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Spatio-temporal ecology of cervids in *Eucalyptus* plantations

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Abstract

Human population growth has led to an increase in demand for forest and agroforestry products (e.g., wood). Deforestation caused by the exploitation of these resources is partially compensated by planting of new production forests, as is the case with eucalyptus plantations. These anthropogenic environments often affect the occurrence of animal and plant species due to their biological, structural and management characteristics. In Portugal, eucalyptus plantations are widespread, occupying a quarter of the total forested area. The roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are Cervidae species whose population has been growing in recent years in the country and as sympatric species they are ideal study models to understand how eucalyptus plantations change the spatial and temporal behavior of animals. In this study, using camera trapping methods, we analyzed the interaction between roe deer and red deer in eucalyptus plantations and areas of native vegetation and the occupancy and activity patterns exhibited by these species. We used conditional occupancy models of two species to obtain species interaction factors and to assess the spatial patterns we used single season, single species occupancy models. We calculated the temporal patterns using non-parametric kernel density estimator. The presence of eucalyptus plantations had a negative influence on the occupancy probability of both species. The species also have different interactions patterns in distinct eucalyptus plantations production stages, which indicates that the structure of the eucalyptus changes how the species use it. Anthropogenic disturbance has a major impact on the spatial and temporal ecology of these cervids. Human activity and infrastructures promote these species avoidance behavior, abandoning highly disturbed areas or altering their activity pattern, as with red deer that became more active during sunrise time to lower the chance of human encounter in *Eucalyptus* plantations. This study may serve as a reference for the spatial, temporal, and interspecies behavior of roe deer and red deer in the southwestern limit of their geographic range and how these species are affected by the presence of eucalyptus plantations. Therefore, we suggest measures to reduce the impact of *Eucalyptus* plantations on local deer population. Maintaining stands age heterogeneity and reducing work activities during the crepuscular hours to ensure normal deer behavior. Allowing small patches of native vegetation within plantation stands to provide food and refuge to roe and red deer. The knowledge generated by this study will be crucial for the sustainable management of these plantations and the populations of ungulates that inhabit them.

Keywords:

Ungulates; Temporal and spatial activity; *Eucalyptus globulus*; Sympatric species; Exotic plantations.

Resumo

O crescimento populacional humano levou a um aumento da demanda por produtos florestais e agroflorestais (ex. madeira). A deflorestação causada pela exploração destes recursos é parcialmente compensada pela plantação de novas florestas de produção, como é o caso das plantações de eucalipto. Estes ambientes antropogénicos afetam frequentemente a ocorrência das espécies animais e vegetais devido às suas características biológicas, estruturais e de gestão. Em Portugal as plantações de eucalipto são vastas ocupando um quarto de toda a área florestada. O corço (*Capreolus capreolus*) e o veado (*Cervus elaphus*) são espécies de cervídeos cuja população se encontra em crescimento nos últimos anos no país. Sendo espécies simpátricas tornam-se espécies modelo ideais para compreender como as plantações de eucalipto alteram o comportamento espacial e temporal dos animais. Neste estudo, utilizando métodos de fotoarmadilhagem, analisámos a natureza da interação entre o corço e o veado em plantações de eucalipto e em áreas de vegetação nativa e os padrões de ocupação e atividade exibidos por estas espécies. Utilizámos modelos de ocupação condicional de duas espécies para obter fatores de interação inter-espécies e analisámos padrões espaciais recorremos a modelos de ocupação de uma espécie numa estação. Calculámos, de forma não paramétrica, os padrões temporais utilizando o estimador de densidade de kernel. A presença das plantações de eucalipto influenciou negativamente a probabilidade de ocupação de ambas as espécies. As espécies também apresentam interações diferentes em fases de crescimento nas plantações de eucalipto distintas, o que indica que a estrutura do eucaliptal altera como as espécies o usam. A perturbação antropogénica tem um grande impacto na ecologia espacial e temporal destas espécies. As infraestruturas e atividades humanas promovem o evitamento das espécies aos locais onde estas estão mais presentes e modelam o padrão de atividade do veado, que altera o seu pico de atividade para diminuir a chance de encontro com humanos em plantações de eucalipto. Este estudo poderá servir de referência para o estudo do comportamento espacial, temporal e interespecie do corço e do veado no limite sudoeste da sua distribuição geográfica e de como estas espécies são afetadas pela presença de plantações de eucalipto. Assim sendo, sugerimos algumas medidas que poderão reduzir o impacto destas plantações na população de cervídeos local. A manutenção da heterogeneidade etária do eucaliptal e a redução de atividades laborais durante os períodos crepusculares permitirá um comportamento natural destas espécies. Permitir segmentos de vegetação nativa dentro dos eucaliptais para proporcionar alimento e refúgio para o corço e o veado. O conhecimento gerado por este estudo será crucial para uma gestão sustentável destas plantações e das populações de ungulados que nelas habitam.

Palavras-chave:

Ungulados; Atividade temporal e espacial; *Eucalyptus globulus*; Espécies simpátricas; Plantações exóticas.

Resumo Alargado

As atividades antropogênicas provocam, em todo o globo, alterações ao nível da paisagem, resultando em importantes mudanças ambientais. O crescimento populacional humano implica um aumento da produção de gado, produtos agrícolas e agroflorestais, o que levou à necessidade de converter áreas de floresta nativa em terrenos produtivos. A desflorestação que ocorre a nível global, é parcialmente compensada com a plantação de novas florestas com o intuito de responder às demandas por produtos lenhosos e pasta de papel. O uso de espécies exóticas é bastante comum nestas plantações florestais, principalmente por apresentarem características de crescimento rápido, como por exemplo as espécies do género *Eucalyptus* e *Pinus*. O eucalipto é uma das espécies mais plantadas em todo o mundo e foi introduzido em Portugal na primeira metade do século XIX, onde o clima favoreceu a sobrevivência desta espécie em grande parte do território continental do país.

As plantações de eucalipto são geridas de forma intensiva com regimes de limpeza de subcoberto e desbaste regular, com o objetivo de promover um crescimento eficiente das árvores e assim aumentar a rentabilidade da produção. Devido a estas intervenções humanas e pela competição por recursos que o eucalipto exerce sobre as outras espécies vegetais, a biodiversidade nas plantações de eucalipto é, geralmente, baixa. Por isso, estas plantações exóticas de eucalipto influenciam frequentemente os padrões de ocorrência de vida selvagem, inclusive mamíferos. Tanto os padrões espaciais como os temporais das espécies são influenciados pelo clima, disponibilidade de recursos, estrutura do habitat e interações interespecies, como a competição e predação. Quando o alimento escasseia, a competição pode ser mais intensa entre espécies que partilham o mesmo nicho alimentar, o que poderá modificar os padrões de ocupação e atividade das espécies de forma a facilitar a sua coexistência. Predação e perturbação podem atuar em simpatria e induzem pressão nas espécies, criando uma paisagem de medo, que poderá alterar o comportamento das espécies de forma que estas possam evitar áreas/periódos onde o risco é maior. Tendo em conta que as plantações exóticas de eucalipto são ambientes perturbados pelas atividades humanas, estas paisagens antropogênicas poderão afetar as populações de animais residentes, demonstrando estas padrões espaciais e temporais diferentes, comparativamente a populações em áreas não perturbadas.

Na Europa as plantações de *Eucalyptus globulus* já ocupam vastas áreas, especialmente na Península Ibérica. Em Portugal a expansão das plantações de eucalipto ocorreu entre as décadas de 1960 e 1990. Com os terrenos desocupados após o abandono rural dos campos, as plantações exóticas de eucalipto expandiram-se em Portugal, chegando a ocupar em 2015 mais de um quarto da área florestada do território continental. O êxodo rural também beneficiou espécies silvestres como o corço (*Capreolus capreolus*) e o veado (*Cervus elaphus*) que expandiram a sua distribuição em Portugal Continental por dispersão natural e com o apoio de alguns programas de reintrodução. Graças a restrições de caça e políticas de gestão, a pressão sobre a população de corço diminuiu, o que permitiu o crescimento populacional desta espécie. Os poucos estudos que incidem nestas populações mediterrâneas de corço e veado demonstram a existência de diferenças nos padrões espaciais em comparação com populações do norte da Europa. Esta variação, reforça a importância de estudos focados nas populações mediterrâneas com o objetivo de compreender os padrões observados e os mecanismos biológicos a eles associados, especialmente em ecossistemas perturbados pela atividade humana.

O corço e o veado são duas espécies simpátricas e modelo ideais para o estudo de interações interespecies em ambientes perturbados, pois coexistem nos mesmos ambientes e sobrepõem extensivamente na sua distribuição geográfica. Apesar de alguns estudos incidirem sobre os padrões de coexistência entre estas duas espécies, não existe um consenso quanto à dinâmica da interação, porque, enquanto uns estudos indicam a possibilidade de espécies maiores terem um efeito negativo sobre espécies menores como o corço, outros não conseguem evidenciar qualquer relação competitiva entre as espécies.

Neste estudo avaliámos os padrões espaciais e temporais do corço e do veado, através de métodos de fotoarmadilhagem, em plantações de eucalipto e áreas naturais na região centro de Portugal e avaliámos, também, os padrões de coexistência entre as duas espécies em áreas de vegetação nativa e plantações de eucalipto.

Foram escolhidas oito áreas de estudo na região centro de Portugal. Estas foram agrupadas em duas subáreas – oeste e este – cada uma com quatro áreas de estudo, correspondendo três delas a áreas de plantações de eucalipto e uma a área de vegetação nativa.

Para proceder a amostragem com dispositivos de fotoarmadilhagem foram criadas grelhas de 1 km, com 25 armadilhas fotográficas em cada área. As armadilhas estiveram ativas 24 horas por dia, sem isco, durante um período de 30 noites, por época amostral. Foram considerados quatro períodos de amostragem, correspondendo às épocas húmidas e secas dos anos 2019 e 2020.

Simultaneamente à colocação das câmaras foram recolhidos dados ambientais a nível local (ex. estrutura e composição da vegetação, indícios de perturbação). Posteriormente através de sistemas de informação geográfica foram recolhidos dados para variáveis a nível da paisagem (composição e estrutura), tendo para isso sido concebido um buffer de 200 metros de raio em torno de cada câmara, que corresponde à dimensão de uma área semelhante à área vital do corço, o cervídeo com menor área vital no estudo.

Os dados provenientes da amostragem foram analisados utilizando um modelo de ocupação condicional de duas espécies, composto por uma árvore hierárquica de probabilidades de ocupação e deteção, cujo valor final corresponde ao fator de interação das espécies.

Foram realizados modelos de ocupação para cada espécie considerando cada ponto como uma combinação câmara*época, de forma a obter pseudo-replicados ao longo do estudo. Para os modelos de ocupação as variáveis ambientais foram organizadas para corresponderem a quatro hipóteses: (1) Perturbação Antropogénica; (2) Recursos de comida e água; (3) Composição do habitat; (4) Heterogeneidade do habitat. Para cada modelo várias combinações de variáveis foram testadas e após selecionar os melhores modelos, foi realizado um procedimento de cálculo de média dos modelos para se escolher as variáveis cujo intervalo de confiança das estimativas não incluíssem o zero. Seguidamente, foi criada uma quinta hipótese mista que reuniu todas as variáveis escolhidas. Por fim, o melhor modelo para cada espécie foi ajustado para “bootstrapping” paramétrico e foram registados os valores previstos de probabilidade de ocupação, que foram comparados através do teste Mann-Whitney-Wilcoxon.

Os padrões de atividade foram estimados não parametricamente usando o estimador de densidade de kernel. Os gráficos resultantes foram observados e comparados visualmente. Foi calculado o coeficiente de sobreposição para cada subgrupo de dados. Por último, realizaram-se testes de homogeneidade de ângulos, baseados em estatística circular, para evidenciar diferenças entre os padrões de atividade das espécies.

Os resultados obtidos indicam que o corço e o veado têm um comportamento espacial distinto nas plantações de eucalipto quando comparado com o detetado em áreas de vegetação nativa. Dentro destas plantações a interação entre as duas espécies variou consoante a fase de crescimento em que o eucalipto se encontrava. Os padrões de ocupação destas espécies foram definidos por uma combinação das variáveis pertencentes às hipóteses formuladas. Ambas as espécies foram negativamente influenciadas pela presença de espécies exóticas, *i.e.*, eucalipto. A perturbação antropogénica, como estradas e infraestruturas, também provou ser prejudicial à probabilidade de ocupação do corço e do veado. Os padrões de atividade demonstraram diferenças comportamentais entre as duas épocas climáticas, sendo que ambas as espécies reduziram a sua atividade diurna durante a época seca, concentrando a sua

atividade nas horas crepusculares. Nas áreas de vegetação nativa durante a época húmida, o veado e o corço têm padrões de atividade muito distintos que indicam diferenças nas suas estratégias de alimentação e de metabolismo. O veado reduziu drasticamente a sua atividade noturna nesta época apenas em áreas de vegetação nativa, aumentando a sua atividade diurna. A perturbação também foi um importante modelador do comportamento do veado nas plantações de eucalipto, uma vez que influenciou uma alteração nos seus ritmos de atividade, deixando de apresentar dois picos de atividade nas horas crepusculares para apenas um maior pico de atividade ao nascer-do-sol, associado provavelmente com a intenção de evitar o encontro com seres humanos.

De acordo com os nossos resultados sugerimos algumas medidas de gestão como a manutenção da heterogeneidade da estrutura etária dos eucaliptais e a redução de atividade de trabalhos florestais durante os períodos crepusculares, de forma a permitir que o corço e o veado possam demonstrar comportamentos naturais nestes ambientes antropogénicos. Também sugerimos a integração de pequenas secções de vegetação nativa dentro dos eucaliptais que servirão de fonte de alimento e refúgio para os cervídeos. Assim sendo, este estudo servirá como base para o estudo dos padrões de ocupação e de atividade do corço e do veado no limite sudoeste da sua distribuição geográfica e das condições que modelam o comportamento destas espécies em plantações exóticas de eucalipto. Esta informação será fundamental como o primeiro passo para que os gestores possam compreender de que forma as suas ações afetam os ungulados, o que é um conhecimento crucial para uma gestão sustentável destas paisagens antrópicas.

