have an impact on meso and small carnivores, possibly causing an avoidance behaviour. To account for the possibility of this effect, we further calculated the index encounter rate of wild boar accompanied by their litter considering independent records from the camera traps.

3.2.3.2 Modelling procedure and selection

To avoid multicollinearity between the response variables, and therefore an overparameterized model, covariate relationships were estimated based on a pairwise Spearman's correlation test. In situations of high correlation ($|r| > 0.7$), the variable of less biological relevance was discarded from the modelling procedure (Dormann et al., 2013). To facilitate the interpretation process, the covariates were normalized by converting it in z-scores – with the exception of the forest intervention variable, which is categorical.

We followed a two-stage modelling approach. First, we determined the relevant covariates for each species occupancy and detection, through single-season single-species occupancy models, and then we assessed interspecific interactions of each species pair, via two-species occupancy models using the variables selected in the previous stage.

For single-species models, we started by modelling the detection probability as function of environmental covariates, while keeping occupancy constant. We incorporated habitat and disturbance covariates, as they could directly influence carnivores' detectability, or indirectly by affecting their behaviour and activity near the camera-trap stations. Following, using the covariates from the most parsimonious detection model, a set of candidate models (Appendix 8.2) was built based on ecologically meaningful hypothesis to explain each species' occupancy. However, to avoid an overparameterization, we mostly tested for univariate models, or a maximum of two covariates per parameter if it represented a relevant hypothesis.

In the second stage, when studying the species pairs interactions, we assessed if the subordinate species' occupancy and detection was conditional or independent on the presence of the dominant species, by testing different scenarios following the parameterization mentioned above (Table 3.1). For this modelling procedure, we tested for null scenarios as well as for hypotheses combining the covariates of the single-species most parsimonious models. By including covariates to better explain occupancy and detection, both for single-species and two-species occupancy models, we relax the assumption that there is no un-modelled heterogeneity (Mackenzie et al., 2018).

For model selection, we assessed candidate models goodness-of-fit and estimated the overdispersion factor ($\hat{c}$) using the Pearson chi-square statistic with 1000 parametric bootstrap samples. It is advisable to evaluate the goodness-of-fit for each model, as there is no theoretical assumption to know *a priori* which could be the best fitting model (Burnham & Anderson, 2002). The candidates that exhibit good fit (*p-value*>0.1) and no overdispersion ($\hat{c}$ approximately 1) were then ranked using the Akaike Information Criterion corrected for small sample size (AICc) as described by Mackenzie and Bailey (2004). We considered models with ΔAICc$\leq$2, comparatively to the best ranked model, to strongly fit the data and to incorporate covariates that are good predictor for species' occupancy and detection (Burnham & Anderson, 2002). Contrarily, if the candidates exhibited poor fit, the AICc was adjusted through the overdispersion factor, and the models were ranked based on their Quasi Akaike Information Criterion corrected for small samples (QAICc) using the threshold of ΔQAICc≤2 (Mackenzie & Bailey, 2004).

Regarding the two-species occupancy analysis, we used the Akaike's weight (AICw) to select the most adequate hypothesis to the data. AICw represents the weight of evidence in favour of a given model to be the best model in the set (Burnham & Anderson, 2002), allowing the assessment of which hypothesis better represents the data. For this testing, we considered null models and models including the environmental covariates of the most parsimonious single-species occupancy models.

Estimates of occupancy and detection, and covariates effect were assessed through model averaging if more than one model was considered to best fit. We considered a well-supported effect if the 90% unconditional confidence intervals of the average ß estimates did not overlap 0 (Anderson, 2008).

Single-season single-species occupancy modelling was performed with "unmarked" package for R software version 3.6.0. (Fiske & Chandler, 2011), and two-species occupancy models were implemented with the PRESENCE software version 13.1 (Hines, 2006).

3.2.4 Spatio-Temporal Analysis

As a third element of this study on interspecific interactions, we proceeded to an analysis combining space and time use patterns.

The spatio-temporal behaviour displacement was assessed via a multiresponse permutation procedure following Karanth et al. (2017) approach to test for spatio-temporal segregation conditionally on the observed space use and time activity patterns. This is a non-parametric method that compares the test statistic for the observed data to the distribution of the same test statistic for the null hypothesis, knowing that this hypothesis is calculated by randomly exchanging labels of data points and recalculating the test statistic for the simulations (McCune & Grace, 2002). Thus, for each encounter of one species at a certain sampling station, we calculated the minimum time-to-encounter the species pair. Following, we compared the median observed time-to-encounter with the statistically expected time-to-encounter. This last parameter was estimated by generating expected time-to-encounter statistical distributions and randomly attributing encounter times to the sampling stations in 1000 simulations (Karanth et al., 2017). The *p-value* was also calculated, representing the proportion of randomly generated times-to-encounter that are greater than the observed. We considered spatio-temporal segregation if the observed time-to-encounter is longer than the expected. Contrarily, a shorter observed time-to-encounter reflects spatio-temporal aggregation.

4. Results

4.1 *Mesocarnivore capture success*

The 5 month survey period resulted in a sampling effort of 3104 effective trap-days and an average of 124.16 active trap-days per camera-trap station (SD = 24.58). We recorded all the 5 target species, totalizing 724 independent records, which indicates an encounter rate of 23.32 independent records per 100 trapping-days (Table 4.1). The most recorded species was the red fox, with 7.89 independent records per 100 trapping-days, followed by the Egyptian mongoose with 5.83 independent records, and the European badger with 4.38. This last species also showed the highest naïve occupancy, being recorded at 18 of the 25 sampling stations. The Egyptian mongoose and the common genet showed similar *naïve* occupancy, although the former had more independent records registered. The species with the lowest number of independent records, the stone marten, also showed the narrower distribution with a *naïve* occupancy of 0.52 (Table 4.1).

Table 4.1 - Target mesocarnivore species records during the survey period. IER refers to the index of encounter rate, calculated as the number of independent records per 100 trapping days.

Species	Total records	IER	Naïve occupancy
Red fox	245	7.89	0.68
Egyptian mongoose	181	5.83	0.64
European badger	136	4.38	0.72
Common genet	119	3.83	0.64
Stone marten	43	1.39	0.52
All target species	724	23.32	0.92

4.2 *Temporal overlap*

Considering the activity patterns within a 24-hour period, 4 of the 5 pairs showed a high temporal overlap. The highest overlap estimates correspond to red fox paired with the stone marten (Δ_1=0.88) and the European badger (Δ_1=0.86) (Table 4.2). The common genet – stone marten pair also showed a high overlap, even though this estimate is close to the moderate category threshold ($0.66 \leq \Delta \leq 0.76$).

Table 4.2 – Species pairs overlap coefficient (Δ_1) estimates with the respective 95% confidence intervals (CI) and the overlap category following Monterroso et al. (2014) criteria.

Species pair	Overlap coefficient	CI (95%)	Overlap category
European badger - Red fox	0.86	0.78 - 0.92	High
Red fox - Egyptian mongoose	0.15	0.11 - 0.19	Low
Red fox - Common genet	0.82	0.73 - 0.89	High
Red fox - Stone marten	0.88	0.79 - 0.94	High
Common genet - Stone marten	0.78	0.67 - 0.88	High

The species pair showing the lowest overlap was the red fox - Egyptian mongoose (Δ=0.15) (Table 4.2). The mongoose presented a very distinct activity period from the red fox, being active mainly during the day (Figure 4.1). Contrarily, the red fox and the remaining mesocarnivores were active predominantly at night, which resulted in higher overlap coefficients mentioned above (Table 4.2). Both the red fox and the common genet showed a bimodal pattern with two activity peaks, one close to the dawn and another, even more pronounced, at dusk time, while the European badger and the stone marten showed a single activity peak, which was demarked at nigh time.

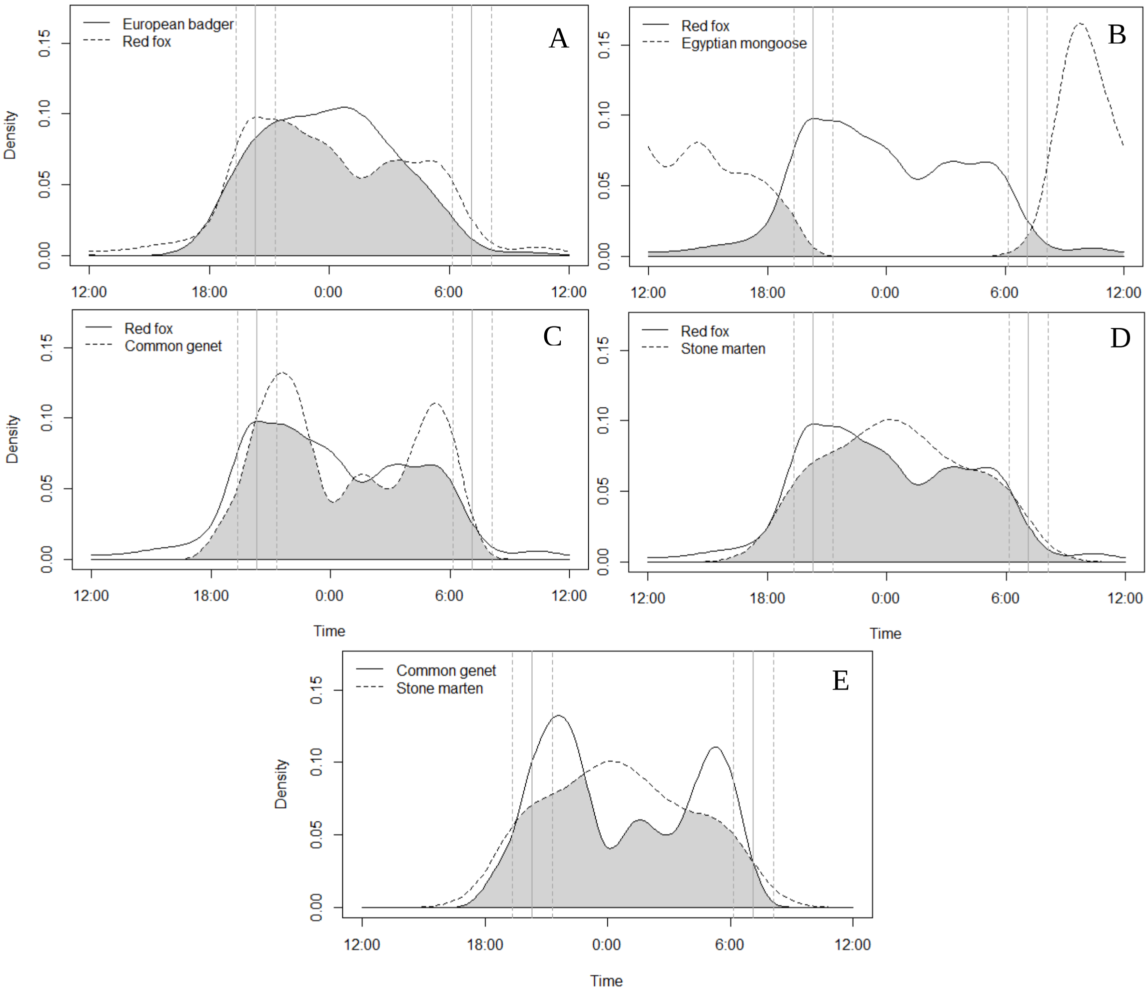


Figure 4.1 - Mesocarnivore diel activity patterns represented by kernel density estimates and pairwise species overlap (darkened area) between European badger – red fox (A), red fox – Egyptian mongoose (B), red fox – common genet (C), red fox – stone marten (D), common genet – stone marten (E). The mean sunset and mean sunrise times are indicated by solid grey lines, while the dashed grey vertical lines indicate one hour before and after those times, delimiting the four diel periods day, dawn, night and dusk (Foster et al., 2013).

4.3 *Spatial overlap*

After testing for covariates correlation, two were excluded from further analysis. Due to high correlation with Simpson's Landscape Diversity index (r = 0.72), Montado with medium shrub (MMS) was excluded, given that it represents a single patch type, while the Landscape Diversity is a more broaden and significant habitat feature (Güthlin et al., 2013; Cruz et al., 2015; Curveira-Santos et al., 2017). Distance to cattle excluded areas was highly correlated (r = 0.72) with Montado without shrub (MNS), therefore was also removed. The existence of shrub or understory has proven to be very important for carnivores in the study area (Gonçalves et al., 2011; Curveira-Santos et al., 2017), hence the absence of that habitat feature should be accounted.

4.3.1 Single-season single-species occupancy modelling

Based on the candidate models goodness-of-fit, only the common genet candidate set had to be adjusted due to overdispersion (*p*-value=0.17, $\hat{c}$=1.17). The remaining species' candidate set - red fox's (*p*-value=0.37, $\hat{c}$=0.99), Egyptian mongoose's (*p*-value=0.72, $\hat{c}$=0.90), European badger's (*p*-value=0.49, $\hat{c}$=0.98) and stone marten's (*p*-value=0.43, $\hat{c}$=0.99) - exhibited good fit.

