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Universidade de Aveiro Departamento de Biologia
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presidente   Professora Doutora Maria Helena Silva, Professora Auxiliar, Universidade de Aveiro

Vogais

                                          Doutor Joaquim Pedro dos Santos das Mercês Ferreira

                                          Doutor Luís Miguel do Carmo Rosalino, Professor Auxiliar Convidado, Faculdade de Ciências da Universidade de Lisboa

palavras-chave

Florestas de produção, eucalipto, mamíferos carnívoros, raposa, padrões de ocupação, armadilhagem fotográfica,

resumo

A transição de áreas naturais para florestas de produção é um fenómeno global crescente com consequências diretas nos níveis de biodiversidade e funcionalidade dos ecossistemas, associadas às alterações da composição e estrutura das florestas naturais. As florestas de produção são frequentemente constituídas por espécies exóticas e de rápido crescimento, usadas com o objetivo de obter rendimento económico, muitas vezes em prejuízo de habitats para a vida selvagem e do bom funcionamento dos ecossistemas. Na região mediterrânica, as florestas de produção compostas por diferentes espécies do género *Eucalyptus* estão amplamente distribuídas, formando paisagens monoespecíficas com impactos em muitos *taxa* e alternando importantes dinâmicas ecológicas. Dada a extensão destas florestas, é importante perceber como e em que medida estas plantações florestais influenciam as dinâmicas ecológicas da biodiversidade nativa. Neste estudo, e baseado em dados recolhidos por armadilhagem fotográfica, avaliámos a influência das florestas de produção de *Eucalyptus globulus* nos padrões de ocupação de mesocarnívoros, usando como espécie-modelo a raposa-vermelha (*Vulpes vulpes*) na região centro de Portugal Continental. A análise uni-sazonal demonstrou que o modelo mais suportado para a probabilidade de deteção da raposa demonstra uma influência negativa da cobertura arbórea. A análise dos padrões de ocupação revela uma influência positiva da cobertura arbórea na ocupação da raposa, mostrando a preferência da raposa por florestas maduras com um substrato arbóreo bem desenvolvido. Áreas naturais demonstram ter uma maior ocupação pela raposa comparativamente a áreas de produção de eucalipto. Os resultados deste estudo evidenciam padrões importantes sobre a influências das florestas de produção de eucalipto na ecologia da raposa e, por isso, são uma importante para a definição de medidas integrativas de conservação de mesocarnívoros em florestas de produção, em consonância com uma exploração sustentável destas plantações.

keywords

Production forests, *Eucalyptus*, carnivore mammals, red fox, occupancy patterns, camera trapping

abstract

The transition of natural areas to forestry plantations is a growing worldwide phenomenon with direct consequences to biodiversity and entire ecosystems by changing forest's composition and structure. Production plantations are often composed by fast-growing exotic species, aiming economic profit, often at the expense of well-suited habitats for wildlife and ecosystems' functionality. In the Mediterranean region, production forests composed by *Eucalyptus* spp. are widely distributed, forming monospecific landscapes with impactful changes in many *taxa* and altering important ecological dynamics. Given the extension of these production forests, it is important to understand how and in what extent this forest transition influences the ecological dynamics of native biodiversity. In this study, and based on camera trapping data, we evaluate the influence of *Eucalyptus globulus* production forests in the occupancy patterns of mesocarnivores, using as species-model the red fox (*Vulpes vulpes*) in Central Portugal region. Based on a single-season analysis, best-fitted model for red fox detection probability shows a negative influence of tree cover. The occupancy analysis revealed a positive influence of tree cover in red fox occupancy, showing a preference this canid for well-developed forests with a mature tree cover. Also, natural and semi-natural forests showed higher red fox occupancy in comparison with *Eucalyptus* production forests. The results of this study unravel relevant insights on the influence of production forests in red fox ecology and thus, may contribute to more integrative measures aiming mesocarnivores conservancy in forestry plantations, in the line with a sustainable exploitation of these plantations.

Index

List of Figures

List of tables

1. Introduction

- Forestry plantations: historical and political background

Human activities and land-use practices related to the development of agriculture, expansion of urban areas and industrialization have deeply transformed the planet's land surface in prejudice of natural landscapes (Foley *et al.*, 2005). The conversion of world's landscapes inflicts changes in ecosystems' functionality, such as in the carbon and water cycles, and serious declines in biodiversity by modifying, degrading, exploiting and fragmenting habitats (Newbold *et al.*, 2015). Accordingly, the unbalanced land use also affects humans themselves in several ways, namely by the depletion of resources (fibers, food, freshwater and many more). Worldwide forestry plantations, although necessary for providing all kinds of resources, are one of such land uses that contribute to landscape changes with deleterious consequences on Earth's ecosystems (Foley *et al.*, 2005).

Historically, the economic development and society industrialization led to major declines of natural forests worldwide due to the conversion of forest land to agriculture and urbanization (Rudel *et al.*, 2005). Later, the increasingly need for wood and wood-derived products, which could not be fulfilled by the remaining natural forests, or whose production was constraint by environmental laws, induced the ongoing expansion of planted forests that currently cover 7% of the global forest area (Payn *et al.*, 2015). This phenomenon of conversion of natural forests to forestry plantations is designated as forest transition (Mather, 1992), and the timing and reasons for this transition varies amongst countries. In Europe, the forest transition initiated centuries ago with the clearance of natural forests in order to favor farming, pastures and timber for fuel, construction and shipbuilding (Reboredo and Pais, 2014). Eventually, timber scarcity inflicted a worldwide crisis in naval construction in 17th century, leading to the implementation of reforestation programs. But it is over the past recent decades, especially in the Mediterranean region, that occurred a conversion of agricultural fields to forestry plantations due to two main reasons: European Union agricultural policies and labor scarcity (Rudel *et al.*, 2005). The monetary incentives included in the agricultural policies of the European Common Market led to a reduction of the agriculture practices in peripheral low wage European countries. Simultaneously, there was a consistent

decrease in agriculture workers availability that encouraged landowners to both abandon the more remote or less productive fields and substitute agriculture productions by forestry plantations as an alternative to agricultural crops associated incomes (Rudel *et al.*, 2005).

Currently, production forests and forestry plantations represent 31% of world's forests and rely mostly on a limited number of fast-growing and often exotic species. The importance of the forestry sector has been increasing, boosting economic changes worldwide, specially to rural areas where forestry activities are often carried out. This importance is highlighted by the contribution of this production sector to the global gross domestic product (GDP) – almost 1% (FAO (Food and Agriculture Organization), 2015).

- Eucalyptus *production forests – the Portuguese context*

The original Portuguese forests, dominated by oak species (*Quercus* spp.) (Reboredo and Pais, 2014) followed the same negative tendency of other Mediterranean countries forests, with a decrease of natural forests due to agricultural expansion, harvesting to the shipbuilding industry and wood for industries/fireplaces and charcoal production (Rego, 2001). However, this decreasing tendency has been reverted by the implementation of forestry plantations in the recent decades, especially based on an Australian species, commonly used the forestry industry: *Eucalyptus globulus* Labill (Myrtaceae). Although this species was introduced into Portugal in the first half of the 19th century (Alves, Pereira and Silva, 2007), only later became a dominant tree species in many Portuguese landscapes. In 1980, as part of a national policy to promote the primary sector and take advantage of the available landscape, it was implemented the Portuguese Forest Project with the support of the World Bank to plant the exotic tree species *E. globulus*, as a strategy to supply the paper industry (Reboredo and Pais, 2014). This reforestation strategy resulted in an homogenization of the Portuguese rural landscapes, where the *E. globulus* is currently the most represented forest species in the Portuguese territory, common in central-North Portugal, and dominating the Atlantic central-western coast and the Tagus river valley (Alegria *et al.*, 2019). Nowadays, it covers 850.000 hectares and occupies 9% of the total area of the country. Many of these monospecific plantations are

spread within and around sites of Natura 2000 Network and in 2006 the area occupied by *Eucalyptus* plantations within these protected areas corresponded to 102.600 hectares (Deus *et al.*, 2018). In 2013, a law decree approved in the Portuguese parliament (Law-decree nº 96/2013) liberalized *Eucalyptus* sp. plantations. However, recently it was decreed a limitation of the *Eucalyptus* plantations' expansion within the scope of the Forest Reform approved in 2017. Although still under debate, *Eucalyptus* plantations, and its intensive management, have often been associated with the increase in the frequency, extension and intensity of forest fires, especially in Portugal (Moreira, Vallejo and Arianoutsou, 2012), which impose new and wider challenges in conciliating forest production and landscape sustainability and wildlife conservation.