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Chapter I - General Introduction

Human activities have induced drastic changes in land use all around the world, leading to globally relevant environmental modifications (Geri, Amici, & Rocchini, 2010). The replacement of native environments by anthropic land uses leads to changes in vegetation cover, which together with unsustainable forestry management practices, promote soil degradation (Bajocco *et al.*, 2012; Reidsma *et al.*, 2006), and ultimately biodiversity loss (Young *et al.*, 2005). The Mediterranean basin is a clear example of this anthropogenic impact, since less than 5% of its original vegetation remains unaltered (Geri *et al.*, 2010). For several decades, extensive native forest areas were severely modified in order to meet human population needs, which growth and expansion led to an increased demand for goods linked to livestock production and agricultural and agroforestry products (Martin *et al.*, 2012).

In the last decades, there has been an abandonment of traditional agricultural practices by rural land exodus, but also an intensification and over-exploitation of the landscape by the overgrowing use of technology, heavy machinery, and of fertilizers and pesticides (Signal & McCracken, 2000; Geri *et al.*, 2010). The rural and agricultural land abandonment was caused by socioeconomic factors. While many people could not sustain their life costs working in these areas and, therefore, migrated to the coastal regions where the main economic activity is located, those that remained were mostly older villagers less capable of implementing agriculture, silviculture, or cattle breeding activities. The depopulation of labor force in rural areas permitted that these areas could be naturally or artificially renaturalized or rewildened (Reidsma *et al.*, 2006).

The world forest area has been decreasing, with an average area of net loss of 4.7 million hectares of forests per year between 2010–2020 (FAO & UNEP, 2020). Nevertheless, while deforestation is occurring in many parts of the world (e.g., Amazon rainforest), new forests are being planted to fulfil paper and wood demands, and therefore, the area of exotic plantation forests has increased globally (FAO & UNEP, 2020). The *Eucalyptus* genus is one of the major species planted, ranging from tropical to temperate zones, covering more than *ca.* 20 million hectares (Forrester & Smith, 2012). These fast-growing tree species, native to Australia, are an economically important asset for some temperate regions of the world (Águas *et al.*, 2014), such as Portugal, where it was introduced in the first half of XIX century (Radich, 2007). Portugal's environmental conditions have both Atlantic and Mediterranean influences providing precipitation rates, annual temperature, and sunlight exposure favorable to *Eucalyptus* survival and recruitment, especially in the coastal and central regions (Águas *et al.*, 2014; Queirós *et al.*, 2020). Due to *Eucalyptus* high rentability and wood quality, its expansion permitted the development of forestry sectors, like the paper and cellulosic pulp industry, in which Portugal places second and third, respectively, as a European producer (Alves, Pereira, & Silva, 2007; CELPA, 2020).

In *Eucalyptus globulus* plantations, the occurrence of other tree species is scarce, limited to terrains where plantation implementation was not legally allowed, or logistically or environmentally possible, like riparian areas (Thomas, 1979), urbanized regions (Germaine & Wakeling, 2001) or protected areas. In these monospecific exotic plantations, understory plant community is particularly underdeveloped, with fewer species present and lower cover percentage than in native forests (Fabião *et al.*, 2007). Such pattern is often the result of intensive management practices implemented in these plantations, where procedures like thinning and understory cleaning are essential to ensure good quality wood production, which are management practices not commonly used on other forestry areas dominated by different genus (e.g., *Pinus*) (Fabião *et al.*, 2007).

Eucalyptus species can create seed banks from which seeds can germinate faster than those of native species, so they interfere with the natural process of native forest habitat regeneration, including

understory (Silva *et al.*, 2011). They have high plasticity and can adapt to different altitude, climate, and soil environments (Silva *et al.*, 2011). *Eucalyptus* trees rapid growth is possible because they are good carbon fixers (Pereira, 2007). This characteristic proves detrimental for the other plant species because they block sunlight (Lomba *et al.*, 2011) and deplete efficiently nutrients and water resources from their vicinity (Blondel *et al.*, 2010), providing unsuitable soil for other species development which ends up affecting understory plant community development (Calviño-Cancela, Rubido-Bará, & van Etten, 2012). The high and efficient resource use by this species is possible because of its deep root system that confers advantage where competition for resources is high (Forrester & Smith, 2012). Its efficiency in water catchment, storage and use allows for great endurance during dry periods (Pereira, 2007). All these physiological characteristics may induce soil degradation in areas where these species flourish, by removing water that maintains soil texture and structure (Lomba *et al.*, 2011). *Eucalyptus* plantations are often characterized by inducing significant environmental impacts due to soil erosion, hydrological cycle disruption (Madeira *et al.*, 2007), biodiversity loss and landscape change (Blondel *et al.*, 2010), although the scale of this impact vary greatly with the implemented management (e.g., Teixeira *et al.* 2017). Plantations are also, more prone to facilitate wildfire spreading than native vegetation forests, endangering species survival, landscape integrity and human well-being (Blondel *et al.*, 2010; Águas *et al.*, 2014).

Faunal species richness and abundance are associated, and depend, of the structural characteristics of these monospecific plantations (Carrilho *et al.*, 2017; Ramírez & Simonetti, 2011). Production forests with low biodiversity tend to be more vulnerable to disturbances and climate change because biodiversity has an important role in supporting ecosystem services and their resilience (Proença *et al.*, 2010). An example of such link is that native understory cover provides both food and shelter resources to several wild animals (Stallings, 1990). Carrilho *et al.* (2017) study, implemented in western Portugal's *Eucalyptus* plantations, verified that understory development, especially shrub cover, promoted small mammal abundance.

The low biodiversity values reported for *Eucalyptus* plantations are a common pattern throughout different taxon. They have been described to host less diverse insect communities, when compared to native forests, with particular emphasis when there is a lack of understory cover (Cunningham, Floyd, & Weir, 2005). Marsden, Whiffin, & Galetti (2001) observed that birds were negatively affected by plantations, especially insectivorous bird species, demonstrating a cascading effect in the trophic chain. However, this pattern does not occur in the whole extension of the plantation. On the plantation's edge plant competition is reduced and there is more understory development, which can promote food and refuge resources for wildlife (Rosalino *et al.*, 2014).

Furthermore, certain plantation management strategies can ameliorate the impact that plantations put on biodiversity (Hartley, 2002; Norton, 1998). Clear-cutting is a major disturbance for both fauna and flora because it changes the environment conditions drastically. The absence of the trees that provide shade and protection against strong winds will negatively affect more sensitive species that would be sheltered otherwise (Hartley, 2002). Harvesting methods that differ from clear-cutting can reduce the impact on species inhabiting plantations. Plantations that allow for longer rotations of managed stands are more prone to have higher biodiversity since older plantation stands are ecologically closer to native forest communities than younger stands (Hartley, 2002; Norton, 1998). Therefore, even exotic plantations that have low understory cover can promote biodiversity by changing their forestry practices.

The fast-paced changes occurring due to the expansion of these exotic forests in recent years, linked to an increase of human demand for paper and wood, make information on the ecological impact for native fauna more urgent than ever (Ramírez & Simonetti, 2011). Exotic *Eucalyptus* plantations have been reported to induce negative effects on mammals (Ramírez & Simonetti, 2011). However, not all

mammal groups are equally studied, and thus this pattern cannot be generalized. For example, small mammals and carnivores have more studies assessing their ecological adaptations and challenges in these altered areas (Curveira-Santos *et al.*, 2021; Martin *et al.*, 2012; Teixeira *et al.*, 2020), than other groups, like cervids (Rodrigues *et al.*, 2017).

The family Cervidae, with 56 species, is the second most speciose Ruminantia (Geist, 1998). The presence of antlers on males is a characteristic that unites the species belonging to this family, but they present a wide range of body sizes, habitat preferences and behavior patterns (Janis & Scott, 1987). Cervidae are distributed mainly in the northern hemisphere, South America, and Southeast Asia (Gilbert *et al.*, 2006). However, in the mid-1800s they were introduced in Australia, for hunting purposes, and due to accidental farm escapes and deliberate releases they have established wild populations that expanded from their introduction sites (Davis *et al.*, 2016).

In Europe, the Cervidae family is represented by six native species and five exotic species that were introduced in this region. The native species are the moose (*Alces alces*), the Siberian roe deer (*Capreolus pygargus*), the European roe deer (*Capreolus capreolus*), the red deer (*Cervus elaphus*), the fallow deer (*Dama dama*) and the reindeer (*Rangifer tarandus*) (Temple & Terry, 2009). The exotic species that were introduced in Europe are the white-tailed deer (*Odocoileus virginianus*) (HoMolka, Heroldová & Bartos, 2008), the axis deer (*Axis axis*) (Šprem & Zachos, 2020), the sika deer (*Cervus nippon*) (Bartoš, 2009), the Chinese water deer (*Hydropotes inermis inermis*) (Ward, 2005) and the reeve's muntjac (*Muntiacus reevesi*) (Ward, 2005).

Both roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are widely distributed in the European continent and their populations have increased in the past years (Burbaitė & Csányi, 2009; 2010) and Portugal is no exception (Carvalho *et al.*, 2018). Deer activity can positively influence forest regeneration and vegetation diversity (Reimoser & Gossow, 1996), but high densities can have deleterious effects (Heinze *et al.*, 2011). Damage to crops and production forests are not the only concerns linked to overabundant deer populations. Disease transmissions and deer-vehicle collisions are also a serious threat to human health and animal welfare, causing high expenses to society (Gortázar *et al.*, 2006; Hothorn *et al.*, 2015). Furthermore, some studies have used deer species to understand how heavy metals contamination can accumulate on large herbivore species, in particular game species consumed by humans, when anthropogenic activity, such as industrial production, construction sites, unregulated landfills or mining quarries produce residual pollution (Markov & Ahmed, 2019; Wiczorek-Dąbrowska *et al.*, 2013). Deer can be good bioindicators for forestry management practices at a landscape scale because they require a wide range of habitats characteristics. Thus, if these requirements are met to ensure a sustainable deer population, then it should also meet those needed to guarantee other species survival (Hanley, 1996). Hanley (1996) stated that “deer habitat management is landscape management” due to the large home ranges displayed by several deer species, when compared to those registered for other vertebrates, apart from large birds and carnivores (Hanley, 1996). Roe and red deer have an extensive distribution in the Iberian Peninsula (Lovari *et al.*, 2016, 2018) overlaying each other in some areas as sympatric species. Differences like body size, well represented between these two species, turn interspecies interaction asymmetric, since the larger species has a competitive advantage (Richard *et al.*, 2010; Torres *et al.*, 2012). Several studies focus on their spatial and temporal ecology in distinct regions of Europe, which provides vast knowledge on roe and red deer habitat use and activity patterns (Kamler, Jędrzejewska, & Jędrzejewski, 2007; Pagon *et al.*, 2013; Torres *et al.*, 2011; Torres, Santos, & Fonseca, 2014). Therefore, the extensive knowledge on these species' biology, ecology and physiology makes them excellent targets to study the possible impacts of *Eucalyptus* plantations on Mediterranean vertebrates in the Iberian Peninsula.

Chapter II - Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) co-occurrence, occupancy, and activity patterns in the central Portugal

2.1 Introduction

Planted forests are cultivated forest ecosystems, implemented by afforestation or reforestation processes (Carnus *et al.*, 2006). Since 1990, the global area of planted forest has increased to 294 million hectares, from which 45 percent are intensely managed plantation forests. However, this increase rate has slowed down since 2010 (FAO & UNEP, 2020). The worldwide demand for wood and cellulosic products creates an overexploitation pressure on native forests resources, endangering its biodiversity (Alves, Correia, & Pereira, 2012). In response to this increasing pressure, planted forests have been pointed as a solution to minimize native forests exploitation and range decrease (Alves *et al.*, 2012). However, the landscape change caused by increasing non-native planted forest area resulted in native forest habitat fragmentation and degradation, which has the potential to negatively affect native biodiversity (Johnstone, Lill, & Reina, 2014). Therefore, one of the main challenges of modern forestry management is to maintain a balance between fulfilling the increasing raw material demand and reducing pressure on native forests, while minimizing the effects on resident wildlife (Borrvalho, Almeida, & Potts, 2007).

These anthropic systems have several purposes, but the most common is wood biomass production. Plantation forests are, typically, intensively managed stands of a single tree species, such as *Pinus* spp. and *Eucalyptus* spp., native or exotic (Carnus *et al.*, 2006). These plantations are often considered “fake” forests, with fewer and simpler ecosystem processes, lower ecological functionality, lower native species richness and abundance than “real” forests, which are far more ecologically complex (DellaSala, 2020).

Exotic *Eucalyptus* plantations can hold lower biodiversity in comparison to native habitats, which indicates that wildlife occurrence, including mammals, can be influenced by the presence of exotic *Eucalyptus* plantations (Stephens & Wagner, 2007). Both spatial and temporal patterns of mammals are influenced by climate, availability of food resources, habitat structure and species interactions, like competition and predation. Lack of understory in these plantations may determine behavioral changes in browsing and habitat selection of herbivores. As an example, red deer (*Cervus elaphus*) in the Mediterranean region prefer habitats that have complex and well-developed vegetation, which provide rich food sources (Alves *et al.*, 2014). Where food is scarce, competition may be enhanced between species that share dietary niches, meaning that species would have to modify their occurrence or activity patterns to facilitate coexistence in such environments (Di Bitetti *et al.*, 2013). Another interspecies interaction that can alter spatial and temporal patterns is predation, creating a landscape of fear (Lone *et al.*, 2014). Disturbance by human activity can also create a landscape of fear that induces avoidance behavior on the species affected (Frid & Dill, 2002). These can change habitat use or adjust time activity to avoid their predator or source of disturbance. In Europe, adult brown bears (*Ursus arctos*) modified their daily activity of 24h cycles to become predominantly nocturnal, as a strategy to avoid humans (Kaczensky *et al.*, 2006). Since exotic *Eucalyptus* plantations are disturbed habitats, due to logging and other human management activities, animal populations inhabiting these plantations can display altered spatial and temporal patterns in comparison to populations in undisturbed native areas (Oberosler *et al.*, 2017).