When analysing species' detection and occupancy candidate model set (Appendixes 8.1 and 8.2), as mentioned we mostly followed the criteria ΔAICc or $\Delta QAICc \leq 2$. However, for the Egyptian mongoose, only one model fulfilled this criterion, with AICcw=0.76 (Table 4.3). Given that is not advisable to select only one model unless it represents AICcw>0.9, we decided to select the second best fitting model as well (ΔAICc<4), which can still be assumed to have considerable support, and together with the first model allowed the total AICc weight to be 0.9 (Burnham & Anderson, 2002) (Table 4.3).

Table 4.3 - Occupancy model selection results for target species' detection (ρ) and occupancy (Ψ), with the respective Akaike Information Criterion corrected for small sample size delta and weight (ΔAICc and AICcw) and the number of parameters in each model (K). See table 3.2 for covariates description.

Species	**Model**	**ΔAICc**	**AICcw**	**K**
Red fox	ρ(RIP) Ψ(.)	0.00	0.21	4
	ρ(RIP) Ψ(LAGO)	0.05	0.20	5
	ρ(RIP) Ψ(MSS)	0.57	0.16	5
	ρ(RIP) Ψ(SS_juv)	1.35	0.11	5
	ρ(RIP) Ψ(S)	1.46	0.10	5
	ρ(RIP) Ψ(SS_juv+LAGO)	1.48	0.10	6
Egyptian mongoose	ρ(MDS) Ψ(SS_juv+LAGO)	0.00	0.76	5
	ρ(MDS) Ψ(LAGO)	3.34	0.14	4
European badger	ρ(MDS) Ψ(LD)	0.00	0.38	5
	ρ(MDS) Ψ(LD+SS_juv)	0.53	0.29	6
	ρ(MDS) Ψ(MNS)	1.82	0.15	5
Stone marten	ρ(MDS+Cattle) Ψ(MNS+LAGO)	0.00	0.51	6
	ρ(MDS+Cattle) Ψ(MNS)	0.18	0.47	5
Species	**Model**	**ΔQAICc**	**QAICcw**	**K**
Common genet	ρ(MDS) Ψ(SS_juv)	0.00	0.47	5
	ρ(MDS) Ψ(AGRI+SS_juv)	0.35	0.39	6

The occupancy and detection estimates indicate that all species have a considerably wide distribution but different levels of detection. The most widespread species are the red fox (Ψ=0.70) and the European badger (Ψ=0.71) but both having low detection probabilities - 0.34 and 0.37, respectively (Table 4.4). The Egyptian mongoose showed the narrower distribution with an occupancy probability of 0.63, and the highest detection probability (ρ=0.41) (Table 4.4). The common genet and the stone marten presented similar occupancy (Ψ=0.68); however, the stone marten detection probability is the lowest in this mesocarnivore community (ρ=0.18) (Table 4.4).

Due to its low density in the area and arboreal habits, distinguishing camera-trap stations where the stone marten is present but not detected from those where it is truly absent is hard resulting in a less accurate occupancy estimate. Nevertheless, as ρ >0.15, we proceeded with the occupancy analysis acknowledging that the model estimates require careful interpretation (Mackenzie et al., 2002).

Table 4.4 - Occupancy and detection estimates, and the respective standard errors (SE) and confidence intervals (CI).

Species	Occupancy	SE	CI (95%)	Detection	SE	CI (95%)
Red fox	0.70	0.16	0.28 - 0.92	0.34	0.06	0.24 - 0.45
Egyptian mongoose	0.63	0.15	0.11 - 0.84	0.41	0.06	0.30 - 0.53
European badger	0.71	0.15	0.35 - 0.94	0.37	0.06	0.27 - 0.49
Common genet	0.68	0.11	0.07 - 0.85	0.39	0.06	0.27 - 0.51
Stone marten	0.68	0.08	0.00 - 1.00	0.18	0.05	0.11 - 0.43

Based on the selected models, we identified the most relevant environmental covariates influencing the target species occupancy and detection (Table 4.3). With the exception of the red fox, the habitat type Montado with dense shrub (MDS) had a significant influence on species detection; it seems to benefit the common genet detection probability but negatively influences the detectability of the Egyptian mongoose, the European badger and the stone marten (Appendix 8.3). The riparian area cover (RIP) had a positive and significant influence on the red fox detection (Appendix 8.3). The cattle grazing pressure covariate (Cattle) was also indicated in the stone marten most parsimonious models, however, its effect was not significant.

Considering the covariates modelling the occupancy selected in the most parsimonious models, the encounter rate of wild boar with juveniles (SS_juv) and lagomorphs (LAGO) influenced the majority of the target species (Table 4.3). SS_juv modelled the occupancy of red fox, Egyptian mongoose, European badger and common genet, while LAGO had no influence in this last species, but affected the other 3 species occupancy as well as that of the stone marten's. Except for the Egyptian mongoose, whose occupancy was modelled by disturbance and food source covariates, the different habitat types were considered to influence the mesocarnivore community space use patterns. Montado without shrub (MNS) modelled both stone marten and European badger occupancy, agricultural areas (AGRI) influenced common genet space use, and the red fox occupancy was explained by Montado with sparse shrub (MSS) and Shrubland (S) (Table 4.3). Red fox occupancy most parsimonious set also included a model whit no covariates.

However, most covariates explaining mesocarnivores space use do not significatively influence these species occupancy, with the exception of landscape diversity (LD) and Montado without shrub (MNS) modelling the European badger occupancy, the first with a positive effect while the second negatively influencing it (Appendix 8.4). This result indicates that, in general, the target community is not strongly influenced by the environmental covariates tested.

4.3.2 Interspecific spatial interactions

Based on the *naïve* occupancy information, for all species pairs, the proportion of sampling points where both species were detected is higher than the proportion of stations each species was detected but the pair was not. Of the 17 stations the red fox was detected, the European badger was also detected in 82%. In the Egyptian mongoose case, 88% of the stations the species was detected, the red fox was also registered. The common genet and the stone marten were detected in more stations where the red fox was recorded as well, in both cases representing 69%. The common genet and the stone marten were co-detected in 10 stations, representing 62.5% and 77% of the total number of stations each species was detected, respectively.

Employing single-season two-species occupancy models and testing the scenarios mentioned in Table 3.1, we analysed the pairwise spatial interactions (Table 4.5).

Table 4.5 - Hypotheses tested according to Table 3.1 for each species pair, and its respective Akaike information criteria weight (AICw) represented in percentage (%). The hypothesis most strongly supported is in bold. ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent.

Species pair	**ρ(COND) Ψ(COND)**	**ρ(IND) Ψ(IND)**	**ρ(COND) Ψ(IND)**	**ρ(IND) Ψ(COND)**
European badger - red fox	25.80	5.32	**60.44**	8.42
Red fox - Egyptian mongoose	**66.12**	1.05	15.15	17.68
Red fox - common genet	15.65	30.23	**42.05**	12.07
Red fox - stone marten	27.18	15.81	**49.79**	7.22
Common genet - stone marten	7.24	**44.80**	7.31	**40.65**

In the European badger – red fox pair, the most supported hypothesis represents the red fox detection conditionality on the dominant species presence, but its occupancy is independent (AICw (ρ(COND) Ψ(IND)) = 60.44%) (Table 4.5). Regarding the Egyptian mongoose, the best hypothesis indicates that its detection and occupancy are conditional on the red fox presence, which is far more supported than the remaining hypotheses (AICw (ρ(COND) Ψ(COND)) = 66.12%) (Table 4.5). The most supported hypothesis for both the common genet and the stone marten – red fox pair, demonstrates that the subordinate species detection is conditional on the red fox presence, though its occupancy is considered independent, with AICw for this hypothesis being 42.05% and 49.79%, respectively (Table 4.5). Based on the hypotheses tested, the stone marten is detected and occurs independently of common genet presence (AICw (ρ(IND) Ψ(IND)) = 44.80%) (Table 4.5). However, the second best hypothesis is still strongly supported (ρ(IND) Ψ(COND)) = 40.65%), indicating the conditionality in the stone marten occupancy on the common genet presence (Table 4.5).

After selecting the best hypothesis to represent each species pair interaction, we derived the species interaction factor (φ) and the ratio between species B detection probability when species A is present (*r*BA) and when it is absent (ρB) (Table 4.6).

Table 4.6 - Hypothesis selected for each species pair, with the respective species interaction factor (φ), the ration between the probability of detecting species B when both are present (rBA) and the probability of detecting species B if A is absent (ρB), and the respective standard deviation. ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent.

Species pair	**Best hypothesis**	***r*BA/ρB**	**φ**
European badger - red fox	ρ(COND) Ψ(IND)	3.68 (±0.22)	1.00
Red fox - Egyptian mongoose	ρ(COND) Ψ(COND)	1.02 (±0.09)	1.25 (±0.03)
Red fox - common genet	ρ(COND) Ψ(IND)	1.90 (±0.08)	1.00
Red fox - stone marten	ρ(COND) Ψ(IND)	2.36 (±0.14)	1.00
Common genet - stone marten	ρ(IND) Ψ(IND) ρ(IND) Ψ(COND)	1.00 1.00	1.00 1.23 (±0.00)

Regarding the subordinate species' detection, only the stone marten proved to be detected independently on the dominant species presence, when paired with the common genet, indicating that its detection probability is not influenced, irrespectively of the presence of the common genet (rBA/ρB=1) (Table 4.6). The red fox detection probability, being conditional on the dominant species presence, more than triples in the European badger presence (rBA/ρB=3.68±0.22) (Table 4.6). The Egyptian mongoose detection probability seems conditional on the red fox, being marginally higher when the dominant species is present (rBA =0.37±0.01, ρB=0.36±0.06). The common genet and the stone marten detection probability is conditional on the red fox presence, as presented by the most supported hypothesis, being almost double when the dominant species is present in the case of the common genet (rBA/ρB=1.90±0.08) or more than double for the stone marten (rBA/ρB=2.36±0.14) (Table 4.6).

The red fox – Egyptian mongoose interaction best hypothesis indicated the subordinate species occupancy is conditional on the dominant species presence (Table 4.6). It showed the highest species interaction factor (φ=1.25±0.03), indicating aggregation as φ>1. The spatial interaction between the common genet and the stone marten was similarly supported by the two best hypothesis (Table 4.5). Nonetheless, the average species interaction factor across models representing 90% of the AICw is 1.11 (±0.10), which favours the conditional occupancy hypothesis and indicates a spatial aggregation behaviour.

Considering that the remaining species occurred independently on the dominant species presence, the species interaction factor is 1 (Table 4.6).

When determining if species pairs spatial co-occurrence was influenced by environmental factors, we were not able to obtain results. This method consisted of the performance comparison of models including covariates modelling the occupancy probability of species B with null models for that parameter. However, due to covariates leading to convergence problems when modelling species B occupancy, we had to remove these models from the candidate set (Appendix 8.5 to 8.9). As a result, the European badger – red fox candidate set includes models where species B occupancy, when species A is present, is modelled by environmental covariates, but when species A is absent no covariates modelled the parameter (ΨBA(environmental covariates), ΨBa(.)). In this same pair, for the same reason, the covariate representing the riparian area cover modelling the red fox detection was removed. In the remaining species candidate sets, the species B occupancy, irrespectively of species absence or presence, is not modelled by any covariate (ΨBA(.) ΨBa(.)). Also, as consequence of convergence problems, we removed the covariate cattle grazing pressure modelling the stone marten detection, from both pairs candidate set this species was included, and the covariate representing the encounter rate of wild boar accompanied by their litter modelling the common genet occupancy in the candidate set for the pair common genet – stone marten.

4.4 Spatio-temporal overlap

Calculating the time-to-encounter between each species pair (Appendix 8.10), the median estimates ranged from 2.23 to 5.86 days (Table 4.7). The pair showing the longest median time was the common genet – stone marten (5.86 days), which also had the lowest p-value, indicating that 65% of the randomly generated times-to-encounter are higher than the observed time-to-encounter (Table 4.7).

The time-to-encounter estimated for the red fox – Egyptian mongoose was the shortest (2.23 days), and this interaction was considered to represent spatio-temporal aggregation given that almost all statistically expected times-to-encounter were longer than the observed (Figure 4.2-B). The red fox also showed fine-scale spatio-temporal aggregation behaviour with the stone marten (*p*-value=0.98) and the European badger (*p*-value=0.96) (Table 4.7). The multiresponse permutation procedure did not show an evident intra-guild behaviour displacement when assessing the common genet spatio-temporal interaction with the red fox and the stone marten's, as the observed median minimum time-to-encounter is not clearly longer or shorter than simulated values (Figure 4.2 – C and E).

Table 4.7 - Median minimum time-to-encounter (days) estimate for each species pair and the *p*-value representing the proportion of randomly generated times-to-encounter longer than the observed.