1.1 *Eucalyptus* production forests impacts on biodiversity in general and at vertebrate community levels

- Impacts of Eucalyptus *monocultures on soil characteristics and biodiversity*

The disruption of coevolutive relationships between plant species, soil biota and animals through the conversion of native forests to exotic planted forests might bring significant changes to the ecosystem's characteristics and functions, depending on the planted species and on the management strategies adopted (Carnus *et al.*, 2006). The establishment of intensive monoculture plantations of *E. globulus* is in fact, one such example with major impacts in soil properties, namely by the eroding effect due to the influence of rainwater runoff through the open canopy, which in turn promotes soil compaction through the reduction of pore space and the consequent reduction of water-retention capacity (Bargalli, Singh & Joshi, 1993). Furthermore, *E. globulus* reforestation induces water repellency, i.e. enhances soil hydrophobicity that will reduce the infiltration capacity of the soil by accumulating hydrophobic compounds derived from the tree into the soil surface (Walden *et al.*, 2015). These soil's properties changes alter the functionality of soil dynamics and consequently impacts the biodiversity depending on it. The allelopathic compounds released during leaf degradation affect microbial and fungal growth and activity (Sousa, Jose and Canhoto, 2013). Moreover, allelopathy is induced on soil invertebrates by direct toxicity or by reducing palatable food availability or quality with direct consequences on ecosystem services, such as nutrient cycling through litter

decomposition (Sousa, Jose and Canhoto, 2013). But the effects of allelopathic compounds go even further by suppressing the root growth of native understory plant species and preventing them to reach deeper wetter soil layers and ultimately, leading to a reduction of plant species richness (Becerra *et al.*, 2018). Besides, the widespread and frequent clear-cutting practices and herbicide application in *Eucalyptus* plantations exacerbate the reduction of the understory plant diversity, disrupt the vegetation structural complexity, and homogenize forest and soil structure (Zhou *et al.*, 2018). All these changes in plant communities will have cascading effects over invertebrate communities that depend on it for suitable habitat both on land (Zahn *et al.*, 2010) and on water streams adjacent or running through *Eucalyptus* stands (Abelho and Graça, 1996). These invertebrate community changes will affect higher trophic level species.

- Changes in vertebrate communities' structure in Eucalyptus *monocultures*

The complex interconnection of different groups of organisms through trophic relationships determine the changes and consequences of ecological disruption induced by the implementation of intensive production forests (Matos, 2011; Silva *et al.*, 2019). The reduction of resource availability in these altered systems hinders the existence of diverse higher trophic level assemblages in *Eucalyptus* stands, namely of vertebrate communities (Matos, 2011; Silva *et al.*, 2019). The scarcity of well-established invertebrate communities in *Eucalyptus* plantations is reflected in the lower diversity and abundance of higher trophic level species, such as, for example, bird species that rely to a great extent on invertebrates as their main food source (Calviño-cancela, 2013). Beyond the trophic relationships, the secondary metabolites of *E. globulus* induce major constraints to fundamental processes of vertebrate's ecology. Leachates from *E. globulus* leaves interfere with amphibians' ability of predator detection, mate finding and mate choice, by affecting pheromonal signals (Iglesias-carrasco *et al.*, 2017a; Iglesias-carrasco *et al.*, 2017b). Furthermore, *Eucalyptus* metabolites dissolved in runway water can inhibit fish reproduction (Morrongiello *et al.*, 2011), as well as the growth and survival of juvenile freshwater fish species (Morrongiello *et al.*, 2013). Moreover, the lowering of water level due to high evapotranspiration rates of *E. globulus* in adjacent or running-through water

streams affects larval niches characteristics of stream-dependent amphibian species (Arntzen, 2015).

In *Eucalyptus* stands, logging imposes cyclic disturbances in vertical vegetation structure and bird communities composition change accordingly to different plantations age, with younger stands being characterized by the presence of shrubby and open habitat species and the older stands by species more associated with canopies (Calviño-cancela, 2013). Moreover, areas where forestry management practices of short harvest are implemented (*e.g.* usually of 10-12 years for *E. globulus* in Portugal (Carneiro *et al.*, 2009; Mirra *et al.*, 2017; Alegria *et al.*, 2019), show less favorable conditions for the establishment of specialist bird species due to regular logging and clear-cutting of the understory vegetation (Ramirez-collio, Vergara and Simonetti, 2017). *Eucalyptus* plantation's impacts on soil characteristics and general biodiversity patterns, and together with its temporal structure heterogeneity, it has a cascading effect in mammals (Timo, Lyra-jorge and Gheler-costa, 2015).

1.2 Impacts in mammal's dynamics

- *Overall direct impacts on mammal diversity and dynamics patterns*

The crucial functional role of mammals in ecosystems - top-down regulation (Estes *et al.*, 2011), seed dispersal facilitation (Rosalino, Rosa and Santos-reis, 2010), improved ecosystem resilience against introduced invasive species (Carlsson *et al.*, 2010; Wallach *et al.*, 2010), disease breakouts control (Pongsiri *et al.*, 2009; O'Bryan *et al.*, 2018) and their ecological bioindicator character for a wide type of ecosystems (Pearce and Venier, 2005; Jones *et al.*, 2009) enhance the scale of the impact of changes in ecosystem's processes due to alterations in mammal's dynamics occurrence and patterns. The intensive monocultures of *E. globulus* impose such modifications to mammals' communities by replacing native forest areas that provide suitable, and more predictable, resources (*e.g.* habitat and food) for a wide variety of mammal's orders (Pereira *et al.*, 2012; Cruz, Sarmento and White, 2015; Silva *et al.*, 2019).

Even-aged *E. globulus* monocultures with reduced native understory cover, devoid of logs, physical obstacles and large decaying trees show low habitat heterogeneity (Carey and Johnson, 2016; Salazar and Fontúrbel, 2016) resulting, therefore, in reduced

abundance and diversity of small mammals due to lack of food and low availability of refugees against predators (Teixeira *et al.*, 2017), such as burrows, natural cavities, and tree holes. Although population numbers can be increased by adopting mitigation measures, for instance by maintaining native patches within or adjacent to plantations (Carrilho *et al.*, 2017), species abundance and diversity of small mammals in *Eucalyptus* stands are often lower when compared with native habitats (Moreira-arce *et al.*, 2015; Esposito *et al.*, 2016). In the trophic context, consequences of reduced and less diverse small mammals' populations are noticeable to their consumers - meso and top predators - (Moreira-arce *et al.*, 2015) since they are an important food source for a plethora of mammal predators (Verdade, 2011), and thus, changes in their occurrence patterns will contribute to significant changes in other mammal communities' structure and composition.

The tendency of lower population numbers of small mammals in *Eucalyptus* stands is also applicable to bat's populations, which are intimately related with invertebrate communities' availability and composition (Jones *et al.*, 2009). The lower plant diversity resulting from intensive stand establishment techniques (Wagner *et al.*, 2005) and the allelopathy effects of *Eucalyptus* presence (Sousa, Jose and Canhoto, 2013), will constrain the ability of plantation to sustain similar invertebrate abundance and diversity patterns as those found in native forests (Rainho, 2007). Therefore, bat activity, population dynamics and space use patterns will vary accordingly (Cruz *et al.*, 2011).

Lack of rich understory plant communities in *Eucalyptus* plantations may determine behavioral changes in other herbivore species, such as alterations in browsing and in habitat selection patterns. For example, populations of European rabbit (*Oryctolagus cuniculus*) inhabiting *Eucalyptus* stands show higher seedling browsing, a behavior related to low availability of their preferred food sources (Becerra and Bustamante, 2009). Moreover, low or absent understory cover promotes the avoidance of *E. globulus* plantations by ungulates, such as the red deer (*Cervus elaphus*) in the Mediterranean region that favors habitats with complex and diverse vegetation that can provide rich food sources. (Alves *et al.*, 2014).

Finally, the generalized reduction of habitat suitability for mammal's populations associated to *Eucalyptus* stands, when compared to native habitats, results in communities dominated by generalist species at the expense of niche-specialized species (Verdade, 2011; Law *et al.*, 2017; Teixeira *et al.*, 2017), which reduces local and regional species diversity and richness.

- Effects of plantation structure's in temporal heterogeneity on mammal population dynamics and space use patterns

Eucalyptus production forests, planted in vast areas, show a simplified forest structure and a monoculture character. Nevertheless, forestry management practices privilege even-aged plantations followed by short clear-cut harvesting cycles that results in greater temporal heterogeneity of *Eucalyptus* stands (Timo, Lyra-jorge and Gheler-costa, 2015). In younger plantations, vegetation structure presents a shrubby structure with open canopies whereas well-developed stands, in a pre-harvesting stage, show a tree stratum resembling grown up forests (Calviño-cancela, 2013). In this context, species that recognize *Eucalyptus* plantations as suitable habitats or the ones that can use these areas in some way, *e.g.* as feeding or refuge grounds, are greatly influenced by this temporal variation of the system's structure, namely in terms of population abundance and occurrence patterns (Martin *et al.*, 2012; Rosalino, Martin and Verdade, 2014). Young *Eucalyptus* stands, often colonized by habitat generalist small mammal species, which take advantage of the few available resources, shifting towards the most abundant resources, thus reducing the competition (Rosalino, Martin and Verdade, 2014). But over the course of a the plantation's commercial cycle, as vegetation structure changes, it occurs a species turnover, with some specialist small mammals start using those older forests (Martin *et al.*, 2012). Therefore, some species occur solely in certain *Eucalyptus*' growth stages and this is a pattern that spans across different trophic levels, from small mammals to the middle and large-sized mammals that prey upon them (Timo, Lyra-jorge and Gheler-costa, 2015). Lastly, in the later commercial pre-harvest stage, often occurs a severe decline in the number of species and occurrence frequency of all trophic levels due to the increasing removal of understory vegetation in order to facilitate the harvesting

process. Although there is a gap knowledge in this later stage, it is suggested that these management practices influence space use patterns of mammals and overall biodiversity (Timo, Lyra-jorge and Gheler-costa, 2015).

1.3 Changes in carnivore ecology associated to forestry plantations implementation

Carnivore mammals' populations are highly influenced by habitat quality and availability and necessarily dependent on the ecological performance of lower trophic levels (Sasaki *et al.*, 2008; Alston *et al.*, 2019). Accordingly, altered environments may modify different aspects of the ecology and dynamics of carnivore mammals. Thereby, habitat modification/disturbance, together with the low multidimensional structure heterogeneity of *E. globulus* plantations, hinders the occurrence of carnivore populations. The use of such anthropic forests is restrained by the low structure diversity of *Eucalyptus* stands that negatively affects carnivore species, such as medium-sized carnivores in Mediterranean ecosystems (Mangas and Lozano, 2008). In fact, the European badger (*Meles meles*) is highly affected by habitat disturbance, namely by the conversion of shrublands to forestry plantations and by the inexistence of shrubs in these production forests (Revilla, Palomares and Fernández, 2001). Consequences are noticeable due to carnivores' habitat requirements, such as the lack of shelter against hazardous weather conditions and by not providing cover for predatory activities, such as prey finding and predator's avoidance, which minimize predatory risk (Mangas and Lozano, 2008).