In 2016, *Eucalyptus globulus* plantations covered 1,3 million hectares in Europe, with more than 80% occurring in the Iberian Peninsula (Cerasoli *et al.*, 2016). In Portugal, predominantly in the central region (Alves *et al.*, 2007), the notorious expansion of these plantations occurred between 1960 and 1990

(Borrvalho *et al.*, 2007). Rural land abandonment gave space for these plantations to be established as an alternative to low productivity agriculture or previous forestry areas, even though some of these regions are prone to wildfires (Fabião *et al.*, 2007), which can be promoted by unmanaged *Eucalyptus* plantations. Forests are the main land cover in mainland Portugal, occupying 36% of its territory (ICNF, 2019). The most dominant species is *Eucalyptus* spp., an exotic tree used in production forests for its fast growth. This specie's expansion has steadily increased during the last fifty years which resulted in an area of 844 thousand hectares in 2015, making up 26% of the total forested area in mainland Portugal (ICNF, 2019).

Rural exodus in Portugal did not only benefit *Eucalyptus* plantations but it also benefited some wildlife species, such as red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) (Carvalho *et al.*, 2018). While roe deer is the most abundant and widespread cervid specie in Europe, due to its ecological adaptability (Apollonio, Andersen, & Putman, 2010; González *et al.* 2013; Tellería & Virgós, 1997), red deer is only absent from northern Scandinavia, Finland, and Iceland (Zachos & Hartl, 2011). In Portugal, both species have expanded their distribution range due to natural dispersion, linked to re-naturalization of abandoned rural land, reinforced with reintroduction programs (Torres *et al.*, 2015; Carvalho *et al.*, 2018). For roe deer, hunting restrictions and management policies have diminished the harvesting pressure, which resulted in a population increase (Torres *et al.*, 2015). The few studies targeting the Mediterranean populations of both deer species often show distinct spatial patterns when compared to northern populations (Carranza *et al.*, 1991). This scenario highlights the importance of studies focusing southern populations (Torres *et al.*, 2014) to understand the mechanistic link between the observed patterns and the underlying processes, especially concerning novel and human disturbed ecosystems.

These two sympatric species are ideal models to study interspecific interactions, and how they are shaped by novel habitats, because they have extensive overlap in their geographical ranges (Carvalho *et al.* 2018) and may co-exist in the same environments (Torres *et al.* 2012). Different habitats can alter their sympatric behavior demonstrated in comparison to native habitats, which can indicate that these novel habitats have low quality and are detrimental to the equilibrium between the two species. The coexistence patterns and its consequences for both species have been the target of several studies, but there is no consensus as to the dynamics of their interaction. In central and western Europe, some studies point that larger deer species can displace roe deer (Ferretti, Sforzi, & Lovari, 2008; Latham, Staines, & Gorman, 1999). However, Borkowski & Ukalska (2008) did not find evidence of such competition or interference. For north-eastern Portugal, Torres *et al.* (2012) suggested that in a Mediterranean environment the interspecific competition between these two species is asymmetrical as roe deer seems to be negatively affected by red deer presence, while the opposite cannot be confirmed.

By using a camera trapping approach, we assessed roe and red deer spatial and temporal patterns in *Eucalyptus* plantations, in the central region of Portugal and evaluated the co-existence patterns between these two species in native vegetation areas and in *Eucalyptus* plantations. To achieve these goals, we defined the following hypothesis, according to the detailed objectives:

For the coexistence patterns, we hypothesized that the presence of red deer negatively influences the probability of roe deer presence in the different scenarios (native vegetation and *Eucalyptus* plantations), because red deer presents a higher body size that can displace roe deer through direct competition (Ferretti *et al.*, 2008) or by depleting the resources available for roe deer, since they have overlapping dietary niches (Storms *et al.*, 2008), which would cause spatial segregation between roe and red deer (Richard *et al.*, 2010; Torres *et al.*, 2012).

To understand which drivers affect roe and red deer spatial patterns we delimited four hypothesis. Each

encompassing different environment characteristics that could influence deer behavior (see table 2.3 for detailed reasoning). We expected both species occupancy patterns to be mostly negatively influenced by anthropogenic disturbance factors. Higher resources availability should determine higher occupancy probability of roe and red deer. The Habitat composition drivers shape both species occupancy variation, and habitat heterogeneity should promote deer occupancy where habitat diversity is higher.

Red and roe deer activity patterns are expected to overlap more during the dry season, because the temperatures during daylight time are higher and these species reduce activity at these hours (Rivrud, Loe, & Mysterud, 2010), which leads to more overlapped activity during nighttime. In *Eucalyptus* plantations both species will show higher overlap patterns since the higher anthropic disturbance typical of this environment (Timo *et al.*, 2015) will induce species to concentrate their activity in period where humans are absent from plantations.

2.2 Methods

2.2.1 Study Area

Our study was carried out in central Portugal, in eight different study areas (Figure 2.1). These study areas were grouped in two sub-areas - western and eastern - each one with four study sites: three located within *Eucalyptus* plantations (in different harvest phases) and the other located in a control zone, dominated by native vegetation (e.g., oak or conifer forests). Each study site comprised an area of, at least, 20 km², and was distant 10 km from the nearest one.

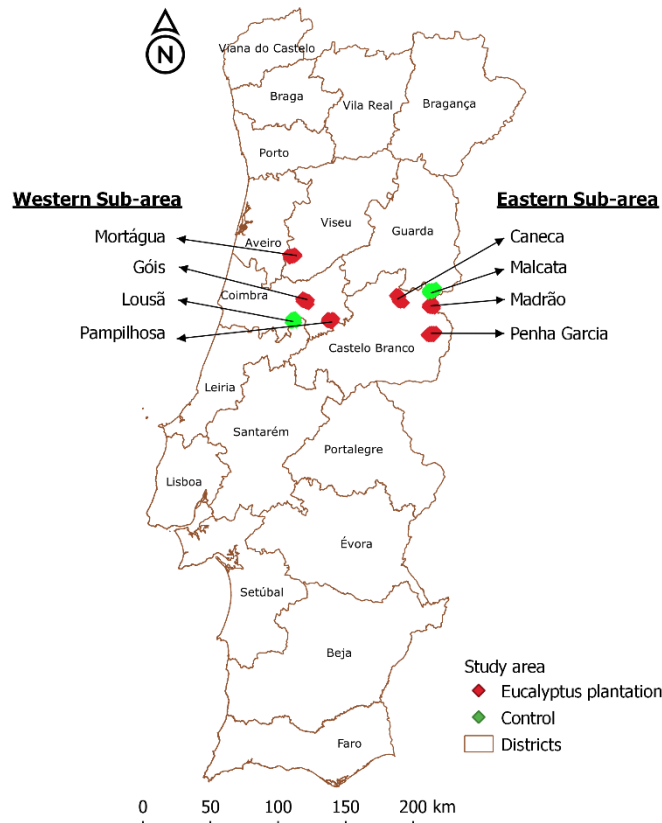


Figure 2.1 – Location of the eight study areas in Portugal, divided in two sub-areas: western and eastern. Study areas within *Eucalyptus* plantations are coloured in red and the control areas in green.

Both sub-areas have a Mediterranean climate, characterized by hot and dry summers and cold and wet winters, with a mean annual temperature and mean annual rainfall reaching 16°C and 750mm, respectively (data from the Portuguese Institute for Sea and Atmosphere – IPMA – collected from 1971 to 2000). Main economic activities in Central Portugal are linked to the production of cellulosic pulp for the paper industry, which has impacted Portugal’s forest structure for decades (Caetano & Gama, 2004; ICNF, 2019; Kardell, Steen, & Fabiao, 1986). In this region, forestry plantations dominate the landscape, and *Eucalyptus* plantations are an important landscape component. Nevertheless, some variations occur between the eastern and western subareas. In the western sub-area, the landscape is characterized by *Eucalyptus globulus* and *Pinus pinaster* plantations, with patches of native woodlands mainly composed by oak woodlands (e.g., *Quercus robur* and *Quercus suber*) and strawberry tree shrublands (*Arbutus unedo*), that also occur scattered within plantations. In the eastern sub-area, plantations of *E. globulus* dominate the landscape, although *Pinus* spp. plantations can also occur, intercalated with native woodlands, composed by oak woodlands (*Q. suber*), and Mediterranean shrublands, predominantly *A. unedo* and *Cistus ladanifer* (Table 2.1). *Eucalyptus* plantations are temporally heterogeneous, and therefore we can identify several harvesting stages in plantations, from

seedling establishment to full growth tree, prior to harvesting (Table 2.2).

Table 2.1 – Percentage of each land cover per study area.

		Native mixed forests	<i>Eucalyptus</i> plantations	Conifer forests	Shrublands	Native broadleaf forests	Mosaic
Eastern	Madrão	3%	97%				
	Penha Garcia		99%		1%		
	Malcata	2%		92%	3%	3%	
	Caneca		100%				
Western	Góis		96%		1%		3%
	Pampilhosa		100%				
	Lousã	11%		67%	10%	12%	
	Mortágua		100%				

Table 2.2 – Percentage of cover of each *Eucalyptus* production stage per plantation study area (1 correspond to a young plantation and 3 to a pre-harvesting stage).

		<i>E.</i> production stage 1	<i>E.</i> production stage 2	<i>E.</i> production stage 3
Eastern	Madrão	2.06%	90.72%	7.22%
	Penha Garcia	7.07%	82.83%	10.10%
	Caneca	5.10%	83.67%	11.22%
Western	Góis	12.50%	57.29%	30.21%
	Pampilhosa	23.00%	77.00%	
	Mortágua	5.00%	78.00%	17.00%

2.2.2 Study design

In each study site, 25 camera traps (Cuddeback 20 Megapixel IR H-1453 white series) were set, based on a 1 km grid, to ensure camera site independence (Figure 2.2), diminishing the possibility of detecting the same individual in multiple sites (Rovero & Zimmermann, 2016). The cameras were active for 24 hours a day during a period of 30 consecutive days (30 trap-nights), per season. No bait was used, and four surveys periods were considered: February-May and June-September of 2019, and January-May and July-September of 2020, corresponding to the wet and dry season of each year. Due to logistic constraints, each sampling period was divided into two phases: in the first 30 days of each sampling period, we monitored the western sub-area, and then we relocated the cameras to the eastern sub-area for another 30 days sampling period, to assure that all the study sites were surveyed within the same season.

Cameras were set at a height of 40-60 centimeters, attached to trees or, when trees were absent or could not provide a stable support for the camera, to wooden stakes (Figure 2.3). Cameras were set facing areas with less vegetation and better visibility to increase the chance of detection, but also to avoid triggering the camera due to the movement of vegetation. Additionally, they were directed towards North, whenever possible, to prevent the activation of the heat sensor (and thus triggering the camera) due to direct sunlight and the flaring of the photo, which can make animal's identification more challenging or even impossible. Camera settings were defined to take three photos at each detection, with a 30 second time interval between any subsequent detection.

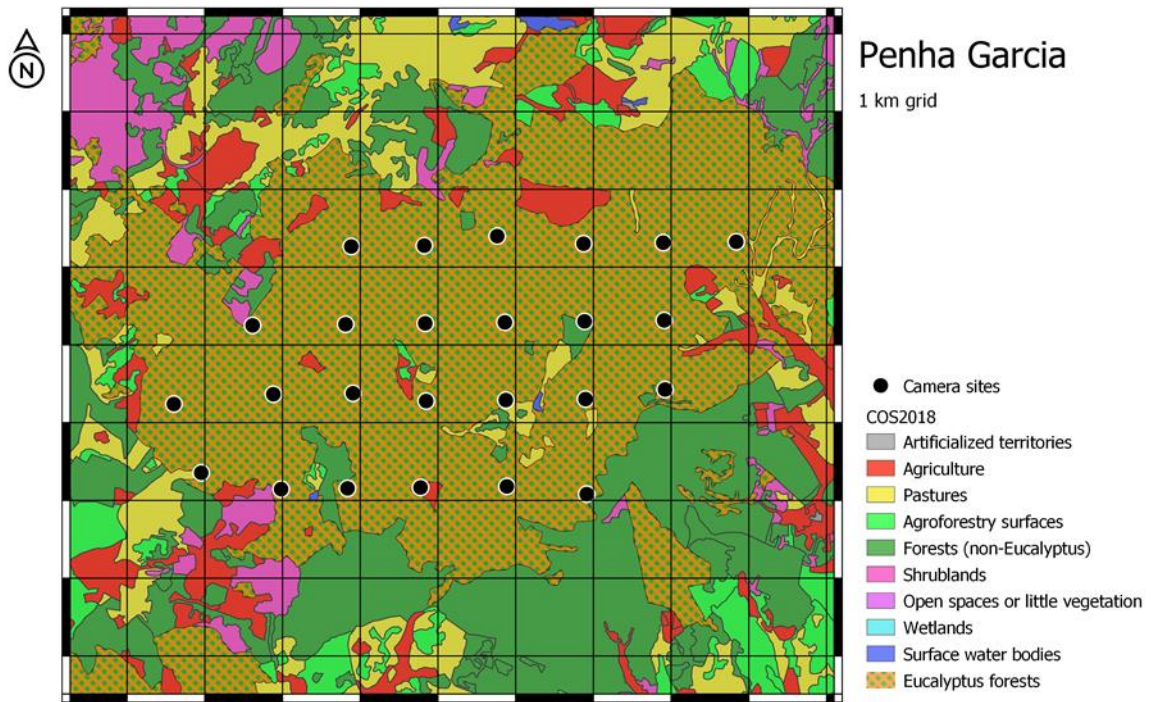


Figure 2.2 - Example of camera-traps distribution in Penha Garcia study area, showing the 1 km grid to help perceive the distance between each adjacent camera site. The camera sites are represented by black dots. The land cover, extracted from COS2018 (DGT, 2018), is represented by the coloured areas indicated in the legend.