Species pair	**Observed (days)**	***p-value***
European badger - red fox	3.44	0.96
Red fox - Egyptian mongoose	2.23	0.99
Red fox - common genet	3.86	0.69
Red fox - stone marten	4.78	0.98
Common genet - stone marten	5.86	0.65

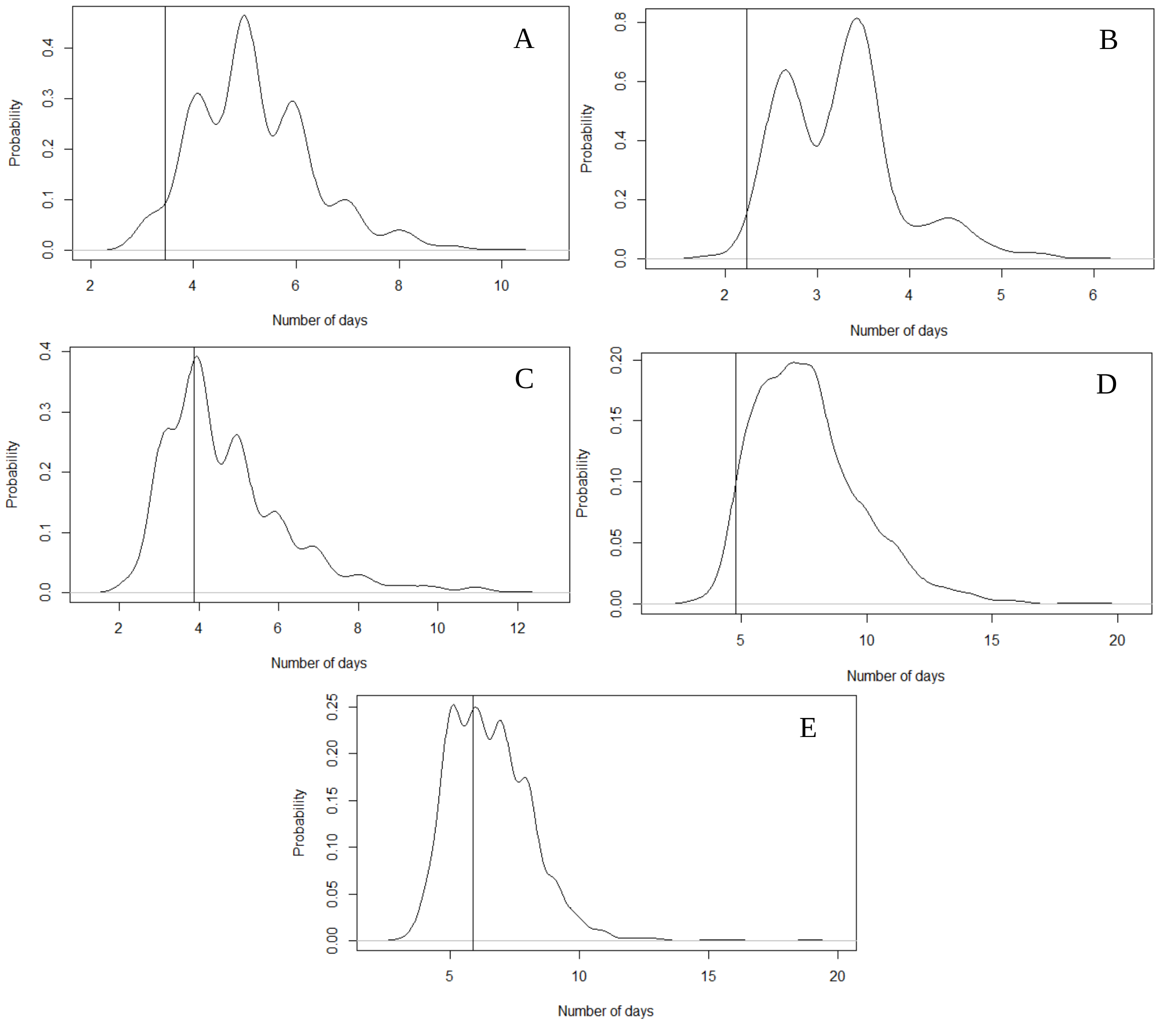


Figure 4.2 - Statistically expected times-to-encounter randomly generated by a multiresponse permutation procedure for each species pair: A – European badger – red fox, B – red fox – Egyptian mongoose, C – red fox – common genet, D – red fox – stone marten, E – common genet – stone marten. The vertical line represents the observed median minimum time-to-encounter.

5. Discussion

The analysis of species interactions along the temporal, spatial and spatio-temporal dimensions revealed the mesocarnivore community in Companhia das Lezírias, S.A., shows aggregation patterns, probably as a result of the high levels of disturbance that force species into scenarios of coexistence. However, fine-scale segregation or partition along other axes of their ecological niche allows the persistence of a resilient community in a context of coexistence.

Regarding the temporal interactions, and according to the expected (H1), we observed a high overlap in the night period with partial time segregation facilitated through activity patterns desynchrony. This partial time partitioning allows species to coexist, while decreasing the probability of agonistic encounters.

On the spatial dimension, we expected spatial aggregation (H2), which was only detected in two species pairs, although the remaining species detection probability increased in the presence of the pair. We were also able to identify the environmental factors influencing species detectability and European badger occupancy. However, the effect of habitat features, food resources and disturbance factors on the community and the negative influence of cattle grazing was not clear. Despite the environmental factors' effect was not evident, based on the species response documented in the literature (Santos-Reis et al., 2005; Santos et al., 2007; Rosalino & Santos-Reis, 2009; Carvalho et al., 2011; Curveira-Santos et al., 2017; Monterroso et al., 2020), we identified patterns of fine-scale spatial segregation (H2).

Considering the spatio-temporal interactions among the assemblage, species pairs did not show a behaviour displacement towards segregation, contrary to H3 expectations. Therefore, for cases where aggregation was identified, we concluded niche partitioning regarding dietary patterns allowed species coexistence.

5.1 Partial temporal segregation through diel cycle asynchrony

Similarly to other studies in Mediterranean areas (Monterroso et al., 2014; Curveira-Santos et al., 2017; Vilella et al., 2020) and according to the expected (H1), given the majority of mesocarnivores detected present activity patterns demarked at the night period, most species pairs showed a considerable temporal overlap, the highest being the red fox – stone marten overlap. Contrarily to the remaining species, the diurnal Egyptian mongoose presented a very low temporal overlap with red fox.

The only strictly diurnal species registered was the Egyptian mongoose, which, considering this ecological trait previously documented (Monterroso et al., 2014, Curveira-Santos et al., 2017), shows a very low temporal overlap with red fox. Nonetheless, it is admissible to consider the possibility of sporadically encounters since a previous study conducted in Companhia das Lezírias characterised this canid as facultative nocturnal (Curveira-Santos et al., 2017), and given the moderate preference for the crepuscular time, it may overlap with the Egyptian mongoose activity period at certain times.

The nocturnal species show a high temporal overlap with red fox activity pattern, the highest being the overlap with the stone marten. This mustelid, as well as the common genet, can take advantage of their arboreal adaptation to avoid agonistic encounters with the red fox (Pereira et al., 2012) and therefore facilitate the temporal overlap with the dominant species.

The European badger – red fox temporal overlap observed in the present study is higher than the one reported in other Iberian study areas by Almeida (2016) and Monterroso et al. (2014), possibly as a result of the higher levels of anthropogenic influence in Companhia das Lezírias, S.A., forcing species to strongly select periods of less disturbance. Despite the high temporal overlap, the red fox cathemeral bimodal activity differs from the European badger unimodal pattern demarked at night. Curveira-Santos et al. (2017) showed similar results, suggesting this difference might be explained by dietary patterns, given that the generalist red fox uses the crepuscular periods possibly to follow the European rabbit activity pattern (Monterroso et al., 2013).

Regarding the pair common genet – stone marten, the temporal overlap observed is categorized as high, which could be a result of habitat features. Higher understory density is associated with an increased temporal overlap between these two species (Almeida, 2016), and 6 of the 10 sampling stations where the common genet and the stone marten were both detected are partially occupied by the patch type Montado with dense shrub. However, the overlap coefficient is close to the moderate category threshold, probably due to the viverrid bimodal activity pattern being distinct from the mustelid unimodal pattern, more demarked at approximately midnight. Common genets have been described to be more active in the first half of the night (Palomares & Delibes, 2000), while stone marten's unimodal patterns have been registered in Mediterranean areas (Monterroso et al., 2014). Knowing these species share their ecological niche (Santos-Reis et al., 2005), the desynchronized activity periods and increased resources, such as refugee or food, that result from higher density in the understory cover, facilitate their coexistence and therefore decrease a potential competition effect. Nevertheless, the temporal overlap is still lower than the one registered in Serra de Grândola (Almeida, 2016), a less intervened study area in southern Portugal, suggesting that, apart from the mechanism mentioned before, these species might respond to competition caused by management factors by displacing a fine-scale segregating behaviour.

Overall, the overlap in the Companhia das Lezírias mesocarnivore community is higher than other Mediterranean areas (Monterroso et al., 2014; Almeida, 2016), which can be a result of increased levels of disturbance, forcing the mesocarnivores to select or to be more active during the less disturbed day period, the nigh time. In response, there is asynchrony among the mesocarnivores activity peaks, given the distinction between bimodal, common genet and red fox, and unimodal patterns, European badger and stone marten. This result suggests a sequential use of the diel cycle, as reported in Mediterranean mesocarnivore communities studies (Monterroso et al., 2014; Almeida, 2016), and inferred to represent a behavioural strategy to avoid agonistic encounters, to facilitate foraging and to benefit niche partitioning (Curveira-Santos et al., 2017; Vilella et al., 2020). Therefore, despite the needs to endogenously regulate their activity patterns according to solar time and circadian rhythms (Monterroso et al., 2013), these mesocarnivores are able to adapt in response to interspecific interactions and, consequently, facilitate the coexistence between competitors.

Nonetheless, a cautious temporal overlap interpretation should account for the possibility that the observed activity patterns are highly dependent of species-specific ecological traits, and, in reality, might not represent a result of interspecific interactions (Curveira-Santos et al., 2017).

5.2 The complexity of spatial interactions

The majority of the analysed species pairs tend to co-occur independently, but, in most cases, the subordinate species detection is conditional on the dominant species presence – which does not robustly corroborate H2. Contrastingly, two species pairs, common genet – stone marten and red fox – Egyptian mongoose, do not co-occur independently, showing spatial aggregation, according to expected in H2. Despite the environmental factors effect was not clearly identified in this study, based on previous knowledge (Santos-Reis et al., 2005; Santos et al., 2007; Rosalino & Santos-Reis, 2009; Carvalho et al., 2014; Curveira-Santos et al., 2017; Monterroso et al., 2020), we believe a heterogenous response to environmental factors contributes to scenarios of fine-scale spatial segregation (H2).

The pairwise interaction indicating the strongest effect of spatial aggregation was the pair red fox – Egyptian mongoose. These two species strongly rely on similar food sources, given that in Mediterranean habitats they both prey on European rabbit and small mammals (Santos et al., 2007; Monterroso et al., 2020). Notwithstanding, a previous isotopic analysis on red fox scats from the study area (Baptista, 2013) revealed a generalist diet, which includes, besides from mammals, insects and vegetable food sources. The carnivores' adoption of a richer and more diverse diet in plant sources has been described in Mediterranean habitats, particularly when fruit becomes more abundant (Rosalino & Santos-Reis, 2009). The canid may benefit from a profitable food source, like the European rabbit, and contribute to spatial aggregation with the Egyptian mongoose, while still relying on its generalist behaviour to minimize competition risk. Given that interaction, the spatial aggregation and the fine-scale spatial segregation due to different use of food resources corroborate H2.

Analysing the two arboreal species interaction, the common genet presence does not influence the stone marten detection, although the analysis of its influence in the mustelid occupancy is not as clear. The most strongly supported occupancy analysis hypothesis (independent occupancy) explains the data variability only 1.1 times better than the second most supported hypothesis (conditional occupancy). Nevertheless, the average species interaction factor is 1.11, which indicates some degree of spatial aggregation, and corroborates the first part of H2. Similar body size and locomotory activity contribute to a greater niche overlap between the common genet and the stone marten (Santos et al., 2007), as it can result in the adoption of similar feeding habits and habitat preferences. A study by Santos-Reis et al. (2005) conducted in southern Portugal showed these two species have similar home range sizes, intraspecific spatial patterns, habitat preferences and food resources. These similarities can explain some degree of spatial overlap, furthermore the habitat characteristics might contribute to this moderate aggregation as well. Resting sites, mainly on trees or shrubs, are very important for both species (Santos-Reis et al., 2005; Rödel & Stubbe, 2006). The common genet will use shrubs as resting site in areas of high density understory (Carvalho et al., 2014), which is probably why its detection probability was not negatively affected by this habitat type (MDS), like other species. While the resting site availability might not be limited in areas of less intervention, however, in managed systems like Companhia das Lezírias, the cork extraction and shrub clearing will lead to its decline. In this environment, the viverrid will rely on tree hollows to rest (Carvalho et al., 2014), similarly to the stone marten (Santos-Reis et al., 2005) and probably increase their spatial overlap.

Both the common genet and the stone marten do not co-occur more often than expected with the red fox, contrary to the spatial aggregation hypothesis (H2), although, their detection probability increases in the dominant species presence. The stone marten detection probability is negatively influenced by the habitat type Montado with dense shrub (Appendix 8.3), leading us to assume that it is more likely detected in open areas. These areas can be used by the red fox to hunt for its prey (Jędrzejewski et al., 1992; Carvalho & Gomes, 2001), and for the stone marten to dislocate in this kind of environment, it requires movement more at ground level, where camera visibility increases and stone marten's detectability can be associated with areas used by the red fox. As an arboreal species, we assume the common genet adopts a similar behaviour to the stone marten on open areas, also resulting in a higher detection probability in the red fox presence.