Fire can also modify carnivore species habitats in several ways. *Eucalyptus* forests are some of the most fire-prone forests worldwide and its characteristic intensive fires can, in short-term, eliminate, reduce and limit carnivores populations, through habitat destruction and food resource limitation (Cunningham, Kirkendall and Ballard, 2006; Chia *et al.*, 2016). This phenomenon of wildfires affecting wildlife population numbers was described for some carnivore species, namely for the gray fox (*Urocyon cinereoargenteus*), as food availability is drastically reduced after wildfires (Cunningham, Kirkendall and Ballard, 2006). In long-term and due to the rapid post-fire recovery of native vegetation and *Eucalyptus* trees, burned stands may provide suitable habitat to some generalist carnivores due to high small mammal recruitment in these areas (Birtsas,

Sokos and Exadactylos, 2012; Chia *et al.*, 2016), that increase the area's carrying capacity. However, other species may take longer to repopulate burned areas due to more demanding habitat requirements and low reproduction rates (Birtsas, Sokos and Exadactylos, 2012; McLean *et al.*, 2018).

Regarding food resource availability, the simplified vegetation structure of *Eucalyptus* stands does not offer enough variety and abundance of food resources, for example fruits and small mammals, to predators or to species which carnivores prey on (Rosalino, Rosa and Santos-reis, 2010; Moreira-arce *et al.*, 2015). Therefore, resource scarceness related with reduced habitat complexity may interfere with interspecies interactions of carnivore communities and their dynamics. In fact, lower food availability in *Eucalyptus* plantations demand higher foraging effort, which entail direct consequences, such as *i)* greater energetic costs while searching for prey with reduced populations numbers, sacrificing feeding rates for safety in relation to other predators and while being more vigilant when active in more risky habitats (Brown, 1978); *ii)* and increased predation risk due to higher spatial overlap of competitor species (Cruz, Sarmento and White, 2015).

Additionally, reduced population numbers of preferred prey species can alter prey selection patterns of carnivores that inhabit *Eucalyptus* plantations, namely specialist species with narrow diet requirements (Moreira-arce *et al.*, 2015). These prey selection changes may result in less efficiency in searching, pursuing, and capturing the more abundant prey species, such as described by Moreira-arce *et al.* (2015) regarding the lack of preferred prey (arboreal small mammals) by the kodkod cat (*Leopardus guigna*). The low availability of preferred prey is a consequence of habitat simplification in forestry plantations, affecting negatively the kodkod cat predation success and thus, its individual survival. Such changes may have further consequences on trophic relationships throughout the food web (Gorini, 2012).

From a community perspective, all the habitat and trophic-related changes imposed by *Eucalyptus* plantations may modify the balanced dynamics that are predicted by the niche partitioning theory, which states that behavioral adjustments allow the coexistence of competitor species through greater segregation over the different niche dimensions –

spatial, trophic, and temporal (Schoener, 1974). Trophically, reduced food diversity, as a result of low prey diversity and fruit availability, may lead to higher diet overlapping of some carnivore species (Wiens, 1993) and, therefore, to the displacement or avoidance behavior of competitor carnivores, namely between the red fox, european badger and the common genet that compete for the same food resources (Pereira *et al.*, 2012). Temporally, activity overlap has been reported to occur amongst carnivore species in *Eucalyptus* production forests due to higher foraging efforts due to food shortage and temporal adjustments in diel activity to avoid the diurnal human disturbance associated to managing and harvesting activities (Cruz, Sarmento and White, 2015), which suggests higher interspecific competition for available prey species (trophic overlapping). In the spatial dimension, the aforementioned food resource changes induce avoidance behaviors by less competitive predators (Rosalino, Macdonald and Santos-Reis, 2004; Sarmento *et al.*, 2010) and promote the displacement of sympatric competitors in *Eucalyptus* production forests, for example, in stone marten (*Martes foina*) that avoids *Eucalyptus* stands due to the presence of other competitors (*e.g.* common genet, *Genetta genetta*) (Pereira *et al.*, 2012). In fact, positive selection for *Eucalyptus* stands has been reported for some carnivore species, especially the common genet that choose these habitats because of the absence of other competitors, such as the red fox, related with the previously described dynamics (Pereira *et al.*, 2012).

However, there is still a lack of information about how forestry plantations impact spatial patterns of carnivores in a single species basis but also as in a community level in order to understand how forestry and conservation efforts can adapt to those influences.

1.4 Red fox ecological adaptation to altered environments and knowledge gaps

As natural habitats are consistently altered by human land use changes, species must adapt to the new habitat characteristics in order to maintain population levels that assure their survival. As a generalist species, red fox is one of the mesocarnivores that better adapts to habitat change (Francisco and Luis, 2011; Alexandre *et al.*, 2019) and therefore, can function as a species model to understand the ecological adaptations of

mesocarnivores species to disturbances and habitat change (Sinclair, White and Newell, 2010).

Habitat fragmentation due to conversion of natural areas for agriculture, urban areas and production forests influence how red fox occupies the territory. Despite the discontinuity of natural habitats, agriculture areas can present a positive influence in red fox occupancy (Matos, 2011; Cruz, Sarmento and White, 2015), especially when forested areas represent less than 25% of regional land cover (Alexandre *et al.*, 2019), due to a mosaic pattern with great habitat variability (Pita *et al.*, 2009). Agriculture areas present food resource availability for a plethora of carnivore species (Pita *et al.*, 2009; Matos, 2011), especially for red fox due to its generalist habits, which include diverse and abundant rodent communities, fruits and seeds (Francisco and Luis, 2011). Nonetheless, agriculture areas can also have a negative effect in red fox occupancy when regional landscape is dominated by forested areas because of human disturbances imposed by agricultural practices that destabilize suitable habitats (Alexandre *et al.*, 2019). Even though fragmented habitat and altered land uses are dominant in many world regions, study evidences showed a red fox noticeable preference for forested habitats (Pereira *et al.*, 2012). Regarding to forest type, some studies highlight that native forests favor the occupancy of red foxes in relation to plantations of exotic species, namely of *Eucalyptus globulus* (Pereira *et al.*, 2012; Cruz, Sarmento and White, 2015)*,* due to higher protection for moving throughout the territory, food resource availability, and refugee sites for predatory activities and lower predatory risks (Curveira-Santos *et al.*, 2017). Notwithstanding, E*ucalyptus* plantations may have some ecological value for red fox occupancy in a landscape fragmentation context by functioning as shelter sites, since they have little to no human disturbances for long periods of time (Pita *et al.*, 2009). In intensively altered environments, such as in *E. globulus* plantations in post-fire conditions, higher red fox occurrence, *i.e.* higher occupancy, and abundance, may occur due to a huge small mammals' recruitment in the affected areas (Birtsas, Sokos and Exadactylos, 2012; Chia *et al.*, 2016). Conversely, fire affected areas show low vegetation structural variability (Birtsas, Sokos and Exadactylos, 2012), and because red fox has the ability to increase its home range in areas with reduced habitat richness (Lucherini and Lovari,

1996), more energetic costs are presumably faced by foxes. These costs may have a direct consequence on individual's fitness when searching for areas with more food abundance. However, no long-term studies were done in order to acknowledge if in these burned areas the red fox occupancy follows the same occupancy tendency after the first years after the fire event.

2. Study aims

Given the widespread distribution of *Eucalyptus* plantations in the Portuguese territory, and the lack of information regarding how this forestry landscape affect the spatial patterns of mesocarnivores, this study aims to: a) give new insights on how *Eucalyptus* dominated landscapes influence occupancy patterns of the red fox (*Vulpes vulpes*); and b) assess what are the drivers associated to *Eucalyptus* dominated landscapes that influence the most the detected occupancy patterns. Based on red fox's ecological features, and the drivers determining the use of *Eucalyptus* plantations identified for several taxa, we formulated a set of ecological hypotheses as candidate explanations to test the influence of different landscape variables on the occupancy patterns of the target species.

i) Hypothesis #1 (H1): landscapes characterized by native dominant habitats show higher fox occupancy relative to *Eucalyptus* dominated areas due to habitat differences (Cruz, Sarmento and White, 2015).

ii) Hypothesis #2 (H2): Forest areas with higher mosaic diversity on a landscape scale (*i.e.* more diversity of habitats) provide more ecological benefits, such as diverse food resources (fruits and prey species associated with each habitat) and therefore, will present higher fox occupancy than monospecific landscapes.

iii) Hypothesis #3 (H3): *Eucalyptus* stands with more complex understory vegetation provide broader resource availability, specially food sources (Carrilho *et al.*, 2017) and more coverage from predatory activities and competitors (*i.e.* shelter (Mangas and Lozano, 2008)) than *Eucalyptus* stands with low or inexistence vegetation diversity; and thus, the former will show higher occupancy probabilities. As relevant ecological requirements for the presence and establishment of red fox populations, it expected they influence fox occupancy according to the characteristics of *Eucalyptus* stands.

iv) Hypothesis #4 (H4): Forest areas with low human activity are expected to show higher red fox occupancy than areas with high human, since human activities – *i.e.* disturbance - are often associated with negative impacts in wildlife dynamics (*e.g.* in reproduction rates (Patten and Burger, 2018)).

v) Hypothesis #5 (H5): Different *Eucalyptus* growth stages imposed by commercial cycles have different phenological and structural features that may influence carnivore's occupancy patterns, namely by the avoidance of the last growth stage due to understory vegetation clearance in order to ease the harvesting process (Timo, Lyra-jorge and Gheler-costa, 2015).