Figure 2.3 - Example of camera traps attached to a tree (left) and to a wooden stake (right).

2.2.3 Explanatory variables

As ungulates respond to variations of environmental determinants at several spatial scales (Torres *et al.*, 2011), we considered multiple scales in habitat use. Therefore, we used ecological descriptors that ranged from patch to landscape scales. In the field, we measured micro-habitat variables that were used together with other derived from Geographical Information System (GIS) (QGIS Development Team, 2016) to estimate several macro-habitat and landscape metrics.

- Field collected data

While setting up the camera traps in the field, we collected in situ, environmental data at a microscale. We defined a 100 m radius buffer around each camera trap, where data was collected. To test our hypotheses, we selected predictor variables within that buffer, known to influence the species' distribution range: type of habitat, percentage of tree, shrub, herbaceous and rocky soil cover, percentage of exotic tree and shrub species, shrub vegetation mean height, number of landscape units, dominant *Eucalyptus* harvesting phase (Figure 2.4), human access to the site and presence of watercourses. We also registered the season when the sampling was implemented (Table 2.3). The 100m radius was defined to allow researchers to visually estimate vegetation cover accurately, as well as assess the other micro-habitat variables within the buffer, in both open and closed environments. As our study areas included steep regions this buffer allowed us to accurately characterize each camera site, according to the selected environmental data. Data collection was done by the same persons minimizing inter observer variations.



Figure 2.4 – *Eucalyptus* stands structure in different development stages. Initial development stage on the left, intermediate on the center and pre-harvesting stage on the right.

- Remote collected data

Additionally, more variables were included in our set of covariates to test our working hypothesis, which were collected remotely using a GIS, produced with the software QGIS version 3.2.1 with GRASS version 7.4.1 (QGIS Development Team, 2016). In the GIS we measured the distance to the nearest artificial land (*e.g.*, houses, warehouses), agricultural patch, unpaved roads, paved roads, and highways.

We also defined a buffer with a 200 m radius around each camera trap to estimate the number of different habitats present, the habitat's Shannon-Wiener index and the density of habitat edges. The 200m radius (buffer's area *ca.* 12 ha) was defined based on the median size of roe deer's core home range (the small cervid targeted), which is around 10 ha (Melis, Cagnacci, & Lovari, 2005; Torres *et al.*, 2011).

Previous studies identified which habitat are preferred by roe and red deer in Mediterranean landscapes. Therefore, to uncover if those patterns of habitat selection were also applicable to the population we studied, two extra variables were considered, and estimated within the 200m buffer: proportion of roe deer's preferred habitat [conifer forests and Pyrenean oak forests; (Torres *et al.*, 2011; Virgós & Tellería, 1998)] and red deer [shrublands; (Alves *et al.*, 2014; Torres *et al.*, 2014)] (Table 2.3).

Table 2.3 – Variables used in the single-species occupancy modelling procedure, grouped by working hypothesis: acronym, description, range, expected influence, data source and the underlying rationale used for each selection.

Description	Variable acronym	Mean [range]	Influence	Data Source	Rationale
<i>H1 - Anthropogenic disturbance</i>					
Ease of human access to camera site	Human_access	Categorical [1 (low); 2 (medium); 3 (high)]	-	Field Observation	Anthropogenic disturbance may alter animal's behavior and activity patterns (Reimoser, 2012). We considered ease of human access as a variable that evaluates access roads and path's usage to deduce if the site is a frequent source of disturbance. Human activity associated to infrastructures is a major disturbance factor (Hewison <i>et al.</i> , 2001), thus we calculated the distance from camera site to nearest artificial land. We also calculated the distance to nearest roads, which were categorized in unpaved, paved and freeways, because they represent different levels disturbance and collision risks, that can result in mortality hazard (Torres <i>et al.</i> , 2014).
Distance in meters from camera site to nearest artificial land	Dist_artificial	1979 [93-5947]	+	Land use and landcover map of continental Portugal - COS2018 (DGT, 2018)	
Distance in meters from camera site to nearest unpaved road	Dist_unpaved	126.5 [0-1020]	+	OpenStreetMap Extracts (OSM, n.d.) Data	
Distance in meters from camera site to nearest paved road	Dist_paved	1144 [4-4928]	+		
Distance in meters from camera site to nearest highway	Dist_highway	23195 [5846-38461]	+		
<i>H2 – Food and Water resources</i>					
Distance in meters from camera site to nearest agricultural land	Dist_agricultural	985.6 [0-4216]	-	Land use and landcover map of continental Portugal - COS2018 (DGT, 2018)	Food and water are basic survival resources, and their availability may change throughout the annual cycle. The Mediterranean summer is hot and dry, while winter is cold and wet. During summer both plants and animals have little water available. Herbivores, such as roe and red deer, must feed on plants that can withstand such hydric stress or that exist in spaces where water is available (Storms <i>et al.</i> , 2008). With that in mind, we registered watercourse presence within the camera site's buffer and season, because both influence water and subsequently food availability. On the other hand, we calculated the distance to nearest agricultural land because it can provide food all year around (Putman, 1986; Szemethy <i>et al.</i> , 2003).
Presence of watercourse within the 100m buffer around camera site	Watercourse	Binary [0-absent; 1-present]	+	Field Observation	
Season when the camera was active	Season	Nominal [Wet; Dry]	Wet season will have a negative influence (-)		
<i>H3 - Habitat composition</i>					

Main habitat of camera site	Habitat	Nominal [<i>Eucalyptus</i> plantations; Conifer forests; Mosaic; Native broadleaf forests; Native mixed forests; Shrublands]	<i>Eucalyptus</i> plantations will have a negative influence (-)	
Percentage of area covered by exotic species within 100m buffer	Exotic	63.36 [0-100]	-	Field Observation
Percentage of area covered by trees within 100m buffer	Tree_cover	Categorical [2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]	+	
Percentage of area covered by shrubs within 100m buffer	Shrub_cover	Categorical [1 (0%); 2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]	+	
Percentage of area covered by herbaceous plants within 100m buffer	Herbaceous_cover	Categorical [1 (0%); 2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]	+	
Percentage of area covered by rocky soil or rocks within 100m buffer	Rock_cover	Categorical [1 (0%); 2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]	-	
Shrub vegetation mean height within 100m buffer	Shrub_height	Categorical [1 (<0.5m); 2 (0.5m-1.5m); 3 (>1.5m)]	+	
200m buffer proportion of preferred habitat for roe deer (conifer forests and Pyrenean oak forests)	Pref_roe_hab	0.244 [0-0.986]	+	
200m buffer proportion of preferred habitat for red deer (shrublands)	Pref_red_hab	0.058 [0-0.881]	+	
<i>H4 - Habitat Heterogeneity</i>				

Roe and red deer habitat selection may not be dependent solely on food availability. Other characteristics like cover can be relevant for protection against adverse weather conditions and protection against predatory and hunting pressure (Mysterud & Østbye, 1999). We considered variables that characterize camera site's composition: habitat type (macro variable which we narrowed down to six different options, according to our study areas); percentage of exotic species present within the buffer to understand the influence that these areas with different flora composition may have on roe and red deer occupancy comparing to native environments; tree, shrub, herbaceous and rocky soil cover, and shrub vegetation mean height to evaluate cover effect. Furthermore, we selected some specific habitats that are known to be preferred by roe and red deer based on previous studies and calculated the proportion that they occupy in each camera site's buffer (Alves *et al.*, 2014; Torres *et al.*, 2014; Virgós & Tellería, 1998).

Number of habitats within 200m buffer	N_habitats	2.278 [1-7]	+	Land use and landcover map of continental Portugal - COS2018 (DGT, 2018)	Heterogeneous landscapes are known to positively influence deer spatial behavior by reducing deer home range (Kie <i>et al.</i> , 2002), which increases site-occupancy probability, but also by increasing the number of edges and therefore ecotone. We registered the number of habitats remotely and the number of landscape units observed in the field. We, also, calculated habitat's Shannon-Wiener index value to provide a habitat's diversity value within the camera site's buffer. To understand possible margin effects, we calculated habitat edge density.
Habitat's Shannon-Wiener index within 200m buffer	Shannon	0.447 [0-1.511]	+		
Density of habitat edge for 200m buffer (m/m ²)	Edge_density	0.004 [0-0.015]	+		
Number of landscape units observed from camera site within 100m buffer	Landscape_units	1.945 [1-5]	+	Field Observation	

2.2.4 Statistical analysis

- Data manipulation

All the registered photos were reviewed and consequently tagged according to the species detected (Figure 2.5), using Digikam 6.2.0 version software (www.digikam.org). Subsequent statistical analyses of the collected data were conducted using R Statistical Software (R Development Core Team, 2020). To assure temporal independence between each event, we only included in the analysis events that were separated by a minimum time interval of 30 minutes from a previous detection of the same species. This sub-sampling of the data was implemented using the `camtrapR` package of the R software (Niedballa *et al.*, 2016). All the detections of each target species were grouped into 5 days occasions, starting at midnight of the first monitoring day. In each of these occasions, we register if the species was detected (1) or non-detected (0). The produced matrix also included an extra category: non-functional camera (NA), corresponding to periods when the camera was inactive (*e.g.*, obstacle blocking the camera lens). The final matrixes corresponded to the detection history of each target species.



Figure 2.5 – Roe (left) and Red deer (right) photos captured by camera traps during our survey periods.

- Co-occurrence between roe and red deer

Co-occurrence patterns between roe and red deer was analyzed using the “`occ2sps`” function in “`wiqid`” R package (Richmond, Hines, & Beissinger, 2010). This analysis is based on a conditional two-species occupancy model, composed by a hierarchical tree of conditional occupancy and detection probabilities, where species A is established to be dominant and species B subordinate. The model provides the unconditional probability of species A occupancy (ψ^A), the conditional probability of occupancy of species B when species A is present (ψ^{BA}) and conditional probability of occupancy of species B when species A is absent (ψ^{Ba}). Also, the probability of dominant species being detected when the subordinate species is present (R^A), the probability of dominant species being detected when the subordinate species is absent (P^A), the probability of subordinate species being detected when the dominant species is not present (P^B), the probability of subordinate species being detected when the dominant species is present and detected (R^{BA}) and the probability of subordinate species being detected when the dominant species is present but not detected (R^{Ba}) (Richmond *et al.*, 2010). Besides those occupancy estimates we also calculated the Species Interaction Factor (SIF), which is a metric that allow us to infer if the species are

avoiding themselves or co-occurring. The SIF was calculated using the following formula:

$$1.1 \quad SIF = \frac{\psi^A \psi^{BA}}{\psi^A (\psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba})}$$

If $SIF = 1$ the two species are considered to occur independently; if $SIF < 1$ then species B is less likely to co-occur with the dominant species A (avoidance hypothesis); and if $SIF > 1$ then species B is more likely to co-occur with species A (aggregation hypothesis) (Richmond *et al.*, 2010). In our study we considered *C. elaphus* as the dominant species due to their larger body mass [male Iberian red deer average body weight range: 152.9 – 201.3 kg (Gaspar-López *et al.*, 2010); male Iberian roe deer average body weight: 23.9 kg (Horcajada-Sánchez & Barja, 2016)], but mostly based on the literature regarding these two species interactions, where red deer seems to displace roe deer (Richard *et al.*, 2010). We estimated these metrics for the entire dataset, and subsequently we divided the data into two sets: locations within *Eucalyptus* plantations sites and in native vegetation control sites, to test if the roe deer would adopt a distinct occupancy pattern in relation to the red deer occurrence in native and exotic plantations dominated landscapes. Plantation sites were also divided into distinct harvesting phases, to identify possible differences in co-occurrence patterns between distinct *Eucalyptus* development stages, as the structural composition of the landscape changes greatly between harvesting phases (Timo *et al.*, 2015).

- Single-species occupancy modelling

Camera sites were treated as pseudo replicates because multi-season occupancy models are overparameterized and we had no interest in local colonization or extinction probabilities (Hines, Nichols, & Collazo, 2014). Therefore, our sampling points were organized in a camera*season combination (Monterroso *et al.*, 2020). Occupancy models were built using the “occu” function, in the “unmarked” R package (Fiske & Chandler, 2011), which fits single season occupancy models (MacKenzie *et al.*, 2002). Species occupancy was estimated under a maximum likelihood-based approach, accounting for imperfect detection. The single-season occupancy model collects information on sampling occasions (5 days occasions, in our study) over multiple camera sites to construct a likelihood estimate based on probabilistic arguments that correct false-negative surveys by estimating detection probability (MacKenzie *et al.*, 2017), assuming imperfect detection.

For the occupancy model analysis, we grouped the candidate environmental covariates in the four hypotheses defined previously, related to the drivers type that shape occupancy patterns of both species: (1) Anthropogenic disturbance; (2) Food and water resources; (3) Habitat composition; and (4) Habitat heterogeneity (see introduction and table 2.3). For each hypothesis, all the covariates were tested for collinearity by using the “corvif” function in “AED” R package (non-cran) (Zuur *et al.*, 2009) that calculates the Variance Inflation Factors (VIF). Variables were considered collinear if $VIF > 3$ (Zuur *et al.*, 2009) and were candidates to be excluded. In each run we excluded the one that reached the higher VIF. The remaining covariates were then tested again for collinearity, and the process would be repeated until none reached a $VIF > 3$ (Zuur *et al.*, 2009).