Similarly to the stone marten and the common genet, the red fox detection probability is higher in the dominant species presence. The European badger occupancy probability is significantly affected by the habitat type Montado without shrub and benefits from landscape diversity (Appendix 8.4), which is in accordance with Curveira-Santos et al. (2017) and Rosalino et al. (2008) that suggest semi-disturbed cork oak with aggregated shrub mosaics favours this species feeding habits, locomotory ability and refugee opportunities. Possibly, the red fox size would potentiate its detection in a habitat type where the absence of dense understory might facilitate camera visibility, and therefore conceivably increase the canid detection probability in areas occupied by the European badger. Nonetheless, given the mustelid high occupancy probability and the fact that 82% of stations the red fox was recorded, the European badger was also detected, there might not be enough data to irrefutably infer about the subordinate species detection in the absence of the dominant.

The environmental covariates effect was not evident, which contrasts with the results of a previous study conducted in the same study area, where a significant effect of environmental covariates on mesocarnivores occupancy was found (Curveira-Santos et al., 2017). However, given the literature (Santos-Reis et al., 2005; Santos et al., 2007; Rosalino & Santos-Reis, 2009; Carvalho et al., 2014; Curveira-Santos et al., 2017; Monterroso et al., 2020), we were able to identify a species-specific response to habitat, food and disturbance factors, as explained in each species pair interaction discussion. This heterogenous response to a complex ecosystem reflects in mesocarnivores using the resources differently, according to the species needs and resources availability, while also aiming to avoid competition – which promotes a scenario of coexistence through fine-scale spatial segregation (H2). The covariate weak association outcome can also be a result of mesocarnivores' ecological plasticity and their ability to use the resources at a landscape level, which can possibly be less evident when accounting for site-specific effects in the analysis, as suggested by Monterroso et al. (2020) regarding carnivores' interactions in natural Mediterranean areas.

A critical analysis of occupancy results should include careful interpretation, and consider the possibility that the absence of spatial interaction among species pairs might be a consequence of the low spatial replicate, that could have affected the model performance to adequately explain most of the data heterogeneity, also leading to convergence problems. Possibly for the same reason, the occupancy analysis showed a weak association between the mesocarnivores spatial patterns and the selected environmental covariates. One covariate that was expected to have a significant effect on the mesocarnivore community was the cattle grazing intensity. Previous studies have shown this disturbance factor can have an impact on Mediterranean mesocarnivores' occupancy (Verdade et al., 2011; Hipólito et al., 2016b; Curveira-Santos et al., 2017; Alexandre et al., 2020). However, as a management option of Companhia das Lezírias, the cattle herds are moved from Charneca do Infantado to Lezíria throughout the year, and during the last 3 months (approximately) of the sampling period, there were no herds in the study area. Consequently, the cattle effect might not have been evident in this study, given it only occurred in the beginning of the study period.

Despite the less significant effect of environmental covariates and the negligible influence of cattle, the impact of intervention or exploitation activities, such as cattle grazing and forest management, should not be disregarded. Both these practices can influence the target community by altering the vegetation structure, and therefore affecting mesocarnivores' habitat use patterns, food and refugee resources, and consequently species interactions (Loureiro, 2008; Verdade et al., 2011; Alexandre et al., 2020). Thus, these management practices can indirectly affect the mesocarnivore community which would reflect in species masking their response to disturbance effects (Curveira-Santos et al., 2017).

In man-shaped ecosystems, like Companhia das Lezírias, where management options may vary along the years and can severely influence the environmental conditions, only by resorting to long-term data, would we be able to identify a reliable pattern and establish robust conclusions on the environmental factors effect.

5.3 Spatio-temporal aggregation and generalist dietary patterns

Overall, opposing to the expected (H3), the mesocarnivore community in Companhia das Lezírias did not displayed patterns of spatio-temporal segregation, as shown by the aggregation behaviour adopted by the European badger – red fox, red fox – Egyptian mongoose and red fox – stone marten pairs. Contrarily, the common genet did not show a fine-scale tendency to spatio-temporal aggregate with the species it was paired, the red fox and the stone marten.

One of the pairs exemplifying the pattern of spatio-temporal aggregation, contrary to H3, is the European badger – red fox. The tendency to observe an overlap between these two species diets is highly dependent on the seasonality (Barrull et al., 2014; Toretta et al., 2016). In the winter, when the resources are limited, red fox significatively consumes insects (Baptista, 2013), one important food source for the European badger (Hipólito et al., 2016a), however, during spring, the canid also preys on mammals, and later in the summer it relies on plant sources (Rosalino & Santos-Reis, 2009; Baptista, 2013), decreasing the overlap. This study was conducted during late winter and early summer, which could indicate that the red fox preyed on small mammals and lagomorphs, but still relied on insects as a part of its diet, resulting in some overlap with European badger feeding sources.

Also contributing to the same pattern, in spite of the documented European badger dominance over the red fox, previous studies have reported the canid using the badger setts (Macdonald, Newman, et al., 2004; Mori et al., 2015). A study conducted in Companhia das Lezírias (Silva, 2017) documenting the badger setts in the area, reported cases of red foxes using secondary setts, which were temporarily unoccupied and therefore could be occasionally used by other species. The number of badger setts in the area and the red fox use might not be considerable for occupancy models to indicate spatial aggregation (although this factor was not directly included as a covariate), however, through a finer-scale, behaviour displacement towards spatio-temporal aggregation could be detected.

The Egyptian mongoose and the red fox show dissimilarities in activity patterns, despite the possibility of overlap in crepuscular times. This divergence facilitates a strong spatial aggregation while also resulting in a short time-to-encounter between the two competitors. The same mechanisms that allow these two species to co-occur spatially, also contribute to a fine-scale spatio-temporal aggregation. Both mesocarnivores showed a significant negative influence of cattle (Curveira-Santos et al., 2017; Marques, 2017), which can consequently be reflected in a finer-scale overlap. Nonetheless, the red fox can slightly diverge its diet and diel activity patterns when necessary to avoid agonistic encounters. This behaviour might not agree with the general assumption that the overlap in space and/or time with the dominant species results in behaviour displacement from the subordinate, however, in response to disturbance factors, the generalist species, in this case the dominant red fox, can adapt its behaviour more easily to promote coexistence (Di Bitetti et al., 2010; Monterroso et al., 2014).

Despite the different physiognomy presented by stone marten and red fox regarding their body size and locomotory adaptations, these species can share dietary patterns (Serafini & Lovari, 1993; Santos et al., 2007; Papakosta et al., 2010), depending on the resources availability. Both adopt a generalist diet, which includes small mammals, fruit and insects (Santos et al., 2007), knowing the proportions of each item vary according the Mediterranean seasonal fluctuations of food resources, which therefore influence the dietary overlap between the red fox and the stone marten. At Southern Portugal, these species have shown to decrease their consumption of Muridae, such as *Apodemus sylvaticus*, *Mus spretus*, and *Rattus rattus*, in warmer seasons (Santos et al., 2007), resulting in a greater overlap when other resources, like fruit, become more abundant (Padial et al., 2002). The stone marten specially benefits from the increased fruit availability as an arboreal species, while the red fox, as morphologically terrestrial adapted, can more easily rely on coleoptera and fallen fruits (Santos et al., 2007; Baptista, 2013).

Regarding the habitat preferences, the stone marten shows a specialization for forested areas, especially for cork oak systems in the Mediterranean basin, whilst still occasionally using other habitats as a supplementing strategy (Dunning et al., 1992; Santos & Santos-Reis, 2010), while the red fox, even though occupancy patterns indicate the use of Montado with dense understory (Curveira-Santos et al., 2017), it can still heavily use riparian habitats and open areas to hunt its prey (Jędrzejewski et al., 1992; Carvalho & Gomes, 2001; Grilo et al., 2016).

The similarities among these species potentiate an aggregative interaction, although the stone marten's arboreal behaviour that allows it to exploit the vertical and horizontal habitat components (Padial et al., 2002) and the red fox's ability to use alternative food sources and other patches besides the dense cork oak woodlands, certainly minimize the competition risk and benefit a coexistence scenario.

Contrarily to the stone marten, the common genet did not show a behaviour displacement upon the red fox influence. Despite the similarities, the common genet does not have a diet as generalist as the stone marten (Vilella et al., 2020). It might eat fruit occasionally (Rosalino & Santos-Reis 2009) but the main food source is still the wood mouse *Apodemus sylvaticus* (Rosalino & Santos-Reis, 2002). As mentioned above, the red fox can adopt a very generalist diet, adapting to most conditions and available resources. It will certainly rely on small mammals, however, given the Companhia das Lezírias' context, the consumption of more accessible resources, such as insects or fruit, can be more profitable in certain occasions. This feature, along with the common genet ability to use trees or dense shrubs as a refugee (Carvalho et al., 2014), is in accordance with the independent occupancy and suggests these two species can coexist without showing a spatio-temporal aggregation behaviour.

The spatio-temporal analysis regarding the interaction between the common genet and the stone marten enlightens the moderate spatial and temporal aggregation observed in this study. These two species have similar ecological features that allow them to share food resources or habitat use patterns, which can contribute to a certain degree of aggregation as shown before. However, at a finer-scale the niche partitioning strategies became more evident, as it was described these species' core areas can be mutually exclusive (Santos-Reis et al., 2005). When the resources are limiting, the common genet and the stone marten might display a behaviour displacement in order to minimize competition. The conditions in an exploited ecosystem, like Companhia das Lezírias, can determine the resources characteristics and availability, and therefore influence intraguild interactions. Contrary to other species, the common genet and the stone do not respond to disturbance factors by tolerating interspecific spatio-temporal aggregation. This may also explain why the occupancy analysis was not clear and did not indicate a strong spatial aggregation behaviour in the first place.

The pairwise analysis did not reveal spatio-temporal segregation, opposed to the expected (H3), however, as described before, mesocarnivores' ecological plasticity proved to be a valuable asset. These species generalist dietary habits, by relying on plant, insects and mammals as food sources, according to each item availability, and the ability to use different habitat features, promoted by the heterogenous landscape, contribute to decrease competition risk and ultimately facilitate coexistence.

The spatio-temporal analysis, representing the study of fine-scale use of space and time, is an important complement to better understand interspecific interactions. Approaches considering only temporal or spatial dimensions may misrepresent how species benefit from or avoid possible interspecific interactions, if they alter their behaviour simultaneously on time and space (Farris et al., 2020). As proved in this study, it can enlighten certain ecological features and behaviours adopted by the target community, that would not be evident if assessing only spatial or temporal interactions. As an example, if considering interactions through time and space separately, the stone marten and the common genet could be considered to aggregate. However, when proceeding to a fine-scale spatio-temporal analysis, it does not corroborate a scenario of aggregation. This result illustrates the intricacy of carnivores' interactions and the need to incorporate several niche axes in the study to better understand this complex topic.

6. Conclusion and research needs

This study enlightens the importance of Mediterranean mesocarnivores ecological plasticity to promote coexistence, by: i) desynchronizing their diel cycle use, and therefore partially time partitioning; ii) diverging species responses to environmental factors, promoting fine-scale spatial segregation; and iii) segregating in their diet, to facilitate spatio-temporal coexistence. This knowledge is crucial to improve the current management decisions in man-shaped ecosystems and prioritize the alignment of exploitation aims and conservation efforts.

The mesocarnivores' occupancy patterns in the study area have been described, allowing inferences about possible scenarios of segregation or aggregation; however, this study complements previous research through a single-season two-species occupancy analysis, which presents a more robust understanding of species interactions along the spatial axis of their ecological niche. Secondly, by including the spatio-temporal analysis, this study provides new information on fine-scale use of space and time simultaneously. To our knowledge, this is the first study to perform this analysis in a Mediterranean area, and we certainly recommend future research to consider this approach.

This study, as short-term research, represents only a snapshot of the effects of environmental factors and interspecific interactions during the sampling period, which can constraint the applicability of its conclusions, particularly on man-shaped ecosystems where the environmental factors vary seasonally and yearly, largely due to changes in management options and practices. As a result, generalist species, like Mediterranean mesocarnivores, present varied and dynamic responses to the ecosystem changes. Therefore, to corroborate or contradict the conclusions presented in this study, and more importantly, to reliably determine a pattern in mesocarnivores' response, long-term data is a requirement. Only then can conservation efforts, based on robust scientific evidence, be adequately directed to the target assemblage in a context of ecosystem exploitation. By complementing previous research, and incentivising future studies to continue to do so, we aim to promote long-term assessments and contribute to implement sustainable management options in Mediterranean production systems.

Nonetheless, we still acknowledge some limitations. The limited spatial replicate in this study, given the low number of sampling stations, might have constrained the occupancy analysis, misrepresenting the local landscape heterogeneity. Moreover, research in man-shaped ecosystems where production and management decisions play a major role, like Companhia das Lezírias, S.A., a fine-scale habitat description is a requirement, given the landscape heterogeneity and environmental factors dynamic change. This aim can be achieved through higher spatial replicate and by characterizing the habitat features according to their functionality and ecological relevance to the target species. Incorporating in the analysis the trophic niche dimension, by assessing each species dietary patterns and food resources availability, would represent an added-value to this study, providing analysis on all 3 dimensions of species ecological niche and eventually corroborating some of our predictions, namely that mesocarnivores' generalist diet promotes coexistence. Lastly, local characteristics of our study area, like seasonal cattle transhumance, diverse forest management activities (varying in space and time) and contrasting climatic conditions along the year (dry *versus* wet season) require multi-season long-term sampling to adequately survey its effects on the animal communities.

