



Management of *Eucalyptus* plantations influences small mammal density: Evidence from Southern Europe



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ABSTRACT

Forestry plantations, and particularly those of exotic *Eucalyptus*, are important man-made systems in Europe, and especially in Portugal, where these represent now the largest fraction of forested areas. *Eucalyptus* plantations may have impacts on vertebrate communities in Europe; however, these have been seldom assessed. Although it is commonly understood that such impacts are contingent on type, shape size and spatial arrangement of landscape elements. Thus, in this study we tested the effects of *Eucalyptus* plantations and the surrounding native semi-natural ecosystems on small mammal density in Central Portugal. We used a Spatially Explicit Capture-Recapture (SECR) model to estimate density, and Generalized Linear (Mixed) Models (GLM/GLMM) to test the effects of habitat type and understory composition and structure on mammal density. Our results showed no significant effect of *Eucalyptus* plantations on density of small mammals, but the presence of a developed understory was positively related to density, likely because it provides food and refuge resources. At the species level, we only found a negative effect of *Eucalyptus* plantations on wood mouse (*Apodemus sylvaticus*) density, most likely because these forests do not provide its preferred food resources (e.g. acorns); this hypothesis was further supported by the positive effect of proximity to ecotone habitat that likely resulted in increased food provisioning. These results highlight that the impact of *Eucalyptus* plantations on small mammals is mostly species-dependent and determined by management and the location of native habitat patches.

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1. Introduction

Human-shaped ecosystems are dominant in many parts of the world (Martin et al., 2014) and are expected to continue expanding alongside with the projected growing global population. These ecosystems represent a gradient ranging from relatively low use to intensive use, often with irreversible change (Kehoe et al., 2015). The human-driven alteration of ecosystems results in changes in composition and structure of natural communities, likely modifying underlying ecological processes (Foley et al., 2005). The type and intensity of use and its management impacts flora and fauna differently (Flynn et al., 2009). For example,

conversion of native ecosystems for vast wood production monoculture plantations threatens the persistence of the native biological communities (e.g. Laiolo et al., 2003), by limiting dispersal and gene flow (e.g., Banks et al., 2005), reducing food and shelter availability (e.g., Rishworth et al., 1995; Parker, 1986), and changing microclimate, nutrient and water conditions (e.g., Liechty et al., 1992). Nonetheless, such human-shaped ecosystems can also be neutral or beneficial in their impacts to the natural communities. For example, Martin et al. (2014) showed that Neotropical *Eucalyptus* plantations had no influence on small mammal body condition, showing/suggesting that some species can even nest inside plantations, although other native species were only detected within its limits.

Globally, exotic forest plantations have been expanding in the last decades and cover now >264 million hectares (FAO, 2010). *Eucalyptus* spp. is one of the most important forestry species, occupying >20 million hectares in temperate and tropical regions (Forrester and Smith, 2012). This increase in *Eucalyptus* production

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areas is associated with its high yield, short production cycle, diverse uses of its wood (e.g. fiber, sawtimber, construction, etc.), high capacity to withstand variable climatic conditions, and ability to be manipulated to produce hybrids and clones with higher wood quality and resilience to regional climates (Campinhos, 1999). In Portugal, *Eucalyptus* spp. are already the most important forestry species, covering 26% of Portuguese forests (ICNF, 2013) that amount to 47% of the *Eucalyptus* production forests in Europe (Iglesias-Trabado et al., 2009). The plantation of exotic *Eucalyptus* have raised several environmental issues associated with the replacement of native ecosystems, namely invasiveness potential, fire risk, unsustainable water use, and production sustainability (Stanturf et al., 2013).

Nonetheless, the impact of *Eucalyptus* plantations on native vertebrate communities is variable and contingent on taxa and landscape context (i.e. type, shape size and spatial arrangement of other landscape components, such as native patches). For example, *Eucalyptus* plantations have shown limited impact on amphibians in the Iberian Peninsula (i.e., constraining the occurrence of some species, but promoting other and not affecting many; Cruz et al., 2015), while in the Brazilian state of São Paulo *Eucalyptus* forests are inhabited by half of the bird species found in native vegetation (Penteado et al., 2016). Further, the presence of native vegetation strips (“cerrado”) within *Eucalyptus* plantations was shown to enhance insect diversity to a value very close to that measured in “cerrado” reserves of Mina Gerais state, Brazil (Zanuncio et al., 1998). The use of *Eucalyptus* plantations by vertebrates may also vary with plantation age. For instance, generalist small mammal species are early colonizers of *Eucalyptus* plantations while more specialist species only appear in latter management stages (e.g., Martin et al., 2012). Larger mammals, on the other hand, avoid pre-harvesting stands at latter management stages (Timo et al., 2014).