For both roe and red deer, the modelling scheme was the same. First, we tested what variables were deemed more relevant to influence detection, by altering the animal visibility for the camera-trap. We built a group of candidate models in which the detection probability varied as a function of three environmental covariates (tree cover, shrub cover and shrub vegetation mean height), tested isolated and simultaneously, while maintaining the occupancy constant (i.e. $\psi=1$). We used the “dredge” function, in “MuMIn” R package (Barton, 2015), to produce models corresponding to all the possible combinations

of the three candidate covariates for influencing detectability. All produced models were ranked by their Akaike Information Criterion (AIC) (Burnham & Anderson, 2002) and the one that reached a lower AIC value was considered that most fit to explain detectability variations. Then, we produced occupancy models for all the hypothesis, by including: 1) in the detectability section of the model the variable(s) identified as influential for detectability in the previous modelling phase, and; 2) in the occupancy section those covariates grouped in each hypothesis. For each hypothesis we produced models corresponding to all combination of the candidate variable and all models with a $\Delta AIC < 2$ (*i.e.*, difference between the AIC of the models and the lowest AIC model) were selected as the best models for each hypothesis (Burnham & Anderson, 2002). These models were considered to properly estimate species-specific occupancy states and identify important environmental drivers shaping those estimates. When more than one top-ranked models were identified, a model averaging procedure was adopted to draw inferences on the variables coefficients and to compute site-occupancy estimates. The effects of covariates on detection and occupancy probability were treated as well-supported when 95% unconditional CIs of averaged β estimates did not include zero (MacKenzie *et al.*, 2017).

Well-supported covariates from all hypotheses (*i.e.*, with 95%CI not including 0) and those included in the single top ranked model (when only one model was selected as best) were used as candidate covariates to test a fifth hypothesis (named “mixed”), to understand if the combination of variables linked to distinct hypothesis would better explain the occupancy probability variation for our model species. This mixed hypothesis models were built using the strategy described for the previous models. The model with the lowest AIC of all the hypotheses, for each species, was deemed the best overall model.

The goodness-of-fit of the best overall model for each species, determined by the lowest AIC, was tested using three different methods included in a single function named “fitstats” created by Wilkinson (2020): 1) sum of squared errors [SSE]; 2) Pearson’s Chi-squared [Chisq] (MacKenzie & Bailey, 2004); 3) and Freeman-Tukey Chi-squared [Freemantukey] (Read, 1993). The function model was fitted to parametric bootstrapping (1000 samples). For this goodness-of-fit test, a “good” model should return a p-value $> 0,05$ for each of the different methods (Wilkinson, 2020).

Finally, based on these two best models (one per species), we created an occupancy probability prediction for each camera site, for roe and red deer. The occupancy prediction values were divided per type of landscape (plantation and native vegetation sites), and the estimates were tested for normality with Shapiro-Wilk normality test (Ws) (Royston, 1995) and then, their average compared through Mann-Whitney-Wilcoxon Test (U) (Bauer, 1972), to test if there was a significant difference in occupancy probabilities between plantation and native vegetation sites, for both species.

- Activity Pattern

The independent detection records for each target species were regarded as a random sample, assuming an underlying continuous temporal distribution, meaning that an animal is equally likely to be photographed when the cameras are active. The probability density function was estimated nonparametrically using a kernel density estimator (Ridout & Linkie, 2009).

The time registered in the photos is related to the region where the camera is located, which varies with the longitude, depending on the time zone, and day of the year. Therefore, the time data was converted from local to solar time, to standardize the temporal data, using “solaR” R package (Perpiñán, 2012) in R software (R Development Core Team, 2020). This step is essential because it allows comparisons between different studies and overcomes the biased associated to the study area’s location in the world

and to political decisions (summer and winter official time). After correction, the time was scaled into a 0-1 range and then transformed into radians ($\text{time} \cdot 2\pi$).

Then, in order to visualize the daily activity patterns of *C. capreolus* and *C. elaphus*, we created probability density functions plots with different subsets of our data to uncover pattern variation between location (*i.e.*, native vegetation and *Eucalyptus* plantation sites) and season, using the “overlap” R package (Ridout & Linkie, 2009). We also estimated the activity overlap between both deer species, by simultaneously plotting both probability density functions. Comparisons between activity patterns estimation were made by estimating the coefficient of overlap Δ_4 for every combination of subsets whose samples included more than 50 detections (Linkie & Ridout, 2011). This coefficient of overlap was selected because it is recommended for relatively large sample sizes (Ridout & Linkie, 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap) and is calculated by the minimum of the density functions of the two species compared at each time point. The precision of this estimator was achieved by computing a standard deviation from 999 bootstrap samples (Linkie & Ridout, 2011).

The coefficient of overlap is purely descriptive, not providing a threshold value for two activity patterns to be considered significantly different. Therefore, the Mardia-Watson-Wheeler's test (W) (Batschelet, 1981) [included in the “circular” R package (Lund & Agostinelli, 2007)] was used to compare the detections' distribution across the diel cycle for all the previous combinations of data between *C. capreolus* and *C. elaphus*. This non-parametric test is based on assigning ranks to the combined samples and tests for the homogeneity of angles. Thus, any significant difference between samples will result in a large W test statistic and the consequent rejection of the null hypothesis ($p\text{-value} < 0,05$) (Tasdan & Cetin, 2014).

2.3 Results

From 800 cameras that we planned to install, only 798 were deployed, because two camera sites were burned during a wildfire just prior to the start of the study. From those, only 765 cameras were fully functional during the entire survey periods, due to camera's mechanical problems or disappearance. The four survey periods, over the entire sampling effort, comprised 26 706 active trap days. Roe deer was detected in seven study areas and red deer in six study areas. None of the target species were detected in Mortágua and only roe deer was detected in Pampilhosa. Roe deer was detected in 1.476 events, while red deer was detected only in 576 detection events.

- Co-occurrence models: roe and red deer

Roe deer (B) occupancy patterns, when red deer is present (ψ^{BA}), is higher than when the latter species is absent (ψ^{Ba}). Such pattern was confirmed by the SIF analysis. Roe and red deer showed a tendency for aggregation within our study areas (SIF=1.386). However, this tendency varies according to the habitat of the study area. For native vegetation areas the value of SIF (SIF=0.912) indicates an independent relationship between the two deer species, while in *Eucalyptus* plantation areas it indicates aggregation (SIF=1.467; Table 2.4). For populations occurring in different *Eucalyptus* development stages, we also observed a similar variation pattern, although we could not estimate SIF value for the first development stage because we had few detections, and the model estimation did not reach convergence. For the second stage, the estimated SIF value implies independence (SIF=0.994) and for the third stage it implies aggregation, reaching the strongest aggregation tendency (SIF=2.159; Table 2.4).

Table 2.4 – Occupancy probability of dominant species (ψ^A), *C. elaphus*, of *C. capreolus* when red deer is present (ψ^{BA}) or absent (ψ^{Ba}), Species Interaction Factor (SIF) value, detection probability of *C. elaphus* when the subordinate species is absent (P^A), *C. capreolus* when dominant species is absent (P^B), probability of dominant species being detected when the subordinate species is present (R^A), probability of subordinate species being detected when the dominant species is present and detected (R^{BA}) and probability of subordinate species being detected when the dominant species is present but not detected (R^{Ba}) for each subset of our data.

	ψ^A	ψ^{BA}	ψ^{Ba}	SIF	P^A	P^B	R^A	R^{BA}	R^{Ba}
All data	0.207	0.578	0.375	1.386	0.285	0.333	0.350	0.409	0.272
Native vegetation sites	0.420	0.658	0.767	0.912	0.467	0.383	0.477	0.390	0.236
Plantation sites	0.301	0.613	0.334	1.467	0.102	0.097	0.068	0.484	0.403
<i>Euc.</i> development stage 2 sites	0.346	0.600	0.606	0.994	0.094	0.046	0.061	0.512	0.403
<i>Euc.</i> development stage 3 sites	0.075	0.590	0.248	2.159	0.301	0.298	0.165	0.643	0.316

- Single-species occupancy models

The variables “Habitat” from the Habitat composition hypothesis and “Shannon-Wiener Index” variable in the Habitat heterogeneity hypothesis were removed after being tested for collinearity (VIF>3). The “rock cover” variable was also removed from the Habitat composition hypothesis because it produced extreme values which in turn created “NA” entries for the estimation of site occupancy.

The detectability of our target species was influenced by the shrub vegetation mean height and the tree cover, being included in all models reaching a $\Delta AICc$ lower than 2 (*i.e.*, best models) (Table 2.5 and 2.6). Both roe and red deer occupancy patterns were best described by the mixed occupancy hypothesis

(Tables 2.5 and 2.6). Thus, in our study areas these species' occupancy probabilities are not related only to one set of environmental characteristics. For the roe deer mixed occupancy hypothesis seven models adequately explained our data ($\Delta AICc < 2$). Therefore, we performed an average model procedure to obtain the average model coefficients (Table 2.7 e 2.8). For the red deer mixed occupancy hypothesis only one single model was considered the best model ($\Delta AICc < 2$) (Table 2.9 and 2.10). Goodness-of-fit tests on both species top-ranked models demonstrate that these fitted our data appropriately (Roe deer: SSE p-value = 0.588; Chisq p-value = 0.998; Freeman-Tukey p-value = 0.630 / Red deer: SSE p-value = 0.692; Chisq p-value = 0.997; Freeman-Tukey p-value = 0.703).

Table 2.5 – Roe deer occupancy models ranked by AICc value for each hypothesis. Model’s variables are linked to occupancy (Ψ) and detection (P). Only models that fulfilled the criterion $\Delta AICc < 2$, per hypothesis, are presented. Variables’ acronyms are described in Table 2.3 (AICc – Akaike Information Criterion corrected for small samples; $\Delta AICc$ – difference between the lowest AIC in the set and the models; Akaike Weight – probability of each model being the best among the set of generated models; Overall $\Delta AICc$ – difference between the lowest AIC and the models).

Hypothesis	Model	Df	AICc	$\Delta AICc$	Akaike Weight	Overall $\Delta AICc$
Null Model	$\Psi(\cdot), P(\cdot)$	2	3325.22			207.89
Constant Occupancy Hypothesis	$\Psi(\cdot), P(\text{Shrub_height} + \text{Tree_cover})$	7	3307.82	0.000	0.908	190.49
Occupancy Hypothesis 1 (Anthropogenic disturbance)	$\Psi(\text{Human_access} + \text{Dist_artificial} + \text{Dist_unpaved} + \text{Dist_paved} + \text{Dist_highway}), P(\text{Shrub_height} + \text{Tree_cover})$	13	3173.93	0.000	0.534	56.60
	$\Psi(\text{Human_access} + \text{Dist_artificial} + \text{Dist_unpaved} + \text{Dist_highway}), P(\text{Shrub_height} + \text{Tree_cover})$	12	3175.35	1.419	0.262	58.02
Occupancy Hypothesis 2 (Food and water resources)	$\Psi(\text{Dist_agricultural} + \text{Season}), P(\text{Shrub_height} + \text{Tree_cover})$	9	3262.40	0.000	0.395	145.07
	$\Psi(\text{Dist_agricultural}), P(\text{Shrub_height} + \text{Tree_cover})$	8	3263.17	0.767	0.269	145.84
	$\Psi(\text{Dist_agricultural} + \text{Watercourse} + \text{Season}), P(\text{Shrub_height} + \text{Tree_cover})$	10	3263.94	1.538	0.183	146.61
Occupancy Hypothesis 3 (Habitat composition)	$\Psi(\text{Exotic} + \text{Shrub_height} + \text{Pref_roe_hab} + \text{Shrub_cover} + \text{Herbaceous_cover}), P(\text{Shrub_height} + \text{Tree_cover})$	19	3187.28	0.000	0.717	69.95
Occupancy Hypothesis 4 (Habitat heterogeneity)	$\Psi(\text{Edge_density} + \text{N_habitats}), P(\text{Shrub_height} + \text{Tree_cover})$	9	3294.44	0.000	0.508	177.10
	$\Psi(\text{N_habitats}), P(\text{Shrub_height} + \text{Tree_cover})$	8	3296.33	1.897	0.197	179.00
	$\Psi(\text{Edge_density} + \text{N_habitats} + \text{Landscape_units}), P(\text{Shrub_height} + \text{Tree_cover})$	10	3296.40	1.963	0.191	179.07
Occupancy Mixed Hypothesis	$\Psi(\text{Human_access} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Exotic} + \text{Herbaceous_cover} + \text{N_habitats} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	22	3117.33	0.000	0.132	0.00
	$\Psi(\text{Human_access} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Dist_unpaved} + \text{Exotic} + \text{Herbaceous_cover} + \text{N_habitats} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	23	3118.29	0.954	0.082	0.95
	$\Psi(\text{Human_access} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Exotic} + \text{Herbaceous_cover} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	21	3118.44	1.113	0.076	1.11
	$\Psi(\text{Human_access} + \text{Shrub_cover} + \text{Dist_agricultural} + \text{Dist_artificial} + \text{Dist_highway} + \text{Exotic} + \text{Herbaceous_cover} + \text{N_habitats} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	23	3118.48	1.148	0.074	1.15

$\Psi(\text{Human_access} + \text{Shrub_height} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Exotic} + \text{Herbaceous_cover} + \text{N_habitats} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	24	3118.49	1.158	0.074	1.16
$\Psi(\text{Human_access} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Exotic} + \text{Herbaceous_cover} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	22	3118.94	1.607	0.059	1.61
$\Psi(\text{Human_access} + \text{Shrub_height} + \text{Shrub_cover} + \text{Dist_artificial} + \text{Dist_highway} + \text{Dist_unpaved} + \text{Exotic} + \text{Herbaceous_cover} + \text{N_habitats} + \text{Pref_roe_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	25	3119.21	1.878	0.052	1.88

Table 2.6 - Red deer occupancy models ranked by AICc value for each hypothesis. Model variables are linked to occupancy (Ψ) and detection (P). Only models that fulfilled the criterion $\Delta AICc < 2$, per hypothesis, are presented. Variables' acronyms are described in Table 2.3 (AICc – Akaike Information Criterion corrected for small samples; $\Delta AICc$ – difference between the lowest AIC in the set and the models; Akaike Weight – probability of each model being the best among the set of generated models; Overall $\Delta AICc$ – difference between the lowest AIC and the models).