Despite the referred limitations, this study clearly enlightens the Mediterranean mesocarnivores' strong adapting ability promoted by ecological plasticity. However, as a final remark, we would like to emphasize that these species' adaptive behaviour should not disregard monitoring and conservation efforts, particularly in a dynamic ecosystem like Montado. The partitioning ability along the ecological niche axes is only possible if there are still resources to allow fine-scale segregation, i.e., if the resources are not limited to an extreme level. The situation of agricultural intensification, habitat loss and pour management is aggravating in many areas and, therefore, more scientific-based evidences are needed to properly predict mesocarnivores' response and improve the current management options accordingly, aiming to conciliate production objectives with conservation efforts in exploited ecosystems.

7. References

According to the Journal of Applied Ecology rules, given the focus on wildlife conservation and land use management, aiming to contribute with crucial information that can potentially be useful and impact ecosystem management decisions.

Alexandre, M., Hipólito, D., Ferreira, E., Fonseca, C., & Rosalino, L. M. (2020). Humans do matter: determinants of red fox (Vulpes vulpes) presence in a western Mediterranean landscape. *Mammal Research, 65*(2), 203–214. https://doi.org/10.1007/s13364-019-00449-y

Almeida, A. L. (2016). *Nicho temporal de mesocarnívoros numa área de montado de sobro: efeito do habitat e do ciclo lunar* (Master of Science dissertation). University of Lisbon, Lisbon, Portugal.

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence*. Spring Science & Business Media. https://doi.org/10.1007/978-0-387-74075-1

Baker, A. D., & Leberg, P. L. (2018). Impacts of human recreation on carnivores in protected areas. *PLoS ONE, 13*(4). https://doi.org/10.1371/journal.pone.0195436

Bandeira, V., Virgós, E., Carvalho, J., Barros, T., Cunha, M. V., & Fonseca, C. (2018). Diet footprint of Egyptian mongoose along ecological gradients: effects of primary productivity and life history traits. *Mammalian Biology, 88,* 16–25. https://doi.org/10.1016/j.mambio.2017.11.004

Baptista, A. (2013). *Aplicabilidade da análise isotópica na compreensão da variação sazonal e espacial da dieta da raposa (Vulpes vulpes) num habitat Mediterrânico* (Master of Science dissertation). University of Lisbon, Lisbon, Portugal.

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., & Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. *Mammalian Biology*, *79*(2), 123–131. https://doi.org/10.1016/j.mambio.2013.11.004

Bencatel, J., Sabino-Marques, H., Álvares, F., Moura, A., & Barbosa, A. M. (2019). *Atlas de mamíferos de Portugal* (2nd ed.). Évora: University of Évora. Retrieved from http://atlas-mamiferos.uevora.pt

Blondel, J., Thomas, D. W., Charmantier, A., Perret, P., Bourgault, P., & Lambrechts, M. M. (2006). A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. *BioScience*, *56*(8), 661–673. https://doi.org/10.1641/0006-3568(2006)56[661:ATSOPA]2.0.CO;2

Burnham, K., & Anderson, D. (2002). *Model Selection and Multimodel Inference*. New York: Springer.

Cabral, M. J., J. Almeida, Almeida, P. R., Delliger, T., Almeida, N. F. de, Oliveira, M. E., Palmeirim, J.M., Queirós, A.I., Rogado, L., Santos-Reis, M. (2005). *Livro Vermelho dos Vertebrados de Portugal*. Lisboa: Instituto da Conservação da Natureza.

Carlsson, N. O. L., Jeschke, J. M., Holmqvist, N., & Kindberg, J. (2010). Long-term data on invaders: When the fox is away, the mink will play. *Biological Invasions*, *12*(3), 633–641. https://doi.org/10.1007/s10530-009-9470-z

Carvalho, J., & Gomes, P. (2001). Food habits and trophic niche overlap of the red fox, european wild cat and common genet in the Peneda-Gerês National Park. *Galemys: Boletín Informativo de La Sociedad Española Para La Conservación y Estudio de Los Mamíferos*, *13*(2), 39–48.

Carvalho, J. C., & Gomes, P. (2004). Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). *Journal of Zoology*, *263*(3), 275–283. https://doi.org/10.1017/S0952836904005266

Carvalho, F., Galantinho, A., & Mira, A. (2011). Factors affecting small and middle-sized carnivore occurrence and abundance in Mediterranean agricultural landscapes: Case studies in Southern Portugal. In *Middle-Sized Carnivores in Agricultural Landscapes* (pp. 39–67).

Carvalho, F., Carvalho, R., Mira, A., & Beja, P. (2014). Use of tree hollows by a Mediterranean forest carnivore. *Forest Ecology and Management*, *315*, 54–62. https://doi.org/10.1016/j.foreco.2013.12.013

Case, T. J., & Gilpin, M. E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America*, *71*(8), 3073–3077. https://doi.org/10.1073/pnas.71.8.3073

Cove, M. V., Jones, B. M., Bossert, A. J., Clever, D. R., Dunwoody, R. K., White, B. C., & Jackson, V. L. (2012). Use of camera traps to examine the mesopredator release hypothesis in a fragmented midwestern landscape. *American Midland Naturalist*, *168*(2), 456–465. https://doi.org/10.1674/0003-0031-168.2.456

Cozzi, G., Broekhuis, F., Mcnutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, *93*(12), 2590–2599. https://doi.org/10.1890/12-0017.1

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, *16*(2), 488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Cuevas, M. F., Mastrantonio, L., Ojeda, R. A., & Jaksic, F. M. (2012). Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology*, *77*(4), 299–306. https://doi.org/10.1016/j.mambio.2012.02.003

Curveira-Santos, G., Marques, T. A., Björklund, M., & Santos-Reis, M. (2017). Mediterranean mesocarnivores in spatially structured managed landscapes: community organisation in time and space. *Agriculture, Ecosystems and Environment*, *237*, 280–289. https://doi.org/10.1016/j.agee.2016.12.037

Cruz, J., Sarmento, P., & White, P. C. L. (2015). Influence of exotic forest plantations on occupancy and co-occurrence patterns in a mediterranean carnivore guild. *Journal of Mammalogy*, *96*(4), 854–865. https://doi.org/10.1093/jmammal/gyv109

D'Eath, R. B., & Turner, S. P. (2008). The Natural Behaviour of the Pig. *The Welfare of Pigs*, 13–45. https://doi.org/10.1007/978-1-4020-8909-1_2

Davies, T. J., Meiri, S., Barraclough, T. G., & Gittleman, J. L. (2007). Species co-existence and character divergence across carnivores. *Ecology Letters*, *10*(2), 146–152. https://doi.org/10.1111/j.1461-0248.2006.01005.x

Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: The next generation. *Ecology Letters*, *8*(8), 875–894. https://doi.org/10.1111/j.1461-0248.2005.00791.x

Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E., & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, *36*(4), 403–412. https://doi.org/10.1016/j.actao.2010.04.001

Donadio, E., & Buskirk, S. W. (2006). Diet, morphology, and interspecific killing in carnivora. *American Naturalist*, *167*(4), 524–536. https://doi.org/10.1086/501033

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dotta, G., & Verdade, L. M. (2007). Trophic categories in a mammal assemblage: diversity in an agricultural landscape. *Biota Neotropica*, *7*(2), 287–292. https://doi.org/10.1590/s1676-06032007000200031

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that effect populations in complex landscapes. *Oikos*, *65*(1), 169–175. https://doi.org/10.2307/3544901

Elton, C. S. (2001). *Animal ecology* (Vol. 166). Chicago: University of Chicago Press. https://doi.org/10.1038/166491a0

Estes, J. A. (1996). Predators and ecosystem management. *Wildlife Society Bulletin*, *24*(3), 390–396.

Estes, J. A., Crooks, K. R., & Holt, R. (2001). Predation and diversity. In *Encyclopedia of Biodiversity* (pp. 857–878). San Diego CA: Academic Press.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine1, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R., Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Farris, Z. J., Gerber, B. D., Karpanty, S., Murphy, A., Wampole, E., Ratelolahy, F., & Kelly, M. J. (2020). Exploring and interpreting spatiotemporal interactions between native and invasive carnivores across a gradient of rainforest degradation. *Biological Invasions*, *22*(6), 2033–2047. https://doi.org/10.1007/s10530-020-02237-1

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M., & York, E. C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, *125*(2), 258–270. https://doi.org/10.1007/s004420000448

Ferreira, M. T., & Aguiar, F. C. (2006). Riparian and aquatic vegetation in Mediterranean-type streams (western Iberia). *Limnetica*, *25*(1–2), 411–424.

Ferreras, P., Díaz-Ruiz, F., Alves, P. C., & Monterroso, P. (2017). Optimizing camera-trapping protocols for characterizing mesocarnivore communities in south-western Europe. *Journal of Zoology*, *301*(1), 23–31. https://doi.org/10.1111/jzo.12386

Ferreras, P., DÍaz-Ruiz, F., & Monterroso, P. (2018). Improving mesocarnivore detectability with lures in camera-trapping studies. *Wildlife Research*, *45*(6), 505–517. https://doi.org/10.1071/WR18037

Fiske, I. J., & Chandler, R. B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*(10), 1–23. https://doi.org/10.18637/jss.v043.i10

Foster, V. C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A. T. A., Negrões, N., Fonseca, C. Silveira, L. (2013). Jaguar and Puma activity patterns and predator-prey interactions in four brazilian biomes. *Biotropica*, *45*(3), 373–379. https://doi.org/10.1111/btp.12021

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63.

Gonçalves, P., Alcobia, S., Simões, L., & Santos-Reis, M. (2011). Effects of management options on mammal richness in a Mediterranean agro-silvo-pastoral system. *Agroforestry Systems*, *85*(3), 383–395. https://doi.org/10.1007/s10457-011-9439-7

Gonçalves, P., Alcobia, S., & Santos-Reis, M. (2013). *Atlas dos Mamíferos da Charneca do Infantado*. Benavente and Lisbon: Companhia das Lezirias S.A./ Centro de Biologia Ambiental (FCUL).

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin’s finches. *Science*, *313*(5784), 224–226. https://doi.org/10.1126/science.1128374

Grilo, F., Ferreira, E., Alcobia, S., Simões, L., & Santos-Reis, M. (2016). Do fine-scale factors shape the use of riparian galleries by carnivores in a Mediterranean agro-forested environment? *International Journal of Environmental & Agriculture Research*, *2*(4), 59.71.

Güthlin, D., Storch, I., & Küchenhoff, H. (2013). Landscape variables associated with relative abundance of generalist mesopredators. *Landscape Ecology*, *28*(9), 1687–1696. https://doi.org/10.1007/s10980-013-9911-z

Hardin, G. (1960). Competitive exclusion principle. *Science*, *131*, 1292–1297.

Heithaus, M. R. (2001). Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, *92*(3), 542–554. https://doi.org/10.1034/j.1600-0706.2001.920315.x

Hines, J. E. (2006). *Program PRESENCE: Software to compute estimates patch occupancy rates and related parameters*. Retrieved from http://www.mbrpwrc.usgs.gov/software/presence.html

Hipólito, D., Santos-Reis, M., & Rosalino, L. M. (2016a). European badger (Meles meles) diet in an agroforestry and cattle ranching area of central-west Portugal. *Wildlife Biology in Practice*, *12*(3), 1–13. https://doi.org/10.2461/wbp.2016.eb.1

Hipólito, D., Santos-Reis, M., & Rosalino, L. M. (2016b). Effects of agro-forestry activities, cattle-raising practices and food-related factors in badger sett location and use in Portugal. *Mammalian Biology*, *81*(2), 194–200. https://doi.org/10.1016/j.mambio.2015.11.005

Hunter, J., & Caro, T. (2008). Interspecific competition and predation in American carnivore families. *Ethology Ecology and Evolution*, *20*(4), 295–324. https://doi.org/10.1080/08927014.2008.9522514

Janssen, A., Sabelis, M. W., Magalhães, S., Montserrat, M., & Van Der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology*, *88*(11), 2713–2719. https://doi.org/10.1890/06-1408.1

Jędrzejewski, W., & Jędrzejewska, B. (1992). Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. *Ecography*, *15*(2), 212–220. https://doi.org/10.1111/j.1600-0587.1992.tb00027.x

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*. https://doi.org/10.1038/srep41036

Jones, M. E., & Barmuta, L. A. (2000). Niche differentiation among sympatric Australian dasyurid carnivores. *Journal of Mammalogy*, *81*(2), 434–447. https://doi.org/10.1644/1545-1542(2000)081<0434:NDASAD>2.0.CO;2

Karanth, K., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., & Samba Kumar, N. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1848). https://doi.org/10.1098/rspb.2016.1860

Keddy, P. A. (1989). *Competition*. New York: Chapman and Hall.