3. Materials and methods

- *Study area*

The study was conducted in two different areas (Area A and B, in Figure 1), located in central Portugal.
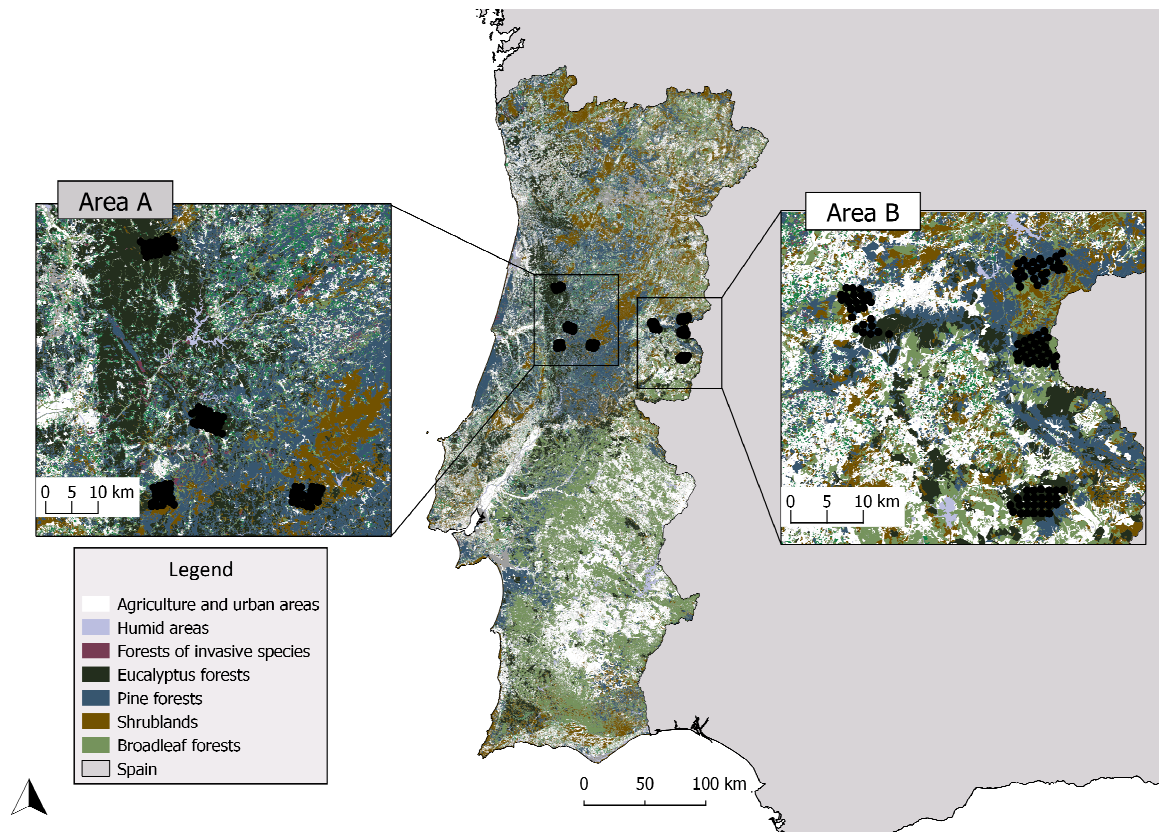
Figure 1. Study areas in Central Portugal and the location of camera traps represented in sampling grids.

The climate in the areas A and B is predominantly Mediterranean, characterized by hot summers and cold winters, with a mean annual temperature of 16 ^{o}C and 15.4 ^{o}C and a mean annual rainfall of 758 mm and 756 mm, respectively (data from the Portuguese Institute for Sea and Atmosphere – IPMA - collected from 1971 to 2000). Average altitude is 907 m and 479 m for area A and B, respectively (data collected from the website www.topographic-map.com). In Area A, vegetation composition is mainly characterized by *Eucalyptus globulus* and *Pinus pinaster* Aiton plantations with remnant patches of native woodlands dominated by *Quercus robur* L. and other Mediterranean vegetation, namely *Arbutus unedo* L. and *Quercus suber* L. In Area B, *E. globulus* and *Pinus* spp. plantations are widely distributed, as well as fruit trees crops (e.g., *Prunus* spp.), in a

mosaic landscape intercalated with native woodlands (*Q. suber* and *Q. rotundifolia* Lam.) and Mediterranean shrublands (*A. unedo* and *Cistus ladanifer* subsp. *ladanifer* L.). In each area, four sub-areas were surveyed: three sub-areas were predominantly dominated by *E. globulus* production forests (Figure 2) and the remnant sub-area characterized by natural or semi-natural habitats, acting as a control area.

Figure 2 – Eucalyptus dominated landscapes

- Study design

In each sub-area we implemented a 16 km^2 grid consisting of 25 sampling sites spaced approximately 1 km apart from each other. This sampling design was designed to ensure site independence, i.e. diminishes the chance that the same individual could be detected over multiple sites (Rovero and Zimmermann, 2016) – as the estimated core area (most used area within home ranges (Powell, 2000) of Mediterranean population foxes) averages 0.11 km^2 (Cavallini, 1996; Pandolfi, Forconi and Montecchiari, 1996). Sampling grids show some deviations to an evenly-spaced grid due to terrain inaccessibility or to logging activity in some sampling points (average distance: 929 meters (m), SD: 143 m, max: 1197 m, min: 613 m). In each sampling point, a Cuddeback

20 Megapixel IR H-1453 white series camera trap was installed in a tree or in a wooden stake at a height of 0.3 – 0.4 m from the ground to increase target species detectability (Swann *et al.*, 2004). No bait was used, and all cameras were set up to take three photos at each event, with a time interval of 30 seconds to any following event, and an image size for each photo of 5 MP. Cameras were set facing zone with less vegetation (to prevent accidental activation of the cameras due to vegetation movement), and the operating time was set to be both during the night and day. The date and time of each event were displayed in all photos. Each camera was charged with a 32 GB MicroSD card. Camera trapping survey was set to 30 days (30 trap-nights) for each sub-area, and the monitoring of all eight study sites occurred between 31st January and 3rd May 2019. In this trapping period it was assumed that population stayed stable (Pereira *et al.*, 2012).

- *Explanatory variables*

Habitat characterization was conducted around each sampling point with two complementary characterization methods: (1) at the time of the setting of each camera trap, we carried out a habitat characterization within a circular buffer area of 100m of radius - approximately corresponding to half of the radius of a theoretical circular core area of the target species of the study (*i.e.*, 0.11 km^2; Cavallini, 1996; Pandolfi, Forconi and Montecchiari, 1996)). The variables considered were: dominant habitat, vegetation cover type and its proportion within the buffer, mean height and native/exotic character, as well as number of landscape units, topography, *E. globulus* growth stage if applicable, presence of large and ecologically important trees (standing or fallen), human perturbation signs (*e.g.*, tourism, buildings hunting areas), and the registration if the sampling areas were recently affected by wildfires (shapefile for rural wildfires of the year 2017 available in: www2.icnf.pt/portal/florestas/dfci/inc); (2) Using QGIS version 2.18 (QGIS Development Team, 2019) and the available land cover map (Land Use and Occupancy Map of Continental Portugal (COS), 2015), a buffer area of 200 meters of radius – red fox core area – centered in each camera-trap, was defined and characterized regarding its relative landcover composition, namely the proportions of each landscape

categories inside each buffer area, the distance to agriculture and urbanized areas, pine forests, deciduous forests, *E. globulus* forests and shrublands (Table 1).

Table 1. Explanatory variables used to test proposed ecological hypotheses relative to occupancy patterns (* - variable measured on field; ** - variable measured by GIS software).

Hypothesis	Variables	Data type	Description
Hypothesis #1 (H1)	Habitat type*	Categorical	Habitat in which the trap camera was set
	Native species presence*	Numerical	Vegetation composition regarding native character (0-100%)
	Exotic species presence*	Numerical	Vegetation composition regarding exotic character (0-100%)
	Prey abundance*	Numerical	Sampled small mammals' abundance for each sub-area
Hypothesis #2 (H2)	Landscape heterogeneity*	Numerical	Number of different habitat units
	Distance to urban and agriculture areas**	Numerical	Distance of camera traps to urban and agriculture areas
	Distance to pine forests**	Numerical	Distance of camera traps to pine forested areas
	Distance to deciduous forests**	Numerical	Distance of camera traps to deciduous forested areas
	Distance to shrublands**	Numerical	Distance of camera traps to shrublands
	Distance to Eucalyptus plantations**	Numerical	Distance of camera traps to Eucalyptus plantation areas
Hypothesis #3 (H3)	Tree cover*	Categorical	Relative tree coverage. Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Shrub cover*	Categorical	Relative shrub coverage (%). Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Herbaceous cover*	Categorical	Relative herbaceous coverage (%). Categories: 0-25%, 25-50%, 50-75%, 75-100%
	Rock cover*	Categorical	Relative rock coverage (%). Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Vegetation mean	Categorical	Categories: < 50 cm, 50 – 150 cm, > 150 cm

	height*		
	Grown up trees*	Categorical	Presence of grown up or ancient trees with cavities with ecological importance
	Water streams*	Categorical	Presence of water streams
	Prey abundance*	Numerical	Sampled small mammal's abundance for each sub-area
Hypothesis #4 (H4)	Topography*	Categorical	Categories: slope, valley, plateau and ridge
	Distance to urban and agriculture areas**	Numerical	Distance of camera traps to urban and agriculture areas
	Accessibility to humans*	Categorical	Accessibility to humans to reach the site where the camera was set. Categories: low, intermediate and high
	Human perturbance*	Categorical	Categories: Touristic, Infrastructures and human activities
Hypothesis #5 (H5)	Eucalyptus growth stage*	Categorical	Categories: Juvenile (< 1 m), initial (> 1 m – 3 m), intermediate (> 3 m) and advanced (grown up trees)
	Tree cover*	Categorical	Relative tree coverage. Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Shrub cover*	Categorical	Relative shrub coverage (%). Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Herbaceous cover*	Categorical	Relative herbaceous coverage (%). Categories: 0-25%, 25-50%, 50-75%, 75-100%
	Rock cover*	Categorical	Relative rock coverage (%). Categories: 0-25%, 25-50%, 50-75% and 75-100%
	Vegetation mean height*	Categorical	Categories: < 50 cm, 50 – 150 cm, > 150 cm