Hypothesis	Model	Df	AICc	$\Delta AICc$	Akaike Weight	Overall $\Delta AICc$
Null Model	$\Psi(\cdot), P(\cdot)$	2	1843.60			128.03
Constant Occupancy Hypothesis	$\Psi(\cdot), P(\text{Shrub_height} + \text{Tree_cover})$	7	1813.76	0.000	0.720	98.19
Occupancy Hypothesis 1 (Anthropogenic disturbance)	$\Psi(\text{Dist_unpaved} + \text{Dist_paved} + \text{Dist_highway}), P(\text{Shrub_height} + \text{Tree_cover})$	10	1757.27	0.000	0.410	41.71
	$\Psi(\text{Human_access} + \text{Dist_unpaved} + \text{Dist_paved} + \text{Dist_highway}), P(\text{Shrub_height} + \text{Tree_cover})$	12	1758.67	1.398	0.204	43.10
	$\Psi(\text{Dist_artificial} + \text{Dist_unpaved} + \text{Dist_paved} + \text{Dist_highway}), P(\text{Shrub_height} + \text{Tree_cover})$	11	1758.75	1.472	0.196	43.18
Occupancy Hypothesis 2 (Food and water resources)	$\Psi(\text{Dist_agricultural} + \text{Season}), P(\text{Shrub_height} + \text{Tree_cover})$	9	1777.07	0.000	0.508	61.50
	$\Psi(\text{Dist_agricultural} + \text{Watercourse} + \text{Season}), P(\text{Shrub_height} + \text{Tree_cover})$	10	1777.27	0.209	0.458	61.71
Occupancy Hypothesis 3 (Habitat composition)	$\Psi(\text{Exotic}), P(\text{Shrub_height} + \text{Tree_cover})$	8	1761.10	0.000	0.213	45.53
	$\Psi(\text{Exotic} + \text{Shrub_height}), P(\text{Shrub_height} + \text{Tree_cover})$	10	1761.65	0.549	0.162	46.08
	$\Psi(\text{Exotic} + \text{Pref_red_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	9	1762.21	1.107	0.123	46.64
	$\Psi(\text{Exotic} + \text{Shrub_height} + \text{Pref_red_hab}), P(\text{Shrub_height} + \text{Tree_cover})$	11	1762.72	1.619	0.095	47.15
	$\Psi(\text{Exotic}), P(\text{Shrub_height})$	5	1763.08	1.979	0.079	47.51
Occupancy Hypothesis 4 (Habitat heterogeneity)	$\Psi(\cdot), P(\text{Shrub_height} + \text{Tree_cover})$	7	1813.76	0.000	0.299	98.19
	$\Psi(\text{Landscape_units}), P(\text{Shrub_height} + \text{Tree_cover})$	8	1815.45	1.691	0.128	99.88
	$\Psi(\text{N_habitats}), P(\text{Shrub_height} + \text{Tree_cover})$	8	1815.76	1.999	0.110	100.19
	$\Psi(\text{Edge_density}), P(\text{Shrub_height} + \text{Tree_cover})$	8	1815.76	2.000	0.110	100.19
Occupancy Mixed Hypothesis	$\Psi(\text{Dist_unpaved} + \text{Dist_agricultural} + \text{Dist_highway} + \text{Dist_paved} + \text{Season} + \text{Exoti}), P(\text{Shrub_height} + \text{Tree_cover})$	13	1715.57	0.000	0.872	0.00

Roe deer detectability was negatively influenced by shrub vegetation mean height higher than 1.5 meters ($\beta = -0.26 \pm 0.09$) and positively influenced by tree cover between 26% and 50% ($\beta = 0.63 \pm 0.25$) (Table 2.7). Occupancy probability was higher when sites were more easily accessed by humans ($\beta = 0.498 \pm 0.175$), with higher number of habitat types ($\beta = 0.14 \pm 0.12$), with those preferred by roe deer ($\beta = 0.39 \pm 0.13$) and far away from artificial lands ($\beta = 0.94 \pm 0.15$) (Table 2.8). Contrary to what was expected, distance to nearest highway had a negative association with roe deer site-occupancy probability ($\beta = -0.68 \pm 0.13$), *i.e.*, occupancy was higher in areas closest to highways. Percentage of exotic plant species decreased occupancy probability ($\beta = -0.58 \pm 0.14$), as did shrub cover of 1-25% ($\beta = -1.38 \pm 0.43$) as well as herbaceous cover between 26-50% and 51-75% ($\beta = -1.18 \pm 0.37$; $\beta = -0.84 \pm 0.30$, respectively).

Table 2.7 - Average coefficients (Coef) of variables included on roe deer top-ranked models for detectability (shaded rows correspond to variables whose coefficients 95% Confidence Intervals (CI 95%) do not including 0). Variables' acronyms are described in Table 2.3 (SE – Standard Error; z-value - standard score; Pr (>|z|)– p-value).

Detection						
Model-averaged coefficients	Coef	SE	z-value	Pr (> z)	CI 95%	
Intercept	-1.009	0.107	9.452	<0.001	-1.185	-0.834
Shrub_height.2	0.124	0.123	1.010	0.312	-0.078	0.327
Shrub_height.3	-0.258	0.092	2.817	0.005	-0.408	-0.107
Tree_cover.3	0.631	0.254	2.486	0.013	0.214	1.049
Tree_cover.4	-0.149	0.202	0.734	0.463	-0.481	0.184
Tree_cover.5	-0.216	0.140	1.544	0.123	-0.446	0.014

Table 2.8 - Average model of roe deer top-ranked occupancy models (shaded rows correspond to variables whose coefficients Confidence Intervals (CI 95%) do not including 0). Acronyms are described in Table 2.3 (Coef – Coefficients; SE – Standard Error; z-value - standard score; Pr (>|z|)– p-value; CI 95% - Coefficient 95% confident interval).

Occupancy						
Model-averaged coefficients	Coef	SE	z-value	Pr (> z)	CI 95%	
Intercept	-0.372	0.177	2.100	0.036	-0.663	-0.081
Human_aces.2	-0.145	0.217	0.666	0.505	-0.502	0.213
Human.aces.3	0.499	0.175	2.846	0.004	0.210	0.786
Shrub_cover.2	-1.383	0.429	3.222	0.001	-2.088	-0.677
Shrub_cover.3	-0.322	0.336	0.958	0.338	-0.874	0.230
Shrub_cover.4	0.027	0.252	0.108	0.914	-0.387	0.441
Shrub_cover.5	-0.272	0.208	1.309	0.190	-0.614	0.070
Dist_artificial	0.937	0.146	6.395	<0.001	0.696	1.177
Dist_highway	-0.682	0.128	5.323	<0.001	-0.893	-0.472
Exotic	-0.581	0.143	4.049	<0.001	-0.817	-0.345
Herbaceous_cover.2	0.091	0.410	0.221	0.825	-0.584	0.766
Herbaceous_cover.3	-1.175	0.368	3.191	0.001	-1.781	-0.570
Herbaceous_cover.4	-0.837	0.304	2.755	0.006	-1.336	-0.337
Herbaceous_cover.5	-0.122	0.260	0.470	0.638	-0.550	0.305
N_habitats	0.140	0.122	1.147	0.251	0.011	0.361
Pref_roe_hab	0.388	0.127	3.049	0.002	0.179	0.598

Dist_unpaved	-0.027	0.071	0.383	0.702	-0.288	0.063
Dist_agricultural	-0.039	0.101	0.383	0.702	-0.409	0.090
Shrub_height.2	0.088	0.207	0.426	0.670	-0.059	0.828
Shrub_height.3	-0.029	0.102	0.284	0.776	-0.424	0.172

Red deer detectability decreased with shrub vegetation mean height between 0.5 and 1.5 meters ($\beta = -1.23 \pm 0.18$) and tree cover between 26-50% ($\beta = -0.59 \pm 0.26$) (Table 2.9). Occupancy probability was lower in areas away from unpaved road ($\beta = -0.46 \pm 0.18$) and highways ($\beta = -0.50 \pm 0.14$), but closer to paved road ($\beta = 0.62 \pm 0.14$). Furthermore, in areas nearby agricultural lands red deer site-occupancy probability occupancy was lower ($\beta = 0.32 \pm 0.12$), as well as in the wet season and in regions with higher Eucalyptus plantations ($\beta = -0.78 \pm 0.24$; $\beta = -0.52 \pm 0.12$) (Table 2.10).

Table 2.9 - Average coefficients (Coef) of variables included on red deer top-ranked models for detectability (shaded rows correspond to variables whose coefficients 95% Confidence Interval (CI 95%) do not including 0). Acronyms are described in Table 2.3 (SE – Standard Error; z-value – standard score; Pr (>|z|)– p-value).

Detection						
Model coefficients	Coef	SE	z-value	Pr (> z)	CI 95%	
Intercept	-0.992	0.120	-8.294	<0.001	-1.227	-0.758
Shrub_height.2	-1.227	0.178	-6.896	<0.001	-1.576	-0.878
Shrub_height.3	0.069	0.148	0.467	0.640	-0.221	0.360
Tree_cover.3	-0.587	0.266	-2.202	0.028	-1.109	-0.064
Tree_cover.4	-0.072	0.218	-0.330	0.741	-0.500	0.355
Tree_cover.5	-0.333	0.174	-1.912	0.056	-0.675	0.008

Table 2.101 - Average model of red deer top-ranked occupancy models (shaded rows correspond to variables whose coefficients 95% Confident Interval (CI 95%) do not including 0). Acronyms are described in Table 2.3 (Coef – Average coefficients; SE – Standard Error; z-value – standard score; Pr (>|z|)– p-value; CI 95% - Coefficient 95% confident interval).

Occupancy						
Model coefficients	Coef	SE	z-value	Pr (> z)	CI 95%	
Intercept	-1.073	0.179	-6.000	<0.001	-1.423	-0.722
Dist_unpaved	-0.464	0.175	-2.650	0.008	-0.807	-0.121
Dist_agricultural	0.315	0.121	2.610	0.009	0.078	0.552
Dist_highway	-0.501	0.141	-3.550	<0.001	-0.778	-0.225
Dist_paved	0.620	0.137	4.520	<0.001	0.352	0.889
Season.Wet	-0.779	0.237	-3.280	0.001	-1.244	-0.314
Exotic	-0.513	0.120	-4.280	<0.001	-0.748	-0.278

Occupancy probability prediction for each species in both native vegetation areas and *Eucalyptus* plantations did not display a normal distribution (Roe deer: native vegetation sites $W_s = 0.913$, p-value < 0.001, and *Eucalyptus* plantation sites $W_s = 0.906$, p-value < 0.001; Red deer: native vegetation sites $W_s = 0.876$, p-value < 0.001, and *Eucalyptus* plantation sites $W_s = 0.905$, p-value < 0.001). Furthermore, we did not detect any significant difference in occupancy probabilities between plantation and native vegetation sites, for both species (Roe deer: $U = 55809$, p-value = 0.708; Red deer: $U = 52424$, p-value

= 0.366). Roe deer mean occupancy probability for native vegetation areas was 0.419 ± 0.277 and for *Eucalyptus* plantation areas was 0.430 ± 0.287 . Red deer presented a significantly lower mean occupancy probability (*Eucalyptus* plantations: 0.239 ± 0.187 ; Native vegetation: 0.264 ± 0.220) for both vegetation types (mean occupancy probability difference between roe and red deer in *Eucalyptus* plantation sites: $U = 231289$, p -value < 0.001 ; and in native vegetation sites $U = 24589$, p -value < 0.001).

- Roe and red deer diel activity overlap

Red and roe deer showed an overall bimodal activity pattern, with peaks at dawn and dusk, although being active throughout all day and night. However, red deer activity peaks had similar density values, while roe deer activity peak at dawn had a much higher density than the peak at dusk (Figure 2.6). Nevertheless, the activity overlap between these two deer species is quite high ($\Delta 4=0.870$), even with different peak activity distribution ($W = 22.842$; p -value < 0.001).

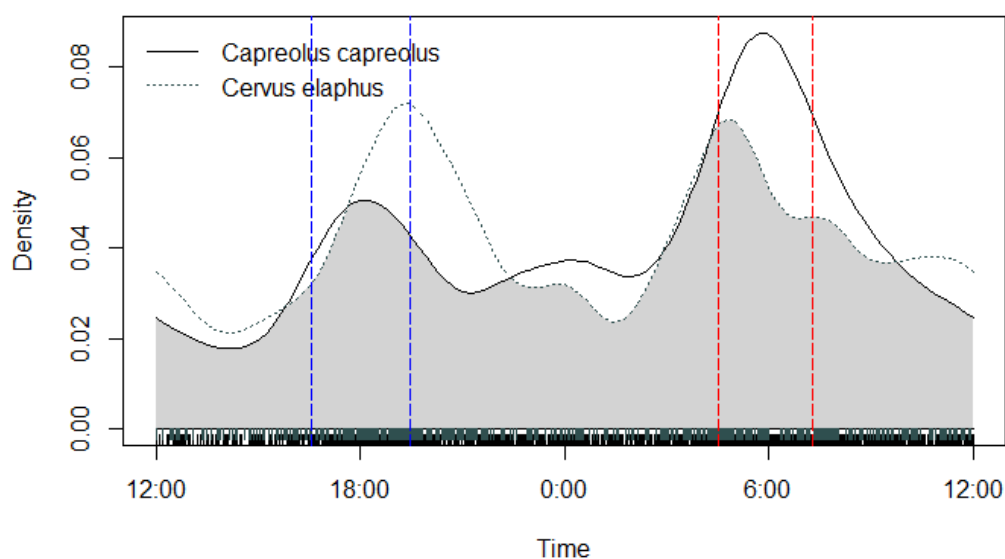


Figure 2.6 - Overall daily activity overlap between roe and red deer. Black line and dotted line represent roe deer and red deer activity densities, respectively. Shaded area is the overlapped activity, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue), throughout the year.