Kelt, D. A., & Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *American Naturalist*, *157*(6), 637–645. https://doi.org/10.1086/320621

Knauer, F., Küchenhoff, H., & Pilz, S. (2010). A statistical analysis of the relationship between red fox Vulpes vulpes and its prey species (grey partridge Perdix perdix, brown hare Lepus europaeus and rabbit Oryctolagus cuniculus) in Western Germany from 1958 to 1998. *Wildlife Biology*, *16*(1), 56–65. https://doi.org/10.2981/07-040

Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecology Letters*, *7*(1), 69–80. https://doi.org/10.1046/j.1461-0248.2003.00551.x

Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE*, *12*(10). https://doi.org/10.1371/journal.pone.0186679

Křivan, V., & Schmitz, O. J. (2004). Trait and density mediated indirect interactions in simple food webs. *Oikos*, *107*(2), 239–250. https://doi.org/10.1111/j.0030-1299.2004.12695.x

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of Time as an Ecological Resource. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Lanszki, Z., Purger, J. J., Bocz, R., Szép, D., & Lanszki, J. (2019). The stone marten and the red fox consumed predominantly fruits all year round: A case study. *Acta Zoologica Academiae Scientiarum Hungaricae*, *65*(1), 45–62. https://doi.org/10.17109/AZH.65.1.45.2019

Lasanta, T., González-Hidalgo, J. C., Vicente-Serrano, S. M., & Sferi, E. (2006). Using landscape ecology to evaluate an alternative management scenario in abandoned Mediterranean mountain areas. *Landscape and Urban Planning*, *78*(1–2), 101–114. https://doi.org/10.1016/j.landurbplan.2005.06.003

Linkie, M., & Ridout, M. S. (2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology*, *284*(3), 224–229. https://doi.org/10.1111/j.1469-7998.2011.00801.x

Loureiro, F. (2008). *Time and Space Use of Key Resources by the Eurasian badger (Meles meles) in a Mediterranean Cork Oak Woodland: Conservation Implications* (Doctoral dissertation). University of Lisbon, Lisbon, Portugal.

Loureiro, F., Bissonette, J. A., Macdonald, D. W., & Santos-Reis, M. (2009). Temporal variation in the availability of Mediterranean food resources: Do badgers Meles meles track them? *Wildlife Biology*, *15*(2), 197–206. https://doi.org/10.2981/07-046

Lozano, J., Virgós, E., Malo, A. F., Huertas, D. L., & Casanovas, J. G. (2003). Importance of scrub-pastureland mosaics for wild-living cats occurrence in a Mediterranean area: Implications for the conservation of the wildcat (Felis silvestris). *Biodiversity and Conservation*, *12*(5), 921–935. https://doi.org/10.1023/A:1022821708594

MacArthur, R., & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist*, *101*(921), 377–385. https://doi.org/10.1086/282505

Macdonald, D. W., Buesching, C. D., Stopka, P., Henderson, J., Ellwood, S. A., & Baker, S. E. (2004). Encounters between two sympatric carnivores: Red foxes (Vulpes vulpes) and European badgers (Meles meles). *Journal of Zoology*, *263*(4), 385–392. https://doi.org/10.1017/S0952836904005400

Macdonald, D. W., Newman, C., Dean, J., Buesching, C. D., & Johnson, P. J. (2004). The distribution of Eurasian badger, Meles meles, setts in a high-density area: Field observations contradict the sett dispersion hypothesis. *Oikos*, *106*(2), 295–307. https://doi.org/10.1111/j.0030-1299.2004.12879.x

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*(3), 300–318. https://doi.org/10.1198/108571104X3361

Mackenzie, D. I., Bailey, L. L., & Nichols, J. D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, *73*(3), 546–555. https://doi.org/10.1111/j.0021-8790.2004.00828.x

Mackenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence* (2nd ed.). Elsevier. https://doi.org/10.1016/C2012-0-01164-7

Mangas, J. G., Lozano, J., Cabezas-Díaz, S., & Virgós, E. (2008). The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. *Biodiversity and Conservation*, *17*(1), 43–51. https://doi.org/10.1007/s10531-007-9229-8

Mangas, J. G., & Rodríguez-Estival, J. (2010). Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. *Forest Ecology and Management*, *260*(8), 1274–1281. https://doi.org/10.1016/j.foreco.2010.07.001

Marques, M. B. (2017). *Mesocarnivore site occupancy in cork oak landscapes: influence of management regimes* (Master of Science dissertation). University of Lisbon, Lisbon, Portugal.

McCune, B., & Grace, J. (2002). MRPP (Multi-response Permutation Procedures) and related techniques. In *Analysis of Ecological Communities* (pp. 188–197). Gleneden Beach, Oregon, USA: MjM Software Design.

Meredith, M., & Ridout, M. S. (2014). Overview of the package ‘overlap’. *R Project*, 1–9.

Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, *124*(3), 383–396. https://doi.org/10.1016/j.biocon.2005.01.045

Miller, B., Dugelby, B., Foreman, D., del Rio, C. M., Noss, R., Phillips, M., Reading, R., Soule, M. E., Terborgh, J., Willcox, L. (2001). The importance of large carnivores to healthy ecosystems. *Endangered Species Update*, *18*, 202–210.

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Robison, T., Millspaugh, J. J., & Montgomery, R. A. (2018). Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems*, *21*(4), 765–778. https://doi.org/10.1007/s11252-018-0758-6

Monterroso, P., Alves, P. C., & Ferreras, P. (2013). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. *Behavioral Ecology and Sociobiology*, *68*(9), 1403–1417. https://doi.org/10.1007/s00265-014-1748-1

Monterroso, P., Alves, P. C., & Ferreras, P. (2014). Ecological interactions and species coexistence in Iberian mesocarnivore communities - Extended summary and main results. *Galemys, Spanish Journal of Mammalogy*, *27*, 47–57. https://doi.org/10.7325/galemys.2015.a6

Monterroso, P., Díaz-Ruiz, F., Lukacs, P. M., Alves, P. C., & Ferreras, P. (2020). Ecological traits and the spatial structure of competitive coexistence among carnivores. *Ecology*, *101*(8). https://doi.org/10.1002/ecy.3059

Mori, E., Menchetti, M., & Balestrieri, A. (2015). Interspecific den sharing: a study on European badger setts using camera traps. *Acta Ethologica*, *18*(2), 121–126. https://doi.org/10.1007/s10211-014-0197-1

Mortelliti, A., & Boitani, L. (2008). Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. *Landscape Ecology*, *23*(3), 285–298. https://doi.org/10.1007/s10980-007-9182-7

Mos, J., & Hofmeester, T. R. (2020). The Mostela: an adjusted camera trapping device as a promising non-invasive tool to study and monitor small mustelids. *Mammal Research*. https://doi.org/10.1007/s13364-020-00513-y

Mpakairi, K. S., Ndaimani, H., Tagwireyi, P., Gara, T. W., Zvidzai, M., & Madhlamoto, D. (2017). Missing in action: Species competition is a neglected predictor variable in species distribution modelling. *PLoS ONE*, *12*(7). https://doi.org/10.1371/journal.pone.0181088

Myers, N., Mittermeler, R. A., Mittermeler, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nagendra, H. (2002). Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography*, *22*(2), 175–186. https://doi.org/10.1016/S0143-6228(02)00002-4

Padial, J. M., Âvila, E., & Sánchez, J. M. (2002). Feeding habits and overlap among red fox (Vulpes vulpes) and stone marten (Martes foina) in two Mediterranean mountain habitats. *Mammalian Biology*, *67*(3), 137–146. https://doi.org/10.1078/1616-5047-00021

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist*, *153*(5), 492–508. https://doi.org/10.1086/303189

Palomares, F., & Delibes, M. (2000). Mongooses, Civets and Genets — Carnivores in Southern Latitudes. In *Acitivty patterns in small mammals* (pp. 119–130). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-18264-8_8

Papakosta, M., Bakaloudis, D., Kitikidou, K., Vlachos, C., & Chatzinikos, E. (2010). Dietary overlap among seasons and habitats of red fox and stone marten in Central Greece. *European Journal of Scientific Research*, *45*(1), 122–127.

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., Millspaugh, J., Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, *56*(8), 1894–1904. https://doi.org/10.1111/1365-2664.13385

Pereira, P., Alves da Silva, A., Alves, J., Matos, M., & Fonseca, C. (2012). Coexistence of carnivores in a heterogeneous landscape: Habitat selection and ecological niches. *Ecological Research*, *27*(4), 745–753. https://doi.org/10.1007/s11284-012-0949-1

Pinto-Correia, T. (2000). Future development in Portuguese rural areas: How to manage agricultural support for landscape conservation? *Landscape and Urban Planning*, *50*(1–3), 95–106. https://doi.org/10.1016/S0169-2046(00)00082-7

Pinto-Correia, T., Ribeiro, N., & Sá-Sousa, P. (2011). Introducing the montado, the cork and holm oak agroforestry system of Southern Portugal. *Agroforestry Systems*, *82*(2), 99–104. https://doi.org/10.1007/s10457-011-9388-1

Pita, R., Mira, A., Moreira, F., Morgado, R., & Beja, P. (2009). Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. *Agriculture, Ecosystems and Environment*, *132*(1–2), 57–65. https://doi.org/10.1016/j.agee.2009.02.008

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics. Vol. 20*, 297–330. https://doi.org/10.1146/annurev.es.20.110189.001501

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, *59*(9), 779–791. https://doi.org/10.1525/bio.2009.59.9.9

Remonti, L., Balestrieri, A., Ruiz-González, A., Gómez-Moliner, B. J., Capelli, E., & Prigioni, C. (2012). Intraguild dietary overlap and its possible relationship to the coexistence of mesocarnivores in intensive agricultural habitats. *Population Ecology*, *54*(4), 521–532. https://doi.org/10.1007/s10144-012-0326-5

Reynolds, J. C., & Aebischer, N. J. (1991). Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox Vulpes vulpes. *Mammal Review*, *21*(3), 97–122. https://doi.org/10.1111/j.1365-2907.1991.tb00113.x

Richmond, O. M. W., Hines, J. E., & Beissinger, S. R. (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, *20*(7), 2036–2046. https://doi.org/10.1890/09-0470.1

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, *14*(3), 322–337. https://doi.org/10.1198/jabes.2009.08038

Ripple, W. J., Wirsing, A. J., Wilmers, C. C., & Letnic, M. (2013). Widespread mesopredator effects after wolf extirpation. *Biological Conservation*, *160*, 70–79. https://doi.org/10.1016/j.biocon.2012.12.033

Ripple, W. J., James A. Estes, Robert L. Beschta, Christopher C. Wilmers, Euan G. Ritchie, Mark Hebblewhite, Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., Wirsing, A. J. (2014). Status and Ecological Effects of the World’s Largest Carnivores. *Science,* 343. https://doi.org/10.1126/science.1241484

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G., & McDonald, R. A. (2012). Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution*, *27*(5), 265–271. https://doi.org/10.1016/j.tree.2012.01.001

Rödel, H. G., & Stubbe, M. (2006). Shifts in food availability and associated shifts in space use and diet in stone marten. *Lutra*, *49*(1), 67–72.

Roemer, G. W., Gompper, M. E., & Valkenburgh, B. Van. (2009). The ecological role of the mammalian mesocarnivore. *BioScience, 59*(2), 165–173. https://doi.org/10.1525/bio.2009.59.2.9

Rosalino, L. M., & Santos-Reis, M. (2002). Feeding habits of the common genet Genetta genetta (Carnivora: Viverridae) in a semi-natural landscape of central Portugal. *Mammalia*, *66*(2), 195–205. https://doi.org/10.1515/mamm.2002.66.2.195

Rosalino, L. M., Santos, M. J., Beier, P., & Santos-Reis, M. (2008). Eurasian badger habitat selection in Mediterranean environments: Does scale really matter? *Mammalian Biology*, *73*(3), 189–198. https://doi.org/10.1016/j.mambio.2007.02.004

Rosalino, L. M., & Santos-Reis, M. (2009). Fruit consumption by carnivores in Mediterranean Europe. *Mammal Review*, *39*(1), 67–78. https://doi.org/10.1111/j.1365-2907.2008.00134.x

Rosalino, L. M., Rosário, J. do, & Santos-Reis, M. (2009). The role of habitat patches on mammalian diversity in cork oak agroforestry systems. *Acta Oecologica*, *35*(4), 507–512. https://doi.org/10.1016/j.actao.2009.03.006

Santos, M. J., Pinto, B. M., & Santos-Reis, M. (2007). Trophic niche partitioning between two native and two exotic carnivores in SW Portugal. *Web Ecology*, *7*, 53–62. https://doi.org/10.5194/we-7-53-2007

Santos, M. J., Rosalino, L. M., Matos, H. M., & Santos-Reis, M. (2016). Riparian ecosystem configuration influences mesocarnivores presence in Mediterranean landscapes. *European Journal of Wildlife Research*, *62*(3), 251–261. https://doi.org/10.1007/s10344-016-0984-2

Santos-Reis, M., Santos, M. J., Lourenço, S., Marques, J. T., Pereira, I., & Pinto, B. (2005). Relationships between stone martens, genets and cork oak woodlands in Portugal. *Martens and Fishers (Martes) in Human-Altered Environments: An International Perspective*, 147–172. https://doi.org/10.1007/0-387-22691-5_7

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, *185*(4145), 27–39. https://doi.org/10.1126/science.185.4145.27

Schoener, T. W. (1983). Field experiments on interspecific competition. *American Naturalist*, *122*(2), 240–285. https://doi.org/10.1086/284133

Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, *158*, 301–312. https://doi.org/10.1016/j.biocon.2012.08.008

Serafini, P., & S.Lovari, S. (1993). Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. *Acta Theriologica*, *38*(3), 233–244.