As simultaneously to our study, a small mammal trapping study was being implemented in the same sampling sites, with the small trapping grid located within our 16 km^2 (unpublished data), we estimated prey abundance for each sub-area and used it as a candidate variable in our modelling procedure.

- Data analysis

All captured photos were tagged through a hierarchical tagging system according to species and number of individuals present in each photo using DigiKam software (version 6.0.0; www.digikam.org/). Detection events in the same camera were considered independent if a minimal time interval of 30 minutes for the target species was registered (Davis, Kelly and Stauffer, 2011). Independent detection records were grouped into 5 days sampling occasions. From tagged photos, a detection history matrix (presence/absence observations; 0 for non-detection and 1 for detection) was built as a response variable to further estimate detection probability and occupancy patterns for the sampled areas. Detection probability (p) was defined as the probability of detecting the target species at a site, given it is present (Rovero and Zimmermann, 2016), and occupancy (Ψ) was defined as probability that the target species occupies a site given that detection probabilities are often smaller than one (Mackenzie, 2002).

We implemented a single-season, single-species occupancy analysis based on fox ecology to model explanatory variables that might influence fox occupancy and detection probability (MacKenzie *et al.*, 2006). We implemented a two-step modelling approach: we first assessed the effect of all the variables that may affect detection probability regardless of the hypothesis they were grouped on, while holding constant occupancy; then, the most supported model for detection probability was selected (see best model selection procedure below), and we incorporated the most significant detection variable into all the subsequent occupancy models (Mackenzie, 2002). Generated models were based on all explanatory variables that may influence site occupancy, taking into account each candidate hypothesis (Table 1). Besides single-variable models, interactions between the most ecological relevant explanatory variables were also modelled. To assess what models showed a higher fit, candidate models were ranked according to the Akaike Information Criterion score, corrected for small sample size (AIC_c) and to the Akaike weights (ω) (Burnham, Anderson and Huyvaert, 2011). Models with $\Delta\,AIC_c$ values ≤ 2 (i.e., difference between the AIC_c of the model and the lowest AIC_c of the all built models) were considered equally robustly supported by the collected data, and when compared with the most parsimonious model they were designated the best models (Burnham and

Anderson, 2004). Goodness of fit was assessed by computing the parametric bootstrap method described by MacKenzie and Bailey (2004). The test was applied to single season occupancy models by producing a Person's chi-square statistic (χ^2). We also evaluated the models' overdispersion by estimating the overdispersion parameter ($\hat{c}$) to assess if we needed to use quasi-likeihood AIC_c ($QAIC_c$) in model selection to account for overdispersion (MacKenzie and Bailey, 2004). The selected models allowed the calculation of the total and *per* sub-area average estimates of seasonal occupancy and detection probabilities.

To avoid collinearity effects (high correlations between explanatory variables), multicollinearity was tested by estimating correlation coefficients through pairwise-correlations (Spearman) for all the numeric variables of the study (Figure 5). For highly correlated pairs ($r > 0.7$; Fowler, Cohen and Jarvis, 1998), the less ecologically meaningful variable was discarded when grouped in the same hypothesis' variable set (Dormann *et al.*, 2013).

All analysis were performed in RStudio version 3.5.0 using camtrapR (Courtiol *et al.*, 2019), ggplot2 (Wickham, 2019), rgdal (Sumner and Hijmans, 2019), plotKML (Roudier and Beaudette, 2019), psych (Revelle, 2019), AICcmodavg (Mazerolle, 2019) and MuMIn (Barton, 2019), stats, base and unmarked packages (Fiske *et al.*, 2019).

4. Results

Throughout the trapping period, a total of 62 independent events of target species was recorded, which 49 were in Area A and 13 in Area B.

All the following results are focused on the analysis of Area A dataset. Area B showed a predominance of the null model for both detection probability and occupancy patterns according to each candidate hypothesis (Table 2 and A2) and therefore, data of Area B was not included in the data analysis and discussion.

Mean detection probability of the red fox for Area A was $\bar{x}$ = 0.32 ± 0.02 and, from all the candidate models tested (N = 22; Table A3), the most supported model that better explained detection probability variation included only the variable tree cover (AIC$_c$ = 191.67, ΔAIC$_c$=0, Table 6, (β = -1.42 ± 0.32, IC = [-2.04, -0.79])). The negative estimate value reveals that detection probability is inversely proportional to tree coverage. Two more models showed a ΔAIC$_c$ < 2 (Table 2), but to assure more parsimony models, we opted to consider only the first one in the following modelling procedures (i.e. we included only tree cover as an influential variable on detectability, when testing occupancy drivers).

Table 2. Detection probability models and its AIC, ΔAIC and model cumulative weights (ω_c) values. Only models that showed ΔAIC ≤ 2 are represented. (Remaining models are presented in Annex II).

Model	AIC$_c$	ΔAIC$_c$	ω_c
p (tree cover), Ψ (1)	191.67	0.00	0.37
p (habitat), Ψ (1)	192.92	1.26	0.57
p (landscape units), Ψ (1)	193.51	1.85	0.71

In the occupancy analysis, we built 72 models (H1: 11, H2: 18, H3: 16, H4: 14 and H5: 13; Table A4), and from all the hypotheses, H5 seems to be the hypothesis with the highest support with the most support model (best model with overall lowest AIC$_c$ and overall ΔAIC$_c$ = 0). Red fox average occupancy was estimated based on the most supported model (from hypothesis #5) to be $\bar{x}$ = 0.38 ± 0.03.

Table 3. Occupancy models and its AIC_c, ΔAIC_c, model cumulative weights (ω_c) values and overall AIC_c. Only models that showed $\Delta AIC_c \leq 2$ are represented.

Hypothesis	Model	AIC_c	ΔAIC_c	ω_c	Overall AIC_c
H1	p (tree cover), Ψ (habitat type + native species content)	189.88	0.00	0.22	11.43
	p (tree cover), Ψ (habitat type)	189.96	0.08	0.43	11.51
	p (tree cover), Ψ (habitat type + exotic species content)	190.44	0.56	0.60	11.99
	p (tree cover), Ψ (habitat type + prey abundance)	191.47	1.56	0.70	13.02
	p (tree cover), Ψ (1)	191.67	1.78	0.79	13.22
H2	p (tree cover), Ψ (distance to pine forests)	190.27	0.00	0.18	11.82
	p (tree cover), Ψ (1)	191.67	1.40	0.27	13.22
	p (tree cover), Ψ (distance to deciduous forests)	191.68	1.42	0.36	13.23
	p (tree cover), Ψ (landscape heterogeneity + distance to pine forests)	191.93	1.66	0.44	13.48
	p (tree cover), Ψ (distance to deciduous forests + distance to pine forests)	192.01	1.75	0.51	13.56
H3	p (tree cover), Ψ (tree cover)	189.85	0.00	0.23	11.40
	p (tree cover), Ψ (tree cover + mean vegetation height)	191.50	1.65	0.34	13.05
	p (tree cover), Ψ (shrub cover)	191.59	1.74	0.43	13.14
	p (tree cover), Ψ (prey abundance)	191.63	1.78	0.53	13.18
	p (tree cover), Ψ (1)	191.67	1.81	0.63	13.22
	p (tree cover), Ψ (herbaceous cover)	191.85	2.00	0.71	13.40
H4	p (tree cover), Ψ (human perturbance + distance to urban/agriculture)	187.46	0.00	0.42	9.01
H5	p (tree cover), Ψ (tree cover + *Eucalyptus* growth stage)	178.45	0.00	0.91	0

No evidence of lack-of-fit and overdispersion for any candidate model was detected (p-value > 0.05 and $\hat{c} \leq 1$) (MacKenzie and Bailey, 2004) and, therefore, model selection was based on AIC_c values.

The models tested using variables included in H1 revealed that habitat type and the presence of native species were the most influential covariates affecting fox occupancy (included in the highest rank model), although other variables seem also to have also some influence on occupancy patterns (presence of exotic species and prey abundance; Table 3). In fact, and as expected, different habitat types influence differently fox occupancy, with the native broadleaf and mixed forests with the highest occupancy when compared with *Eucalyptus* plantations (Table 4). Shrublands and *Pseudostuga menziessi* plantations show a negative effect on occupancy, while *Pinus nigra* plantations and *Pinus pinaster* forests show a slightly higher occupancy in relation to *Eucalyptus* stands (Table 4). Furthermore, native species presence and prey abundance show a slight negative influence, while exotic species show a positive influence. However, the set of models with $AIC_c < 2$ also included the null model and high overall ΔAIC_c values (Table 3), indicating that this hypothesis has low support.