We sub-divided each species data into four datasets to assess the effects of season (wet and dry) and type of vegetation (native vegetation vs *Eucalyptus* plantation), on activity patterns and overlap between both species (Figure 2.7). Overlap in *Eucalyptus* plantations was clearly higher ($\Delta 4=0.949$), and the Mardia-Watson-Wheeler test revealed that these daily activity patterns between both deer species were homogeneous (Figure 2.7a and Table 2.11), indicating a similar temporal behavior within *Eucalyptus* plantations. In native vegetation areas, both deer species seem to present distinct activity patterns with red deer showing an activity peak at dusk while roe deer seem to be more active at dawn, a pattern corroborated by the Mardia-Watson-Wheeler test, which detected a heterogeneity in the activity patterns of both species (Figure 2.7b; Table 2.11: $W = 23.159$; p -value < 0.001). During wet season red deer are more active till 12:00, while the roe deer decreased sharply its activity just after dawn, a pattern evidenced by both species in the dry season (although this decrease is sharper). In the dry season, red and roe deer seem to reduce activity at daylight hours (Figure 2.7c and 2.7d).

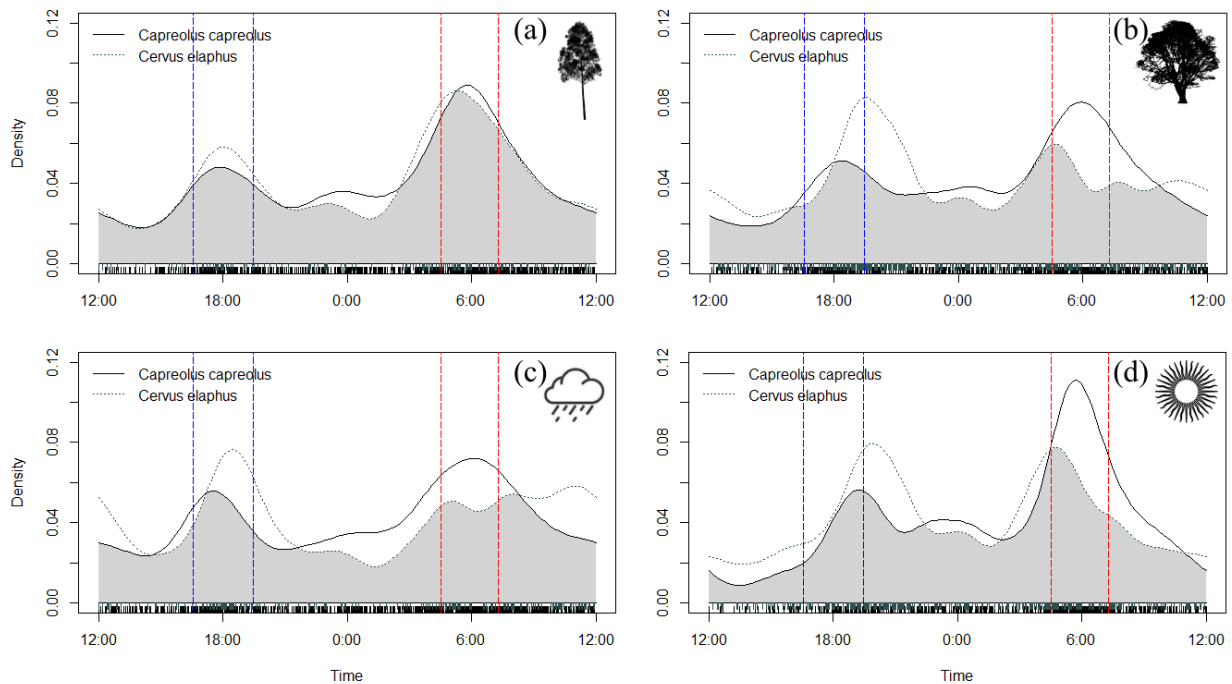


Figure 2.7 - Daily activity patterns of roe and red deer, and corresponding overlap, for *Eucalyptus* plantation areas (a), native vegetation areas (b), wet season (c) and dry season (d). Black and dotted lines represent roe deer and red deer activity density patterns, respectively. Shaded area illustrates the overlapped activity period, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue) throughout the year.

Table 2.11 - Roe and red deer activity overlap, represented by the Δ_4 value, and confidence interval (95%) for each respective subset of our data, and the correspondent Mardia-Watson-Wheeler's W statistic value and p-value for homogeneity in activity.

	Δ_4	CI 95%		W statistic	p-value
Global	0,870	0,832	0,909	22,842	<0,001
Native areas	0,837	0,791	0,884	23,159	<0,001
Plantation areas	0,949	0,902	0,996	0,080	0,961
Wet season	0,836	0,776	0,897	11,690	0,003
Dry season	0,831	0,780	0,882	19,366	<0,001
Native areas during Wet season	0,747	0,668	0,826	12,399	0,002
Native areas during Dry season	0,810	0,748	0,872	20,339	<0,001
Plantation areas during Wet season	0,942	0,880	1,004	0,390	0,823
Plantation areas during Dry season	0,872	0,801	0,943	0,452	0,798

We also divided our data in other four distinct subsets to test the combined effects of location and season (Figure 2.8). Red deer in native vegetation areas, during wet season, maintained higher activity density at daylight hours, a pattern not adopted in *Eucalyptus* plantation areas nor in native area in the dry season (Figure 2.8a and 2.8c). Inversely, roe deer showed a more constant activity throughout a 24h period in native area in the wet season, while in the dry season in both areas and in *Eucalyptus* plantations in the wet period, these ungulates seem to be more active in the dawn phase. Finally, the red deer also seem to concentrate its activity more sharply at dawn in *Eucalyptus* plantation areas during dry season (Figure 2.8d).

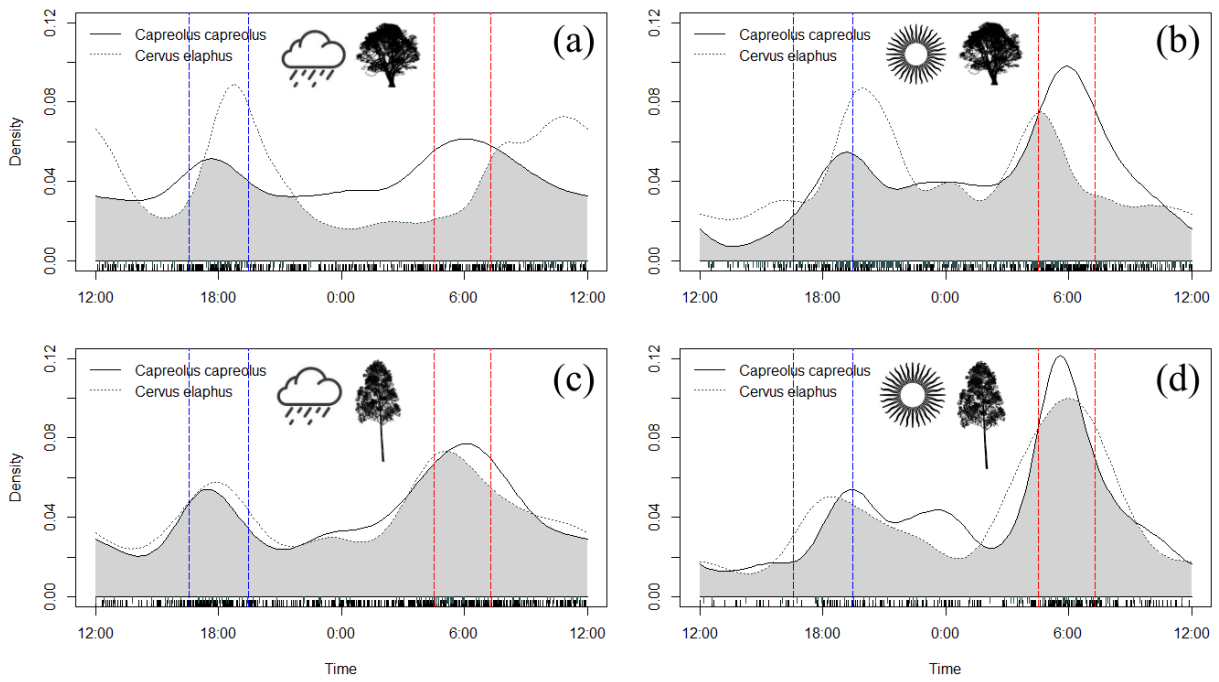


Figure 2.8 - Daily activity overlap of roe and red deer in native vegetation areas during wet (a) and dry season (b), and in *Eucalyptus* plantation areas during wet (c) and dry season (d). Black and dotted lines represent roe deer and red deer activity densities patterns, respectively. Shaded area illustrates the overlapped activity period, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue) throughout the year.

2.4 Discussion

Our results showed that in *Eucalyptus* plantations roe deer and red deer show a distinct spatial behavior, a pattern not detected in areas dominated by native vegetation. However, the heterogeneity of the distinct harvesting phases of *Eucalyptus* plantations seemed to affect species interaction, which can imply that, during the time span of a growing plantation, roe and red deer usage of space can change according to the harvesting phase characteristics. A combination of several factors was responsible to define the occupancy patterns of our target species. The presence of exotic *Eucalyptus* plant species negatively influenced both roe and red deer occupancy probability, which indicates that these areas are detrimental to the occurrence of the species. Anthropogenic disturbance in the form of roads and infrastructures also proved prejudicial to the occupancy of these animals, which may perceive humans as a source of danger. Seasonal changes were observed in the activity patterns of both deer species evidencing behavioral and ecological differences between them. In the *Eucalyptus* plantation areas, which are habitats frequently disturbed by human activity, red deer demonstrated the capacity to alter their activity pattern to avoid human encounter.

- Co-occurrence of roe and red deer in different environments

Interestingly, both species seem to co-exist differently in natural and anthropogenic areas. In *Eucalyptus* plantations, both species tend to aggregate more, as roe deer occupancy is promoted by red deer presence. In Montesinho Natural Park, these species demonstrated an asymmetric relationship by red deer's negative effect on roe deer presence, while roe deer presence had a positive effect on red deer occurrence (Torres *et al.*, 2012). Our results indicate a similar interaction between the two species in native vegetation areas because roe deer occupancy probability decreases when red deer is present. In *Eucalyptus* plantations, the reduction of available resources in these anthropic landscapes (Hobbs *et al.*, 2003) seems to relax the potential interference between species and to induce the need for these species to co-occur in sites/patches where resources are more, and still, abundant. Such resources availability spatial patterns will induce species to use more those resource rich patches, leading to a higher overlap of occupation in these environments.

Our results also show that the different development stages of the *Eucalyptus* plantation are perceived by both species, since different stages induce distinct species interaction patterns. Plantation forests of *Eucalyptus* in intermediate development stage (stage 2) and in pre-cut development stage (stage 3) have structural contrasts, such as leaf structure (James & Bell, 2001), tree canopy height and cover due to spacing between trees and thinning (Henskens *et al.*, 2001; Neilsen & Gerrand, 1999). Older *Eucalyptus* stands have narrower leaves, higher canopies and, due to thinning regimes, fewer lateral branches (Ferraz-Filho *et al.*, 2018). Therefore, in pre-cut development stage sites, cover provided by trees at ground level is scarce, increasing animals' visibility and making them more vulnerable to disturbance. Thus, roe and red deer occupancy probabilities are lower in these older stands and roe deer occupancy probability increases where red deer are present, which means these animals need to share the few sites in the older stands that have better habitat conditions. Contrasting with the pre-cut development stage sites, in intermediate development stage sites red and roe deer showed independent occupancy probabilities. This pattern could be linked to the higher cover provided by trees that creates more suitable areas to be exploited by the animals (*i.e.*, more cover), allowing these populations to interact in a similar way of those registered in native vegetation areas.

- Occupancy of roe and red deer

The occupancy patterns of red and roe deer in heterogeneous Mediterranean landscapes, that include native habitats and exotic plantations were mostly driven by a combination of factors with different underlying mechanistic links. This is corroborated by the fact that the proposed occupancy model Mixed Hypothesis was the one that best fitted to the data of both roe and red deer.

As expected, the multi-origin drivers that affected both species occupancy were related with human disturbance, food resources (food and water) and habitat structure (habitat composition and habitat heterogeneity), which were already described for these species in Portugal (Torres *et al.*, 2011, 2014). Disturbance seems to be one of the major drivers affecting both species occupancy. Paved roads have already been highlighted as an important occurrence driver of cervids (Torres *et al.*, 2014), being a pivotal disturbance source, acting as a mortality hazard for deer species, due to vehicle-deer collision. However, in our study, only the distance to highways had a negative impact for both roe and red deer occupancy probabilities, which contradicts the previously stated negative effect of roads. But this result needs to be carefully interpreted, since our study areas do not represent a reliable gradient for highway effects on red deer populations due to the low density of highways and to the landscape scale as the shortest distance from a highway to our study sites was eight kilometers. At this distance, the effect of disturbance from the highway might be low, and what our model have identified might be the effect of another correlated untested driver. Regarding red deer, we identified a positive association of occupancy probability with the distance to paved roads. This pattern follows the previous identified negative effect of roads, probably due to road kills (Mysterud, 2004), accessibility by illegal hunters (Sage *et al.*, 1983) or traffic (*e.g.*, noise) (Iglesias-Merchan *et al.*, 2018), which can all have a substantial impact on species' survival.