Sévêque, A., Gentle, L. K., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*. https://doi.org/10.1111/brv.12635

Silva, M. G. (2017). *Organização espacial do texugo europeu na Companhia das Lezírias, SA* (Master of Science dissertation). University of Lisbon, Lisbon, Portugal.

Soto, C., & Palomares, F. (2015). Coexistence of sympatric carnivores in relatively homogeneous Mediterranean landscapes: functional importance of habitat segregation at the fine-scale level. *Oecologia*, *179*(1), 223–235. https://doi.org/10.1007/s00442-015-3311-9

Surová, D., Surový, P., de Almeida Ribeiro, N., & Pinto-Correia, T. (2011). Integrating differentiated landscape preferences in a decision support model for the multifunctional management of the Montado. *Agroforestry Systems*, *82*(2), 225–237. https://doi.org/10.1007/s10457-011-9373-8

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(30), 10854–10861. https://doi.org/10.1073/pnas.0403458101

Torretta, E., Serafini, M., Puopolo, F., & Schenone, L. (2016). Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (N-W Italy). *Acta Ethologica*, *19*(2), 123–132. https://doi.org/10.1007/s10211-015-0231-y

Torretta, E., Mosini, A., Piana, M., Tirozzi, P., Serafini, M., Puopolo, F., Saino, N., Balestrieri, A. (2017). Time partitioning in mesocarnivore communities from different habitats of NW Italy: Insights into martens' competitive abilities. *Behaviour*, *154*(2), 241–266. https://doi.org/10.1163/1568539X-00003420

Tsunoda, H., Newman, C., Peeva, S., Raichev, E., Buesching, C. D., & Kaneko, Y. (2020). Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina Mountains, Bulgaria. *Zoology (Jena, Germany), 141*. https://doi.org/10.1016/j.zool.2020.125801

Vandermeer, J., & Perfecto, I. (2007). The diverse faces of ecosystem engineers in agroecosystems. In *Ecosystems Engineers-Plants to Protists* (Vol. 4, pp. 367–385).

Verdade, L. M., Rosalino, L. M., Gheler-Costa, C., Pedroso, N. M., & Lyra-Jorge, M. C. (2011). Adaptation of mesocarnivores (mammalia: carnivora) to agricultural landscapes in Mediterranean Europe and Southeastern Brazil: A trophic perspective. In *Middle-Sized Carnivores in Agricultural Landscapes*, 1–39.

Vilella, M., Ferrandiz-Rovira, M., & Sayol, F. (2020). Coexistence of predators in time: Effects of season and prey availability on species activity within a Mediterranean carnivore guild. *Ecology and Evolution*, *10*, 11408– 11422. https://doi.org/10.1002/ece3.6778

von Essen, M., do Rosário, I. T., Santos-Reis, M., & Nicholas, K. A. (2019). Valuing and mapping cork and carbon across land use scenarios in a Portuguese montado landscape. *PLoS ONE, 14*(3). https://doi.org/10.1371/journal.pone.0212174

8. Appendixes

Appendix 8.1 – Candidate models for each species detectability (*ρ*), while keeping occupancy constant (Ψ). See table 3.2 for covariates description.

Species	Model	ΔAICc
Red fox	*ρ*(RIP) Ψ(.)	0.00
	ρ(SS_juv) Ψ(.)	5.36
	ρ(MNS) Ψ(.)	6.75
	ρ(.) Ψ(.)	7.44
European badger	*ρ*(MDS) Ψ(.)	0.00
	ρ(.) Ψ(.)	3.97
	ρ(Cattle) Ψ(.)	6.25
	ρ(MNS) Ψ(.)	6.50
	ρ(AGRI) Ψ(.)	6.40
Egyptin mongoose	*ρ*(MDS) Ψ(.)	0.00
	ρ(.) Ψ(.)	13.08
	ρ(SS) Ψ(.)	13.56
	ρ(AGRI) Ψ(.)	3.14
Common genet	*ρ*(MDS) Ψ(.)	0.00
	ρ(.) Ψ(.)	4.92
	ρ(Forest_Interv) Ψ(.)	11.43
	ρ(Cattle) Ψ(.)	7.58
Stone marten	*ρ*(MDS+Cattle) Ψ(.)	0.00
	ρ(MNS) Ψ(.)	8.32
	ρ(.) Ψ(.)	9.94
	ρ(Forest_Interv) Ψ(.)	17.19

Appendix 8.2 – Candidate models for each species occupancy (Ψ). See table 3.2 for covariates description.

Species	Model	ΔAICc	AICcw
Red fox	ρ(RIP) Ψ(.)	0.00	0.21
	ρ(RIP) Ψ(LAGO)	0.05	0.20
	ρ(RIP) Ψ(MSS)	0.57	0.16
	ρ(RIP) Ψ(SS_juv)	1.35	0.11
	ρ(RIP) Ψ(S)	1.46	0.10
	ρ(RIP) Ψ(SS_juv+LAGO)	1.48	0.10
	ρ(RIP) Ψ(SM)	2.81	0.05
	ρ(RIP) Ψ(MNS)	2.85	0.05
	ρ(RIP) Ψ(Forest_Interv)	5.35	0.01
	ρ(RIP) Ψ(AGRI+Cattle)	5.82	0.01
Egyptian mongoose	ρ(MDS) Ψ(SS_juv+LAGO)	0.00	0.76
	ρ(MDS) Ψ(LAGO)	3.34	0.14
	ρ(MDS) Ψ(RIP)	6.20	0.03
	ρ(MDS) Ψ(LD)	6.84	0.02
	ρ(MDS) Ψ(.)	7.01	0.02
	ρ(MDS) Ψ(SS)	7.20	0.02
	ρ(MDS) Ψ(MNS)	8.53	0.01
European badger	ρ(MDS) Ψ(LD)	0.00	0.38
	ρ(MDS) Ψ(LD+SS_juv)	0.53	0.29
	ρ(MDS) Ψ(MNS)	1.82	0.15
	ρ(MDS) Ψ(MSS)	2.38	0.11
	ρ(MDS) Ψ(.)	5.01	0.03
	ρ(MDS) Ψ(Alim)	6.24	0.02
	ρ(MDS) Ψ(Cattle)	6.97	0.01
	ρ(MDS) Ψ(P)	7.83	0.01
Common genet	ρ(MDS) Ψ(SS_juv)	0.00	0.47
	ρ(MDS) Ψ(AGRI+SS_juv)	0.35	0.39
	ρ(MDS) Ψ(MDS)	3.16	0.10
	ρ(MDS) Ψ(.)	5.96	0.02
	ρ(MDS) Ψ(RIP)	7.31	0.01
	ρ(MDS) Ψ(Cattle)	8.43	0.01
	ρ(MDS) Ψ(SM)	8.93	0.01
	ρ(MDS) Ψ(Forest_Interv)	17.26	0.00
Stone marten	ρ(MDS+Cattle) Ψ(MNS+LAGO)	0.00	0.51
	ρ(MDS+Cattle) Ψ(MNS)	0.18	0.47
	ρ(MDS+Cattle) Ψ(.)	7.53	0.01
	ρ(MDS+Cattle) Ψ(RIP)	9.74	0.00
	ρ(MDS+Cattle) Ψ(SS_juv)	10.02	0.00
	ρ(MDS+Cattle) Ψ(SM)	10.09	0.00
	ρ(MDS+Cattle) Ψ(Cattle)	10.68	0.00
	ρ(MDS+Cattle) Ψ(Forest_Interv)	19.08	0.00

Appendix 8.3 – Average beta coefficients and standard errors for each species detectability. * represents a well-supported effect (estimate unconditional beta coefficient 90% confidence intervals do not overlap zero). See table 3.2 for covariates description.

Species	MDS	RIP	Cattle
Red fox		0.63±0.23 (0.19, 1.08)*	
European badger	-0.48±0.19 (-0.87, -0.1)*		
Egyptian mongoose	-0.82±0.25 (-1.32, -0.33)*		
Common genet	0.71±0.28 (0.24, 1.17)*		
Stone marten	-0.57±0.26 (-1.08, -0.06)*		-3.75±2.59 (-8.83, 1.33)

Appendix 8.4 – Average beta coefficients and standard errors for each species occupancy. * represents a well-supported effect (estimate unconditional beta coefficient 90% confidence intervals do not overlap zero). See table 3.2 for covariates description.

Species	LD	MNS	MSS	S	SS_juv	LAGO	AGRI
Red fox			-0.70±0.50 (-1.52, 0.12)	1.13±1.45 (-1.25, 3.51)	0.76±0.76 (-0.49, 2.0)	2.22±2.18 (-1.36, 5.81)	
European badger	1.64±0.73 (0.21, 3.08)*	-1.24±0.54 (-2.35, -0.12)*			1.16±0.93 (-0.66, 2.98)		
Egyptian mongoose					2.8±1.66 (-0.45, 6.05)	8.98±10.72 (-12.03, 29.99)	
Common genet					13.78±63.72 (-91.04, 118.59)		7.56±61.94 (-94.31, 109.44)
Stone marten		-45.73±107.51 (-256.44, 164.99)				34.96±38.97 (-41.42, 111.34)	

Appendix 8.5 – Candidate model set for the single-season two-species occupancy modelling for the pair European badger (A) – red fox (B). Red fox detection probability is not modelled by RIP (ρB(.)). This species occupancy is only modelled by environmental covariates if European badger is present (ΨBA(environmental covariates) but ΨBa(.)). ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent. See table 3.1 for hypotheses description and 3.2 for covariates description.

Hypothesis	**Model**	**ΔAIC**	**AICw**
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(MSS)	0.00	0.18
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(MSS)	1.05	0.11
ρ(COND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(MSS)	1.63	0.08
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(MSS)	2.69	0.05
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(.)	2.70	0.05
ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(MSS)	2.80	0.04
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(LAGO)	3.54	0.03
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(.)	3.58	0.03
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(S)	3.70	0.03
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(MSS)	3.76	0.03
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(SS_juv)	4.26	0.02
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(LAGO)	4.34	0.02
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(MSS)	4.42	0.02
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(S)	4.53	0.02
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(.)	4.55	0.02
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(MSS)	4.83	0.02
ρ(COND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(SS_juv+LAGO)	4.99	0.01
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(SS_juv)	5.12	0.01
ρ(COND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(LAGO)	5.35	0.01
ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(.)	5.37	0.01
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(.)	5.45	0.01
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(MSS)	5.52	0.01
ρ(COND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(S)	5.53	0.01
ρ(COND) Ψ(IND)	ΨA(LD) ΨB(SS_juv+LAGO)	5.76	0.01
ρ(COND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(SS_juv)	6.13	0.01
ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(LAGO)	6.17	0.01
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(LAGO)	6.17	0.01
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(MSS)	6.22	0.01
ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(S)	6.36	0.01
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(S)	6.39	0.01
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(MSS)	6.57	0.01
ρ(COND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(SS_juv+LAGO)	6.82	0.01
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(.)	6.94	0.01
ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(SS_juv)	6.95	0.01
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(.)	6.95	0.01
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(SS_juv)	7.02	0.01
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(.)	7.22	0.00
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(.)	7.56	0.00
ρ(COND) Ψ(COND)	ΨA(LD) ΨB(SS_juv+LAGO)	7.62	0.00

ρ(COND) Ψ(IND)	ΨA(MNS) ΨB(SS_juv+LAGO)	7.63	0.00
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(LAGO)	7.80	0.00
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(.)	7.86	0.00
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(LAGO)	7.97	0.00
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(LAGO)	7.98	0.00
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(S)	7.98	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(MSS)	8.00	0.00
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(S)	8.05	0.00
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(S)	8.19	0.00
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(SS_juv)	8.42	0.00
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(LAGO)	8.49	0.00
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(SS_juv)	8.55	0.00
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(S	8.60	0.00
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(LAGO)	8.63	0.00
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(SS_juv)	8.82	0.00
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(S)	8.85	0.00
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(SS_juv)	9.00	0.00
ρ(IND) Ψ(IND)	ΨA(LD+SS_juv) ΨB(SS_juv+LAGO)	9.25	0.00
ρ(IND) Ψ(COND)	ΨA(LD+SS_juv) ΨB(LAGO+SS_juv)	9.29	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(.)	9.40	0.00
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(SS_juv)	9.45	0.00
ρ(COND) Ψ(COND)	ΨA(MNS) ΨB(SS_juv+LAGO)	9.47	0.00
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(.)	9.63	0.00
ρ(IND) Ψ(IND)	ΨA(LD) ΨB(SS_juv+LAGO)	9.74	0.00
ρ(IND) Ψ(COND)	ΨA(LD) ΨB(SS_juv+LAGO)	10.10	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(LAGO)	10.38	0.00
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(LAGO)	10.44	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(S	10.49	0.00
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(S)	10.66	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(SS_juv)	10.88	0.00
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(SS_juv)	11.25	0.00
ρ(IND) Ψ(IND)	ΨA(MNS) ΨB(SS_juv+LAGO)	11.68	0.00
ρ(IND) Ψ(COND)	ΨA(MNS) ΨB(SS_juv+LAGO)	11.95	0.00
ρ(COND) Ψ(IND)	Ψ(.)	19.91	0.00
ρ(COND) Ψ(COND)	Ψ(.)	21.77	0.00
ρ(IND) Ψ(IND)	Ψ(.)	23.86	0.00
ρ(IND) Ψ(COND)	Ψ(.)	23.98	0.00

Appendix 8.6 – Candidate model set for the single-season two-species occupancy modelling for the pair red fox (A) - Egyptian mongoose (B). The subordinate species occupancy is not modelled by environmental covariates (ΨBA(.) and ΨBa(.)). ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent. See table 3.1 for hypotheses description and 3.2 for covariates description.