Table 4. Estimate coefficients (β), standard error (SE), z value and corresponding p-values and confidence intervals (CI) for the variables included in the average models for each hypothesis. In hypothesis #4 and #5, only the most supported models are presented since no other models revealed and $AIC_c < 2$. Estimate variables coefficients values for hypothesis #1 were calculated against Eucalyptus plantations estimated occupancy values. Only full average is presented.

Hypothesis	Explanatory variables	β	SE	z	p(>|z|)	IC 97.5%
	(Intercept)	-1.91	1.45	1.32	0.19	[-4.75; 0.93]
	Native broadleaf forests	9.31	125.74	0.07	0.94	[-274.82; 300.21]
	Native mixed forests	8.34	105.03	0.08	0.94	[-228.74; 251.48]
	Pinus nigra plantations	1.10	1.41	0.78	0.43	[-1.34; 4.34]
	Pinus pinaster forests	1.15	1.73	0.66	0.51	[-2.07; 5.19]
H1	*Pseudostuga menziesii* plantations	-5.16	435.52	0.01	0.99	[-1003.84; 989.75]
	Shrublands	-5.79	100.08	0.06	0.95	[-236.82; 221.03]
	Native species presence	-0.01	0.02	0.40	0.69	[-0.09; 0.02]
	Exotic species presence	0.00	0.02	0.32	0.75	[-0.02; 0.08]
	Prey abundance	-0.01	0.08	0.18	0.86	[-0.54; 0.26]

H2	(Intercept)	-1.13	0.57	2.00	0.05	[-2.24; -1.85]
	Distance to pine forests	-0.00	0.00	0.98	0.33	[-0-00; 4.96]
	Distance to deciduous forests	-0.00	0.00	0.44	0.66	[-0.00; 8.37]
	Landscape heterogeneity	0.03	0.18	0.20	0.84	[-0.55; 1.05]
H3	(Intercept)	-6.70	5.82	1.15	0.25	[-18.11; 4.70]
	Tree cover	1.28	1.39	0.92	0.36	[-1.23; 4.24]
	Vegetation mean height	0.06	0.34	0.18	0.85	[-1.15; 2.07]
	Shrub cover	-0.02	0.15	0.16	0.87	[-0.94; 0.56]
	Prey abundance	0.01	0.09	0.15	0.88	[-0.34; 0.55]
	Herbaceous cover	0.00	0.21	0.02	0.98	[-1.19; 1.26]
H4	(Intercept)	-0.33	0.48	-0.68	0.50	[-1.26; 0.61]
	Human perturbation	-0.55	0.26	-2.10	0.04	[-1.06; -0.04]
	Distance to urban and agriculture areas	-0.00	0.00	-2.04	0.04	[-0.00; -0.00]
H5	(Intercept)	-15.08	6.19	-2.44	0.01	[-27.21; -2.94]
	Tree cover	3.07	1.31	2.35	0.02	[0.51; 5.64]
	Initial eucalyptus growth stage	-1.25	1.57	-0.80	0.42	[-4.32; 1.83]
	Intermediate eucalyptus growth stage	-9.24	48.12	-0.19	0.85	[-103.54; 85.07]
	Advanced eucalyptus growth stage	0.60	1.78	0.34	0.74	[-2.89; 4.09]

The most supported model for H2 shows a slightly negative effect of the covariate "distance to pine forests" in occupancy patterns. Other high ranked models also show that "distance to broadleaf forests" has also the same influence tendency on fox occupancy, while "landscape heterogeneity" shows a positive correlation with fox occupancy, indicating that higher landscape habitat heterogeneity supports higher fox occupancy (Table 8). However, once again the best models for H2, includes the null model, indicating that this hypothesis has lower support (Table 3).

For the H3, "tree coverage" was included as the solely variable in the model with the lowest AIC$_c$ value, revealing a positive correlation between tree cover and fox occupancy. Moreover, "vegetation mean height", "prey abundance" and "herbaceous

coverage" covariates revealed a positive effect on fox occupancy, while "shrub coverage" showed a negative influence (Table 3). Again, the presence of the null model within the set of best models and high overall ΔAIC$_c$ values indicates that this hypothesis seems have lower support (Table 3).

Regarding H4, the model including human perturbation and distance to urban and agriculture areas was considered the most supported model, with all the other models presenting ΔAIC$_c$ values > 2 (Table 3). The covariate "human perturbation" showed a negative influence in fox occupancy, while distance to urban and agriculture areas results shows an inversely proportional tendency with fox occupancy being higher closer to these areas (Table 4).

Finally, the most supported model for hypothesis H5 seem to be the most fitted in explaining overall fox occupancy variation (*i.e.*, lowest overall ΔAIC$_c$ values; Table 3). Only the model accounting for the influence of tree cover and *Eucalyptus* growth stages in occupancy showed a ΔAIC$_c$ ≤ 2 (Table 3). The high model cumulative weight value (ω_c = 0.91) suggests a great relative importance of the two covariates considered in the model for the occupancy patterns of red fox. The model results show a positive influence of tree cover on fox occupancy pattern. Furthermore, occupancy seems to be lower in intermediate stages of the production cycle in relation to juvenile growth stage. The last growth stage shows a positive influence in occupancy (Table 4).

Based on the fittest model, the predicted occupancy per area revealed a higher red fox occupancy for the natural area, in Lousã, in comparison with *Eucalyptus* production forests sites (Table 4).

Table 5. Predicted occupancy based on the most fitted model according to the sub-areas of Area A.

Sub-area	Average occupancy	Standard deviation
Serra da Lousã (natural forests)	0.65	0.04
Góis (*Eucalyptus* production forests)	0.23	0.03
Pampilhosa (*Eucalyptus* production forests)	0.21	0.02
Mortágua (*Eucalyptus* production forests)	0.21	0.03

5. Discussion

Eucalyptus plantations have often been characterized as low diversity landscape units with deleterious effects on species occurrence (*e.g.* Calviño-cancela, 2013; Cruz, Sarmento and White, 2015). Our results showed that although the continuous and monospecific character of Eucalyptus plantations, plantations have distinctive features that induce different effects in the species that are able to use them. Our results reveal an influence of different characteristics of *Eucalyptus* plantations in the detection probability and occupancy patterns of the ref fox within our study area, and thus, partly supporting initially proposed hypothesis to some extent.

For detection probability in Area A, the most supported model revealed a negative influence of higher tree cover, indicating that in low tree cover areas, *i.e.* in more open or new-planted *Eucalyptus* stands, as well as in shrublands, the red fox is more easily detected when compared with areas with high tree cover. Also, the linear characteristics of *Eucalyptus* plantations, especially in areas with steep slopes, the tendency of the red fox is to follow the X, which is the easiest way to travel in such areas, instead of random use of all the possible trail paths. Hence, this may also influence detection probability in *Eucalyptus* production areas.

In the occupancy analysis, although other models showed to be the most supported models for each corresponding hypothesis, the model with the lowest global AIC_c value and an overall $AIC_c = 0$ is the most supported model (Table 3) explaining red fox occupancy patterns variation in Area A. This best model revealed a positive influence of tree cover in fox occupancy, indicating a preference of well-developed forested areas over the newly planted areas or other open habitats, such as shrublands. This might be related with higher protection opportunities offered by forested environments. They provide more refuge sites from human disturbance, more coverage for predatory activities and less predation risk (Mangas and Lozano, 2008). Also, it may suggest that commercial harvesting cycles might interfere with red fox occupancy patterns, and probably with that of other carnivores, due to the temporal heterogeneity associated with forestry production in these plantation forests (from bare soil prior to seedlings plantation to mature forests, often reaching 10 meters high). Conversely, long aged

plantations forests with selective tree harvesting and more native forests mosaics mixed with *Eucalyptus* plantations may favor red fox occupancy rates due to higher tree cover in the temporal scale. Furthermore, the model also shows different occupancy preferences according to each *Eucalyptus* growth stage. However, standard error presented for each growth stage is, in some cases, higher than the coefficient itself, the p-value > 0.05 and 0 is within confidence interval of this variable's coefficient (Table 4). Therefore, and although *Eucalyptus* growth stage has an influence on red fox occupancy patterns, obtained results for this variable are not robust enough to take any conclusions and to support unequivocally hypothesis #5. Nevertheless, it shows that *Eucalyptus* plantations are not uniform landscape units, not only in terms of structure, but also in its effects on wildlife during growth stages (which are logically linked to the temporal variation in plantation structure). Therefore, although not completely unquestionable, the results seem to indicate that any management action, aiming to compatibilized production with wildlife conservancy should definitely consider that each production stage induces distinct challenges and opportunities to wildlife. Thus, management plans targeting sustainability of forestry production will fail if not incorporating the inter-production stage variability of impacts, which might also be taxa-specific (Timo, Lyra-jorge and Gheler-costa, 2015).

The predicted occupancy for each sub-area in Area A revealed that red fox occupancy in the native forest is roughly three times higher than in *Eucalyptus* production forests and thus, partially supporting the proposed hypothesis #1. Thus, this study shows evidences that natural areas are key areas for the studied canid (*i.e.* higher occupancy), and therefore can have a major role for red fox occurrence and conservation, especially in landscapes highly dominated by *E. globulus* plantations in Central Portugal. Also, most of sampled areas are wood production areas with strict regulations for wood certification (*e.g.* Forest Stewardship Council – FSC) that are required the adoption of sustainable forestry practices that maintain and promote biodiversity levels. Therefore, these exotic planted forests should adopt more integrative measures to assure similar red fox (and other mesocarnivores) occupancy rates when compared with neighboring natural forests in order to fulfill certification goals. Some of the most used management approaches to

these conservation goals, are the creation and protection of ecological corridors of native vegetation within production forests, the selective tree harvesting over clear-cutting methods, and avoid forestry works in seasons when wildlife is more sensible to disturbance (*e.g.* reproduction season).