Also linked to human dominated patches and anthropogenic disturbance we identified that the distance to artificial land positively influence the occupancy probability of roe deer. This means that roe deer occurs preferentially in areas away from villages and other artificial areas. Such pattern may be linked not only to the presence of non-natural habitats dominated by infrastructures, but also to the higher disturbance in and around these areas. Roe deer might perceive humans as danger (Oberosler *et al.*, 2017), which would explain roe deer's avoidance of human dominated areas. However, areas surrounding villages are generally composed by small agricultural patches, likely attractive for roe deer, therefore it seems that this species trades-off food resources for disturbance. We could not detect this avoidance pattern for red deer occupancy probability, but we highlighted a positive association with the distance to agricultural land. Agricultural land should be a food source for red deer according to our hypothesis (H2 – Food and Water resources), however these areas can have a high frequency of disturbance due human presence and machinery activities (*e.g.*, tractors) (Frid & Dill, 2002; Szemethy *et al.*, 2003). Therefore, red deer might tend to view agricultural areas as disturbed areas, to be avoided. In summary, both species decrease their occupancy probabilities where disturbance is high, even if from different sources.

Another two factors that are linked to disturbance are unpaved roads and the degree of human accessibility to the areas. Contrary to our expectations, the accessibility to the sampling sites by humans was positively correlated with roe deer occupancy probability and the distance to unpaved roads was negatively correlated with red deer occupancy probability. Both variables were expected to have the opposite effect on deer occupancy, since they should be a factor of human disturbance, due to an easy access to the areas, and thus increasing the anthropic pressure on animals using those sites. A possible explanation for these results is linked to how animals move throughout the landscape. Deer might prefer efficient and easy to travel paths for moving from one place to another, with low obstacles such as dense vegetation. We evaluated the degree of human access during field work, by observing the quality of the

roads that accessed to the sites. Thus, better accesses, like vegetation-free trails (*e.g.*, used by trackers and mountain bikers), dirt and unpaved roads, serve also as good paths for animals (Abrahms *et al.*, 2016; Dickson, Jenness, & Beier, 2005). In our study areas, accesses frequently used by humans have absence or low shrub and herbaceous vegetation densities, to increase safety for trackers, mountain bikers or vehicles (Sage *et al.*, 1983). Therefore, those trails/dirt roads can be used by roe and red deer to travel efficiently and more easily between sites, even if it enhances the risk of human encounters [minimized by showing a more nocturnal activity pattern (see activity patterns below)].

But not only disturbance seems to drive deer occupancy patterns. Habitat composition is also a significant driver. Both deer occupancy probabilities are negatively associated with the land cover percentage by exotic plant species. This pattern was somehow expected and corroborates the negative impact of exotic landcover in ungulates, especially if these patches represent exotic plantations (Torres-Porras *et al.*, 2015; Trammell & Butler, 2016). Some exotic species can replace native species in their environment by competition, or by being actively planted (*i.e.*, plantations), but due to ecological and functional differences, often the exotic species do not deliver the ecological services provided by the native species. Anti-herbivory strategies present in some exotic species can deter herbivore species, like roe and red deer, from being able to feed on these plants (Vavra, Parks, & Wisdom, 2007). An example of those strategies is adopted by *Eucalyptus* spp., large trees species that produce a substance called terpene in their leaves, which makes them undigestible for many animal species (Moore *et al.*, 2004). Roe deer, as a concentrate selector, and red deer, as a browser, have a nutritive disadvantage when they inhabit *Eucalyptus* plantations, as they cannot feed on any vegetative part of *Eucalyptus* spp (Moore *et al.*, 2004), not fulfilling their food requirements. Due to this biological disadvantage/limitation, deer could decrease their occupancy of areas where exotic plant species are dominant, but this habitat seems to provide cover for these species, both from human disturbance but also of adverse climatic conditions. Roe deer occupancy probability is negatively influenced by both shrub and herbaceous cover. Shrub and herbaceous strata develop more when tree stratum is underdeveloped, allowing sunlight to reach lower strata (Anderson, Loucks, & Swain, 1969; Jules, Sawyer, & Jules, 2008). This could indicate that roe deer prefers areas with denser tree cover over shrub and herbaceous higher cover, even though the shrub layer can be big enough to provide them cover. This preference is linked to fact that roe deer needs cover that can provide shelter/refuge from human disturbance. This is corroborated by its preference for forest refuges where is harder to be detected (Coppes *et al.*, 2017). The positive effect of roe deer preferred habitat (*i.e.*, conifer forests and Pyrenean oak forests) on occupancy reinforces this ecological link and shows that the population inhabiting Central Portugal shows similar preference patterns as those found on Atlantic landscapes (Virgós & Tellería, 1998).

Habitat heterogeneity, namely the number of habitats, can also be a promoter of cervids occupancy, namely for roe deer. A bigger number of habitats increases the ecotone's area. This relationship was not observed for red deer, which is a species with a larger home range. Roe deer has a browsing feeding pattern and are, also, very selective regarding its food, choosing quality over quantity (Latham, Staines, & Gorman, 1997). Red deer, on the other hand, are able to fulfil its nutritional needs with low quality food, by increasing the quantity of matter ingested (Demment & Van Soest, 1985). Thus, roe deer chooses sites with more types of habitats available to be able to select the more nutritious food from various sources available throughout the year cycle (Latham *et al.*, 1999).

Finally, occupancy seems to depend on the season. In the wet season the occupancy probability of red deer decreased. During this season, the precipitation is high, and water is a well available resource, allowing a generalized plant growth in most habitats. Plant growth increases the quantity of food available for red deer, a browser ungulate with lower food specificity (Latham *et al.*, 1999). Thus, due to this increase in productivity, each site can provide more resources. Therefore, red deer do not need to

regularly use the food rich patches to fulfil their nutritional needs, because food is more abundant throughout the landscape (Alves *et al.*, 2014). This geographically wider food availability allows red deer populations to be more scattered during the wet season, reducing thus the local occupancy.

- Roe and Red deer activity patterns and overlap

Roe deer and red deer are crepuscular species meaning that activity peaks around dawn and dusk (Cederlund, 1981; Kamler *et al.*, 2007). While their activity peaks at the same time, their activity density differs. In native vegetation areas, red deer had its highest peak at dusk, while roe deer had it at dawn. This contrast was also observed in Reimoser (2012) and could indicate temporal avoidance between sympatric populations of roe and red deer, in low disturbance areas, to reduce interspecific interference. In *Eucalyptus* plantation areas, these species have highly overlap activity patterns, because red deer shifts its highest activity peak from dusk to dawn. This pattern change may be induced by the higher anthropogenic disturbance of these, when compared to native vegetation areas. Forestry activities in the plantation areas begin in the morning and can last until sunset. Therefore, the observed change in red deer temporal pattern could be a response to human activity, aiming to reduce deer-human encounters during daytime. A similar behavior was observed in areas where human outdoor recreation was present (Coppes *et al.*, 2017). Since red deer are game species and can perceive humans as a source of danger, human presence will induce anti-predatory behavior in these animals (Torres *et al.*, 2014), namely a change in the activity pattern, as showed in this study.

But not only between habitats the red deer activity shows some deviation from the overall pattern. This species evidences some generalist behavior in how it used the day and night periods, showing that it can adapt according to different drivers/ecological objectives. This ungulate activity pattern in native vegetation areas, during wet season, reveals a distinct behavior from the overall pattern, with a long period of inactivity at night. Wet season is characterized by high precipitation and low temperature. Night is when the temperature drops the most and this coincides with red deer's inactive period. The observed drop in activity could be explained by red deer's nocturnal hypometabolism to preserve energy during periods of food shortage and harsh climatic conditions (Arnold *et al.*, 2004). Food shortage could not be the cause for this physiological response as winter is not a limiting season in Mediterranean as plant growth is higher than during the hot dry season (Bugalho & Milne, 2003). Therefore, low temperatures at night influence the changes in red deer's activity patterns. Inversely, roe deer maintained a rather constant activity throughout the diel cycle in native vegetation areas during wet season. This absence of an activity reduction during wet season in Mediterranean Iberia, contradict the pattern described for northern European populations territories (Cederlund, 1981). Other studies in Italy (Pagon *et al.*, 2013) and Israel (Wallach, Shanas, & Inbar, 2010), also, did not observed a decrease in roe deer's activity during the wet season, probably because ambience temperature is higher in these locations than in northern European territories. Roe deer are concentrate selectors that have short rumination periods (Cederlund, 1989; Storms *et al.*, 2008) and few fat reserves (Wallach *et al.*, 2010). As such, they feed more frequently (Turner, 1979) throughout the diel cycle to endure the slightly increased thermoregulation energy costs during the Mediterranean wet season. On the other hand, red deer feed on both low- and high-quality food (Gebert & Verheyden-Tixier, 2001), allowing them to satisfy their needs during daytime feeding and accumulate fat reserves for inactive periods (Azorit *et al.*, 2012).

Dry season affects both species activity patterns by inducing a reduction of activity during daylight hours (Rivrud *et al.*, 2010), an increase at both dawn and slight increase at night. These species reduce their activity, by resting during high temperature hours, as a thermal strategy (Myysterud & Østbye, 1995) in low food quality, but high temperatures, periods, such as those found in Mediterranean dry season

(Bugalho & Milne, 2003). This strategy seems to optimize feeding periods and thermal regulation energetic costs (Belovsky, 1981).

- Species detectability and camera limitation

Tree cover and shrub vegetation mean height both determined the detectability of the two deer species, as expected. Camera traps record images by detecting temperature differences made by animals crossing in front of the sensors (Rovero & Zimmermann, 2016). Thus, the more vegetation there is in front of the camera's field of vision the higher the probability of the sensors not detecting the animal. Also, more vegetation can obstruct the animal's identification by the researchers when analyzing the images, limiting the number of viable identifications.

Chapter III - Final considerations

Camera trap methods are quite reliable and provide high quality data. It is a non-invasive detection method that causes minimum disturbance to wildlife, while recording information automatically, day and night, during weeks or months. Camera trapping is more efficient at detecting diurnal species than other direct observation methods like line transects. The major advantage of camera traps compared to indirect methods is that they provide objective records which can be used to study activity patterns, coexistence, and even individual identification for some species (Rovero & Zimmermann, 2016). Nevertheless, there are some specificities that can limit animals' detection (Newey *et al.*, 2015). One of those are that camera traps can only detect animals in front of the sensors and within a few meters. These sensors trigger the camera to capture an image by sensing a difference between the background and the animals' body. Another limitation is linked with the habitat in which the camera is placed as certain habitats are more challenging to sample, such as shrublands, normally characterized with extensive understory vegetation, therefore diminishing the distance that an animal is detected. Additionally, background shadows, vegetation, and certain weather conditions can trigger the camera, which in turn captures a large number of photos with no animal and sometimes filling up memory cards before the sampling time is over, creating gaps on the sampling method by not completing the required sampling time (Newey *et al.*, 2015). The specific placement of the camera trap can *per se* also affect reliability. The height, angle, and distance that the camera is from the targeted area, influences performance and animal detection, and therefore, distinct sites have different performances. Consequently, interpreting camera trap results must account for the imperfect detection and biased errors. Nonetheless, the previous statements do not undermine the advantages that camera trapping presents as a wildlife detection method.

Our results show that roe and red deer use *Eucalyptus* plantations, but these ungulates seem to somehow decrease occupancy in these habitats and adapt their activity patterns to avoid human encounters. The variation within plantations and season also shapes occupancy patterns. Both species seem to optimize the trade-off relationship between disturbance and resource availability, occupying areas with lower disturbance where enough resources exist. This is corroborated by roe and red deer aggregation in sites where this balance can be achieved, like some pre-cut development stage sites where disturbance is lower enough for deer occurrence.

These results have strong impacts on how these anthropic ecosystems should be managed to achieve biodiversity preservation, while still maintaining economical profitability, thus fulfilling forestry certification goals (Gutierrez Garzon *et al.*, 2020). Pre-harvesting phases seem to be the more critical period for deer, managers must guarantee that plantation structure encompasses areas with different tree ages so animals may take shelter in unharvested stands, while others are subject to higher disturbance level due to harvesting. Furthermore, forestry activities should avoid dawn and dusk, to minimize disturbance. Finally, to minimize negative interaction between sympatric guild members, by allowing species to be sparsely distributed (and not clustered in the few undisturbed patches), plantation should include dispersed native patches to which animals may move in search for food and refuge, creating discontinuities within plantations.

Summing up, both species inhabit *Eucalyptus* plantations and are affected by them. However, some ecological questions arose from these observations, which cannot be answered by camera trapping methods alone. In two of our study areas, we did not detect one or both deer species. We could not find a plausible reason to why that happened, but possibilities are that the species did not occur in those areas or that *Eucalyptus* plantations in those regions have different characteristics that could be critical to deer occurrence. Both Mortágua and Pampilhosa have large plantation areas which could indicate that the size of *Eucalyptus* plantation areas and the distance to the edge of plantation are relevant to species

occurring within the plantations. Another question that cannot be answered by our data, is the importance of *Eucalyptus* plantations as a food provider environment in the diet of roe and red deer. We observed that roe deer preferred sites where heterogeneity of habitats was high, which could be related to the need of high-quality food, as this species is a concentrate selector and maybe its food requirements could not be fulfilled within pure *Eucalyptus* stands. Finally, camera-traps are a static and population monitoring method, which does not generate data that allow to understand the individual movement patterns and how individuals behave in the proximity of its conspecific and potential competitor. Thus, we believe that to move forward in understanding the ecological processes determining the use of plantations it is crucial to implement a radio-tracking studies. As this study raised many research questions, which should be addressed to fully understand the impact of *Eucalyptus* plantations on these species, it should be regarded as a steppingstone to understand the ecology of roe and red deer within exotic *Eucalyptus* plantations in the southern edge of their range. Furthermore, it is the first piece of the ecological puzzle that can allow managers understand how their actions affect ungulates, a crucial knowledge to achieve a sustainable management of these anthropic landscapes.

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