Hypothesis	Model	ΔAIC	AICw
ρ(COND) Ψ(COND)	ΨA(LAGO) ΨB(.)	0.00	0.19
ρ(COND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	0.01	0.19
ρ(COND) Ψ(COND)	ΨA(SS_juv) ΨB(.)	1.39	0.10
ρ(COND) Ψ(COND)	ΨA(MSS) ΨB(.)	1.55	0.09
ρ(COND) Ψ(COND)	ΨA(S) ΨB(.)	1.58	0.09
ρ(IND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	2.64	0.05
ρ(IND) Ψ(COND)	ΨA(LAGO) ΨB(.)	2.64	0.05
ρ(COND) Ψ(IND)	ΨA(LAGO) ΨB(.)	3.00	0.04
ρ(COND) Ψ(IND)	ΨA(LAGO+SS_juv) ΨB(.)	3.16	0.04
ρ(IND) Ψ(COND)	ΨA(SS_juv) ΨB(.)	4.03	0.03
ρ(COND) Ψ(IND)	ΨA(MSS) ΨB(.)	4.05	0.03
ρ(IND) Ψ(COND)	ΨA(MSS) ΨB(.)	4.20	0.02
ρ(IND) Ψ(COND)	ΨA(S) ΨB(.)	4.22	0.02
ρ(COND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	4.32	0.02
ρ(COND) Ψ(IND)	ΨA(S) ΨB(.)	4.51	0.02
ρ(IND) Ψ(IND)	ΨA(LAGO) ΨB(.)	8.44	0.00
ρ(IND) Ψ(IND)	ΨA(LAGO+SS_juv) ΨB(.)	8.71	0.00
ρ(IND) Ψ(IND)	ΨA(MSS) ΨB(.)	8.96	0.00
ρ(IND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	9.74	0.00
ρ(IND) Ψ(IND)	ΨA(S) ΨB(.)	9.85	0.00
ρ(IND) Ψ(COND)	Ψ(.)	25.47	0.00
ρ(COND) Ψ(COND)	Ψ(.)	26.82	0.00
ρ(IND) Ψ(IND)	Ψ(.)	30.96	0.00
ρ(COND) Ψ(IND)	Ψ(.)	32.53	0.00

Appendix 8.7 – Candidate model set for the single-season two-species occupancy modelling for the pair red fox (A) - common genet (B). The subordinate species occupancy is not modelled by environmental covariates (ΨBA(.) and ΨBa(.)). ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent. See table 3.1 for hypotheses description and 3.2 for covariates description.

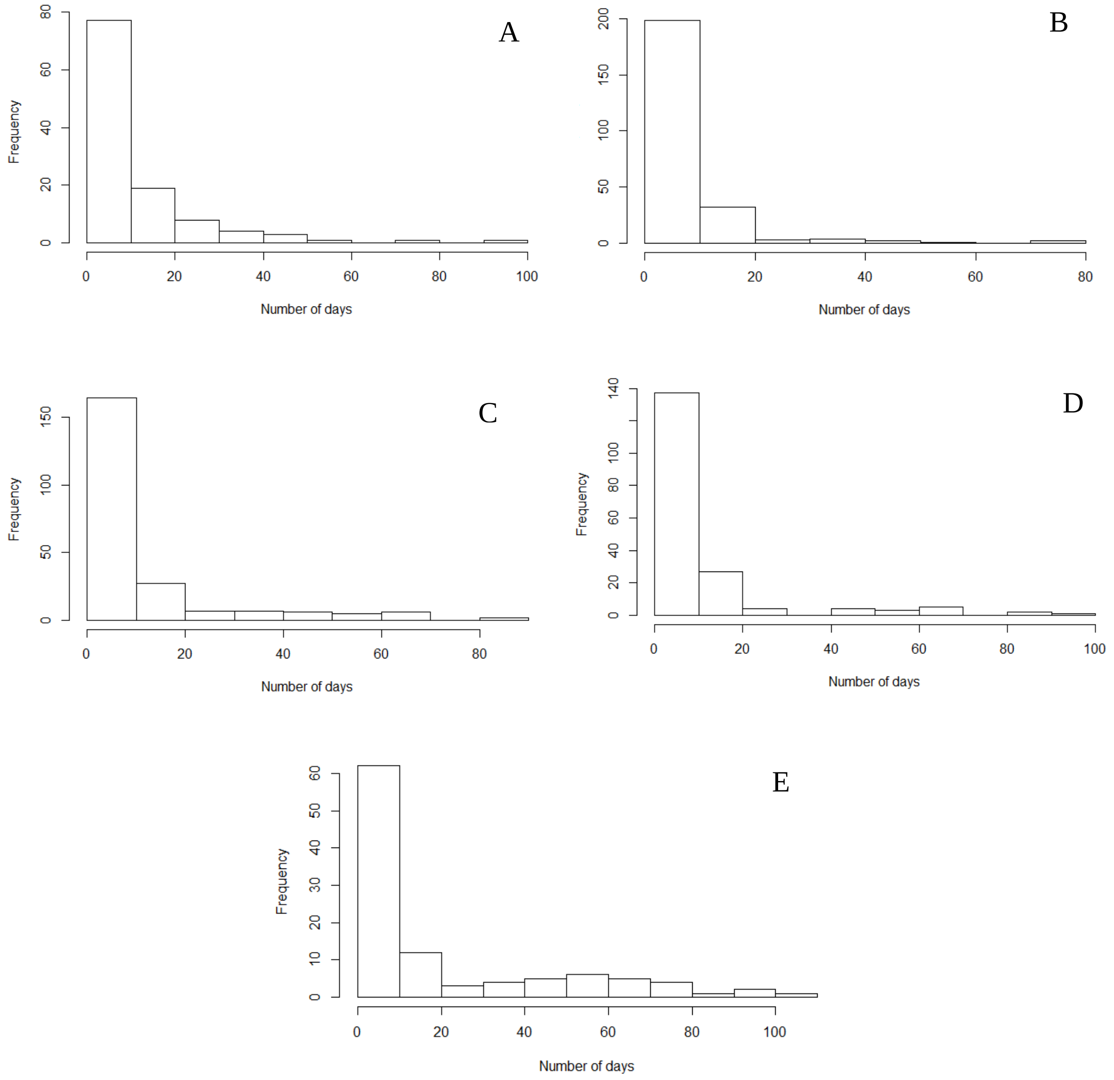
Hypothesis	**Model**	**ΔAIC**	**AICw**
ρ(COND) Ψ(IND)	ΨA(LAGO) ΨB(.)	0.00	0.12
ρ(COND) Ψ(IND)	ΨA(LAGO+SS_juv) ΨB(.)	0.25	0.10
ρ(IND) Ψ(IND)	ΨA(LAGO) ΨB(.)	0.71	0.08
ρ(COND) Ψ(IND)	ΨA(MSS) ΨB(.)	0.76	0.08
ρ(IND) Ψ(IND)	ΨA(LAGO+SS_juv) Ψ(.)	0.98	0.07
ρ(IND) Ψ(IND)	ΨA(MSS) ΨB(.)	1.23	0.06
ρ(COND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	1.35	0.06
ρ(COND) Ψ(IND)	ΨA(S) ΨB(.)	1.42	0.06
ρ(COND) Ψ(COND)	ΨA(LAGO) ΨB(.)	1.97	0.04
ρ(IND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	2.02	0.04
ρ(IND) Ψ(IND)	ΨA(S) ΨB(.)	2.12	0.04
ρ(COND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	2.22	0.04
ρ(IND) Ψ(COND)	ΨA(LAGO) ΨB(.)	2.55	0.03
ρ(COND) Ψ(COND)	ΨA(MSS) ΨB(.)	2.74	0.03
ρ(IND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	2.81	0.03
ρ(IND) Ψ(COND)	ΨA(MSS) ΨB(.)	3.07	0.03
ρ(COND) Ψ(COND)	ΨA(SS_juv) ΨB(.)	3.33	0.02
ρ(COND) Ψ(COND)	ΨA(S) ΨB(.)	3.40	0.02
ρ(IND) Ψ(COND)	ΨA(SS_juv) ΨB(.)	3.85	0.02
ρ(IND) Ψ(COND)	AΨ(S) ΨB(.)	3.96	0.02
ρ(COND) Ψ(IND)	Ψ(.)	14.27	0.00
ρ(IND) Ψ(IND)	Ψ(.)	15.00	0.00
ρ(COND) Ψ(COND)	Ψ(.)	16.22	0.00
ρ(IND) Ψ(COND)	Ψ(.)	16.73	0.00

Appendix 8.8 – Candidate model set for the single-season two-species occupancy modelling for the pair red fox (A) - stone marten (B). The subordinate species occupancy is not modelled by environmental covariates (ΨBA(.) and ΨBa(.)). ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent. See table 3.1 for hypotheses description and 3.2 for covariates description.

Hypothesis	**Model**	**ΔAIC**	**AICw**
ρ(COND) Ψ(IND)	ΨA(LAGO) ΨB(.)	0.00	0.14
ρ(COND) Ψ(IND)	ΨA (LAGO+SS_juv) ΨB(.)	0.18	0.13
ρ(COND) Ψ(IND)	ΨA(MSS) ΨB(.)	0.84	0.09
ρ(COND) Ψ(COND)	ΨA(LAGO) Ψ(.)	1.23	0.08
ρ(COND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	1.32	0.07
ρ(COND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	1.44	0.07
ρ(COND) Ψ(IND)	ΨA(S) ΨB(.)	1.51	0.07
ρ(COND) Ψ(COND)	ΨA(MSS) ΨB(.)	1.93	0.05
ρ(IND) Ψ(IND)	ΨA(LAGO) ΨB(.)	2.35	0.04
ρ(COND) Ψ(COND)	ΨA(SS_juv) ΨB(.)	2.55	0.04
ρ(IND) Ψ(IND)	ΨA(LAGO+SS_juv) ΨB(.)	2.62	0.04
ρ(COND) Ψ(COND)	ΨA(S) ΨB(.)	2.74	0.04
ρ(IND) Ψ(IND)	ΨA(MSS) ΨB(.)	2.87	0.03
ρ(IND) Ψ(IND)	ΨA(SS_juv) ΨB(.)	3.66	0.02
ρ(IND) Ψ(IND)	ΨA(S) ΨB(.)	3.76	0.02
ρ(IND) Ψ(COND)	Ψ(LAGO) ΨB(.)	3.98	0.02
ρ(IND) Ψ(COND)	ΨA(MSS) ΨB(.)	4.16	0.02
ρ(IND) Ψ(COND)	ΨA(LAGO+SS_juv) ΨB(.)	4.32	0.02
ρ(IND) Ψ(COND)	ΨA(SS_juv) Ψ(.)	5.27	0.01
ρ(IND) Ψ(COND)	ΨA(S) ΨB(.)	5.38	0.01
ρ(COND) Ψ(IND)	Ψ(.)	20.20	0.00
ρ(COND) Ψ(COND)	Ψ(.)	20.70	0.00
ρ(IND) Ψ(IND)	Ψ(.)	22.60	0.00
ρ(IND) Ψ(COND)	Ψ(.)	24.59	0.00

Appendix 8.9 – Candidate model set for the single-season two-species occupancy modelling for the pair common genet (A) - stone marten (B). The subordinate species occupancy is not modelled by environmental covariates (ΨBA(.) and ΨBa(.)). ρ(COND) indicates the subordinate species detection is conditional on the dominant species presence and ρ(IND) indicates it is independent. Ψ(COND) stands for subordinate species occupancy conditional on the dominant species presence, while Ψ(IND) indicates it is independent. See table 3.1 for hypotheses description and 3.2 for covariates description.

Hypothesis	**Model**	**ΔAIC**	**AICw**
ρ(IND) Ψ(IND)	ΨA(AGRI) ΨB(.)	0.00	0.44
ρ(IND) Ψ(COND)	ΨA(AGRI) ΨB(.)	0.21	0.40
ρ(COND) Ψ(COND)	ΨA(AGRI) ΨB(.)	3.76	0.07
ρ(COND) Ψ(IND)	ΨA(AGRI) ΨB(.)	3.94	0.06
ρ(COND) Ψ(IND)	Ψ(.)	7.35	0.01
ρ(IND) Ψ(COND)	Ψ(.)	8.28	0.01
ρ(COND) Ψ(COND)	Ψ(.)	9.09	0.00
ρ(IND) Ψ(IND)	Ψ(.)	9.24	0.00



Appendix 8.10 – Observed minimum times-to-encounter for each species pair. A – European badger – red fox; B – red fox – Egyptian mongoose; C – red fox – common genet; D – red fox – stone marten; E – common genet – stone marten.