To assure that future studies manage to collect more robust datasets and therefore present more defined patterns, some considerations are worth mentioning. Prey abundance was assessed by using small mammal sampling protocol by targeting the surrounding areas of just one camera trapping station per each sub-area and the results extrapolated for the entire sub-area. Changes in landscape structure between each camera-trap sampling site may consequently influence differently prey abundance and therefore, the obtained data may have some bias. Also, camera-trap sampling in natural areas may also have induced some bias since i) the natural areas also included other landscape patches of different forestry plantations (some of them with exotic species, such as *Pinus nigra* and *P. menziessi*) and exotic invasive species, e.g. *Acacia* spp.; ii) and even the natural patches showed a simplified natural habitat structure - reduced plant species diversity, low complexity of vertical structure and low age heterogeneity of present tree species. But these characteristics are typical of the entire study area and therefore it was not possible to select pure, well preserved and sufficient wide natural patches to act as control sites. Moreover, due to logistical constrains our *Eucalyptus* sampling stands were not evenly placed according to the different growth stages (juvenile: 12 camera stations, initial: 35, intermediate: 17 and advanced: 9). Therefore, pre-harvesting stages of *Eucalyptus* plantations were not proportionally represented on the sampling effort. A more balanced sampling scheme can contribute to more accurate and robust results, which may mirror better the patterns and processes occurring in *Eucalyptus* plantations. The lack of evidence about the occupancy patterns of red fox and its drivers in Area B (null model predominance), the main reason for the low model performance might be related with the low recorded events (13 independent events) that are not enough to define a clear patterns and therefore understand the contribution of each explanatory variable in occupancy patterns.

Overall, the output combination of tree cover and *Eucalyptus* growth stages variables may suggest a preference of red fox for grown up forests with a mature tree cover rather than newly planted *Eucalyptus* stands or open habitats, such as grasslands.

Other variables not considered *a priori* in our study (and therefore, not collected in the field nor tested in the modelling procedure) that might also be relevant for red fox occupancy patterns, surely would give important insights to the analysis (*e.g.* other food resources availability that may be important for foxes, such as insects or rabbits (Díaz-Ruiz *et al.*, 2013)). Therefore, further studies should be implemented targeting to improve our understanding of the environmental drivers of *Eucalyptus* production forests use by wildlife, by using wider datasets. In fact, including other variables would allow for different and complementary approaches, namely a carnivore community scale approach and a multi-season analysis that would bring important insights for a holistic understanding of red fox ecology in these humanized forests.

6. Conclusions

The study highlights the role of different landscape compositions on red fox occupancy and thus, helps to unravel some important insights on red fox's spatial ecology in *Eucalyptus* dominated landscapes. The results show evidences of a positive influence of tree cover in red fox occupancy, which indicates a preference of red fox for grown up forests with mature tree cover. Also, natural and semi-natural landscapes present higher red fox occupancy when compared with *Eucalyptus* production forests, suggesting a negative influence of *Eucalyptus* plantations and its management practices. Furthermore, a stage specific effect was detected that should be taken into consideration when defining management plans for forestry plantations in order to assure wildlife preservation. The red fox higher occupancy in natural areas suggest the relevance of such areas for the species survival in landscapes highly dominated by *Eucalyptus*, since they may provide most of the ecological requirements needed by the species that, consequently will increase its rate of occurrence in those patches. These insights are valuable knowledge for red fox conservancy, namely for adopting sustainable forest management strategies in production forests that combine forestry activities to assure stands profitability, without overlooking mesocarnivores conservation and overall biodiversity preservation targets.

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8. Annexes

8.1. Annex I - Figures

Figure A1 - Example of a camera trapping station (Cuddeback 20 Megapixel IR H-1453 white series).

Figure A2 - Example of red fox camera trapping photographs

Figure A3. Multicollinearity test of all explanatory variables.

8.2. Annex II - Tables

Table A1. Detection probability candidate models and its AIC_c, ΔAIC_c, model cumulative weights (ω_c) values and overall AIC_c for Area B.

Model	AIC_c	ΔAIC_c	ω_c	Overall ΔAIC_c
p (1), Ψ (1)	127.22	0.00	0.15	0
p (accessibility to humans), Ψ (1)	127.73	0.50	0.27	0.51
p (prey abundance), Ψ (1)	127.97	0.75	0.37	0.75
p (distance to water streams), Ψ (1)	128.27	1.05	0.46	1.05
p (rock cover), Ψ (1)	128.45	1.23	0.54	1.23
p (landscape heterogeneity), Ψ (1)	128.46	1.23	0.62	1.24
p (herbaceous cover), Ψ (1)	128.86	1.64	0.69	1.64
p (vegetation mean height), Ψ (1)	128.97	1.74	0.75	1.75
p (shrub cover), Ψ (1)	129.06	1.84	0.81	1.84
p (tree cover), Ψ (1)	129.16	1.93	0.87	1.94
p (grown up trees), Ψ (1)	129.22	2.00	0.93	2.00
p (topography), Ψ (1)	129.77	2.55	0.97	2.55
p (eucalyptus growth stage), Ψ (1)	131.88	4.66	0.98	4.66
p (human perturbation), Ψ (1)	132.27	5.05	0.99	5.05
p (habitat type), Ψ (1)	133.83	6.60	1.00	6.61

Table A2. Occupancy models and its AIC$_c$, ΔAIC$_c$, model cumulative weights (ω$_c$) values and overall AIC$_c$ for Area B.

Hypothesis	Model	AIC$_c$	ΔAIC$_c$	ω$_c$	Overall AIC$_c$
	p (1), Ψ (1)	127.22	0.00	0.29	0
	p (1), Ψ (prey abundance)	127.68	0.46	0.53	0.46
	p (1), Ψ (native species content)	129.10	1.87	0.64	1.88
	p (1), Ψ (exotic species content)	129.11	1.88	0.76	1.89
	p (1), Ψ (prey abundance + native species content)	129.45	2.22	0.85	2.23
H1	p (1), Ψ (prey abundance + exotic species content)	129.46	2.23	0.95	2.24
	p (1), Ψ (exotic species presence + native species content)	130.89	3.67	1.00	3.67
	p (1), Ψ (habitat type)	137.77	10.55	1.00	10.55
	p (1), Ψ (prey abundance + habitat type)	138.46	11.23	1.00	11.24
	p (1), Ψ (habitat type + native species presence)	138.60	11.38	1.00	11.38
	p (1), Ψ (habitat type + exotic species presence)	138.65	11.42	1.00	11.43
	p (1), Ψ (1)	127.22	0.00	0.28	0
	p (1), Ψ (vegetation mean height)	128.67	1.45	0.42	1.45
	p (1), Ψ (herbaceous cover)	128.96	1.73	0.53	1.74
	p (1), Ψ (shrub cover)	129.11	1.88	0.64	1.89
	p (1), Ψ (shrub cover + vegetation mean height)	130.07	2.84	0.71	2.85
H3	p (1), Ψ (herbaceous cover + vegetation mean height)	130.41	3.19	0.77	3.19
	p (1), Ψ (tree cover + vegetation mean height)	130.52	3.29	0.82	3.3
	p (1), Ψ (tree cover + herbaceous cover)	130.59	3.36	0.87	3.37
	p (1), Ψ (tree cover + shrub cover)	130.75	3.53	0.92	3.53
	p (1), Ψ (shrub cover + herbaceous cover)	130.90	3.68	0.96	3.68
	p (1), Ψ (tree cover)	131.35	4.12	1.00	4.13
	p (1), Ψ (1)	127.22	0.000	0.24	0
	p (1), Ψ (rock cover)	127.31	0.087	0.48	0.09
	p (1), Ψ (vegetation mean height)	128.67	1.448	0.60	1.45
	p (1), Ψ (herbaceous cover)	128.96	1.732	0.70	1.74
H5	p (1), Ψ (shrub cover)	129.11	1.881	0.79	1.89
	p (1), Ψ (vegetation mean height + shrub cover)	130.07	2.841	0.85	2.85
	p (1), Ψ (vegetation mean height + tree cover)	130.52	3.293	0.90	3.3
	p (1), Ψ (shrub cover + tree cover)	130.75	3.529	0.94	3.53
	p (1), Ψ (tree cover)	131.35	4.123	0.97	4.13

p (1), Ψ (eucalyptus growth stage)	133.30	6.071	0.99	6.08
p (1), Ψ (tree cover + eucalyptus growth stage)	134.34	7.111	0.99	7.12
p (1), Ψ (vegetation mean height + eucalyptus growth stage)	134.98	7.751	1.00	7.76
p (1), Ψ (vegetation mean height + shrub cover + eucalyptus growth stage)	136.09	8.866	1.00	8.87

Table A3. Detection probability candidate models and its AIC_c, ΔAIC_c, model cumulative weights (ω_c) values and overall AIC_c for Area A.

Model	AIC_c	ΔAIC_c	ω_c	Overall ΔAIC_c
p (tree cover), Ψ (1)	191.67	0.00	0.38	0
p (habitat), Ψ (1)	192.92	1.26	0.58	1.25
p (landscape heterogeneity), Ψ (1)	193.51	1.85	0.74	1.84
p (distance to deciduous forests), Ψ (1)	194.64	2.98	0.82	2.97
p (distance to pine forests), Ψ (1)	196.16	4.50	0.86	4.49
p (native species presence), Ψ (1)	197.25	5.59	0.89	5.58
p (exotic species presence), Ψ (1)	197.33	5.66	0.91	5.66
p (eucalyptus growth stage), Ψ (1)	198.39	6.73	0.92	6.72
p (herbaceous cover), Ψ (1)	198.45	6.79	0.93	6.78
p (human perturbation), Ψ (1)	198.65	6.98	0.95	6.98
p (rock cover), Ψ (1)	199.67	7.01	0.96	8.00
p (topography), Ψ (1)	199.67	8.01	0.96	8.00
p (1), Ψ (1)	199.75	8.08	0.97	8.08
p (vegetation mean height), Ψ (1)	200.17	8.50	0.98	8.50
p (prey abundance), Ψ (1)	200.58	8.92	0.98	8.91
p (water streams), Ψ (1)	200.90	9.23	0.98	9.23
p (accessibility to humans), Ψ (1)	201.13	9.47	0.99	9.46
p (distance to urban and agriculture areas), Ψ (1)	201.50	9.83	0.99	9.83
p (shrub cover), Ψ (1)	201.75	10.08	0.99	10.08
p (grown up trees), Ψ (1)	201.75	10.08	1.00	10.08
p (distance to shrublands), Ψ (1)	201.75	10.08	1.00	10.08
p (distance to eucalyptus plantations), Ψ (1)	201.75	10.09	1.00	10.08

Determinants of red fox (*Vulpes vulpes*) occupancy patterns in *Eucalyptus* dominated landscapes

Table A4. Occupancy models and its AIC_c, ΔAIC_c, model cumulative weights (ω_c) values and overall AIC_c for Area A.

Hypothesis	Model	AIC_c	ΔAIC_c	ω_c	Overall AIC_c
	p (tree cover). Ψ (habitat type + native species content)	189.88	0.00	0.22	11.43
	p (tree cover). Ψ (habitat type)	189.96	0.08	0.43	11.51
	p (tree cover). Ψ (habitat type + exotic species content)	190.44	0.56	0.60	11.99
	p (tree cover). Ψ (habitat type + prey abundance)	191.47	1.59	0.70	13.02
	p (tree cover). Ψ (1)	191.67	1.78	0.79	13.22
H1	*p* (tree cover). Ψ (native species presence + exotic species presence)	191.98	2.10	0.86	13.53
	p (tree cover). Ψ (exotic species presence)	193.36	3.48	0.90	14.91
	p (tree cover). Ψ (native species presence)	193.44	3.56	0.94	14.99
	p (tree cover). Ψ (prey abundance)	193.61	3.73	0.97	15.16
	p (tree cover). Ψ (prey abundance + exotic species presence)	195.36	5.47	0.99	16.91
	p (tree cover). Ψ (prey abundance + native species presence)	195.43	5.55	1.00	16.98
	p (tree cover). Ψ (distance to pine forests)	190.27	0.00	0.18	11.82
	p (tree cover). Ψ (1)	191.67	1.40	0.27	13.22
	p (tree cover). Ψ (distance to deciduous forests)	191.68	1.42	0.35	13.23
	p (tree cover). Ψ (landscape heterogeneity + distance to pine forests)	191.93	1.66	0.43	13.48
	p (tree cover). Ψ (distance to deciduous forests + distance to pine forests)	192.01	1.75	0.50	13.56
H2	*p* (tree cover). Ψ (distance to urban and agriculture areas	192.31	2.05	0.57	13.86
	p (tree cover). Ψ (distance to *Eucalyptus* plantations + distance to pine forests)	192.35	2.08	0.63	13.90
	p (tree cover). Ψ (landscape heterogeneity)	193.04	2.77	0.68	14.59
	p (tree cover). Ψ (distance to shrublands)	193.07	2.81	0.72	14.62
	p (tree cover). Ψ (distance to *Eucalyptus* plantations)	193.23	2.96	0.76	14.78

	p (tree cover). Ψ (landscape heterogeneity + distance to deciduous forests)	193.45	3.19	0.80	15.00
	p (tree cover). Ψ (distance to deciduous forests + distance to *Eucalyptus* plantations)	193.69	3.42	0.83	15.24
	p (tree cover). Ψ (landscape heterogeneity + distance to deciduous forests + distance to pine forests)	193.74	3.47	0.86	15.29
	p (tree cover). Ψ (landscape heterogeneity + distance to *Eucalyptus* plantations + distance to pine forests)	193.74	3.47	0.89	15.46
	p (tree cover). Ψ (distance to deciduous forests + distance to *Eucalyptus* plantations + distance to pine forests)	193.91	3.64	0.92	15.59
	p (tree cover). Ψ (distance to urban and agriculture areas + distance to *Eucalyptus* plantations)	194.04	3.78	0.95	15.94
	p (tree cover). Ψ (landscape heterogeneity + distance to *Eucalyptus* plantations)	194.39	4.12	0.97	16.20
	p (tree cover). Ψ (landscape heterogeneity + distance to *Eucalyptus* plantations + distance to urban and agriculture areas)	194.65	4.38	0.99	17.23
	p (tree cover). Ψ (tree cover)	189.85	0.00	0.23	11.40
	p (tree cover). Ψ (tree cover + mean vegetation height)	191.50	1.65	0.10	13.05
	p (tree cover). Ψ (tree cover + shrub cover)	191.59	1.74	0.10	13.14
	p (tree cover). Ψ (prey abundance)	191.63	1.78	0.10	13.18
	p (tree cover). Ψ (1)	191.67	1.81	0.09	13.22
	p (tree cover). Ψ (tree cover + herbaceous cover)	191.85	2.00	0.09	13.40
H3	*p* (tree cover). Ψ (shrub cover)	192.44	2.59	0.06	13.99
	p (tree cover). Ψ (prey abundance)	193.61	3.76	0.04	15.16
	p (tree cover). Ψ (herbaceous cover)	193.64	3.79	0.04	15.19
	p (tree cover). Ψ (vegetation mean height)	193.67	3.81	0.04	15.22
	p (tree cover). Ψ (vegetation mean height + shrub cover)	193.92	4.07	0.03	15.47
	p (tree cover). Ψ (shrub cover + herbaceous cover)	194.28	4.43	0.03	15.83

	p (tree cover). Ψ (shrub cover + prey abundance)	194.44	4.59	0.02	15.99
	p (tree cover). Ψ (herbaceous cover + prey abundance)	195.60	5.75	0.01	17.15
	p (tree cover). Ψ (vegetation mean height + prey abundance)	195.61	5.76	0.01	17.16
	p (tree cover). Ψ (vegetation mean height + herbaceous cover)	195.64	5.79	0.01	17.19
	p (tree cover). Ψ (human perturbance + distance to urban/agriculture)	187.46	0.00	0.31	9.01
	p (tree cover). Ψ (human perturbance + distance to urban/agriculture + accessibility to humans)	189.49	2.02	0.43	11.04
	p (tree cover). Ψ (human perturbance)	189.50	2.04	0.54	11.05
	p (tree cover). Ψ (distance to urban/agriculture)	190.27	2.80	0.62	11.82
	p (tree cover). Ψ (distance to pine forests)	190.27	2.80	0.69	11.82
	p (tree cover). Ψ (human perturbance + distance to deciduous forests)	190.56	3.10	0.76	12.11
H4	*p* (tree cover). Ψ (human perturbance + distance to *Eucalyptus* plantations)	191.38	3.92	0.80	12.93
	p (tree cover). Ψ (human perturbance + accessibility to humans)	191.46	4.00	0.85	13.01
	p (tree cover). Ψ (1)	191.67	4.20	0.88	13.22
	p (tree cover). Ψ (distance to deciduous forests)	191.68	4.22	0.92	13.23
	p (tree cover). Ψ (distance to urban/agriculture + accessibility to humans)	192.36	4.90	0.95	13.91
	p (tree cover). Ψ (distance to shrublands forests)	193.07	5.61	0.97	14.62
	p (tree cover). Ψ (distance to *Eucalyptus* plantations)	193.23	5.77	0.99	14.78
	p (tree cover). Ψ (accessibility to humans)	193.67	6.20	1.00	15.22
	p (tree cover). Ψ (tree cover + *Eucalyptus* growth stage)	178.44	0.00	0.92	0.00
	p (tree cover). Ψ (vegetation mean height + *Eucalyptus* growth stage + shrub cover)	184.90	6.46	0.96	6.46
H5	*p* (tree cover). Ψ (*Eucalyptus* growth stage)	185.94	7.50	0.98	7.50
	p (tree cover). Ψ (vegetation mean height + Eucalyptus growth stage)	187.47	9.02	0.99	9.03
	p (tree cover). Ψ (tree cover)	189.85	11.41	0.99	11.41

p (tree cover). Ψ (rock cover)	190.40	11.96	0.99	11.96
p (tree cover). Ψ (vegetation mean height + tree cover)	191.50	13.05	1.00	13.06
p (tree cover). Ψ (shrub cover + tree cover)	191.59	13.15	1.00	13.15
p (tree cover). Ψ (tree cover)	191.67	13.22	1.00	13.23
p (tree cover). Ψ (shrub cover)	192.44	14.00	1.00	14.00
p (tree cover). Ψ (herbaceous cover)	193.64	15.20	1.00	15.20
p (tree cover). Ψ (vegetation mean height)	193.67	15.22	1.00	15.23
p (tree cover). Ψ (vegetation mean height + shrub cover)	193.92	15.48	1.00	15.48