The negative impacts of *Eucalyptus* plantations may be counteracted by management. For example, adequate management of the harvest cycle may enhance the habitat provisioning capacity of *Eucalyptus* plantations for many vertebrates (Verdade et al., 2014). Plantations with remnants of natural vegetation tend to have higher species richness than monocultures (e.g. Zanuncio et al., 1998), as natural vegetation likely serve as a refuge/cover/shade (Hartley, 2002) being also source of colonizers of several species (Vidal et al., 2016). Several studies have shown that understory vegetation is one of the most influential factors for biodiversity in forestry plantations (e.g. Cerda et al., 2015; López and Moro, 1997), with *Eucalyptus* plantations with understory of native shrubs hosting as much as 40% of the small mammals found in primary forests (Barlow et al., 2007). Some authors suggest that to provide habitat for native wildlife (and promote a diversified understory layer) it is possible to thin plantations earlier, to exclude some areas of herbicide application or to reduce clearcutting actions (Hartley, 2002). It is therefore important to understand which is the *Eucalyptus* plantation structure and associated management regime that best enhance vertebrate population densities, a necessary step towards conservation and a sustainable landscape (Sinclair et al., 2006).

In this study, we compared small mammal density in an *Eucalyptus* plantation and in the surrounding native semi-natural ecosystem, testing the effects of habitat type and understory composition and structure. We expected lower small mammal density in *Eucalyptus* stands when compared to native ecosystems because *Eucalyptus* may provide fewer resources (e.g. Majer and Recher, 1999), i.e. lower food availability (Stallings, 1990; Stephens and Wagner, 2007), and/or less refuges (Stallings, 1990).

2. Materials and methods

2.1. Study area

This study was carried out at “Companhia das Lezírias, S.A.” a state farmstead located 40 km northeast of Lisbon, Portugal (38°49′22.34″N, 8°52′3.24″W; Fig. 1). The region is characterized by hot dry summers and cold rainy winters typical of Mediterranean climates, with an average annual temperature of 16.3 °C and 700 mm rainfall (Gonçalves et al., 2012).

Companhia das Lezírias, S.A. (hereafter termed CL) is the largest agro-forestry farmstead in Portugal, including an area of 11,000 ha (Charneca farmstead) where main activities are cattle breeding, forestry and agriculture. The main land use (6725 ha) is the semi-natural forest of the native cork oak (*Quercus suber*), called *montado*, where agroforestry productions co-exist with high biodiversity (Pinto-Correia et al., 2011), mammals included (Gonçalves et al., 2012). Other forestry systems are also present in the farmstead, such as pinewoods (maritime pine *Pinus pinaster* and umbrella pine *Pinus pinea* - 1500 ha) and *Eucalyptus* plantations (*Eucalyptus globulus* - 476 ha). Forestry stands are interspersed with agriculture fields, including rice fields (630 ha), pastures (460 ha), olive yards (59 ha), and vineyards (140 ha) (Companhia das Lezírias, 2010). The present study was conducted in two of CL's forestry systems: exotic *Eucalyptus* plantations and native cork oak *montado*. In each forestry type, a sampling area of 400 ha was defined representing one treatment (*Eucalyptus*) and one control (*montado*) site.

2.2. Small mammal trapping and handling

Small mammal trapping was conducted in the fall (October and November 2014) and repeated again in the spring (March and April 2015) to represent two life-cycle periods: pre and post-reproduction, respectively. The two sampling areas (*Eucalyptus* plantation and cork oak *montado*) were selected in close proximity to ensure similarity in physiographic conditions, but sufficiently far apart to prevent animals to move between the two areas (ca. 9 km). In each area, we established 9 sampling points, forming a 3 by 3 grid, with points spaced 1 km from each other (Fig. 1). On each sampling point we defined a smaller 40 × 40 m grid, with 25 trapping points spaced 10 m apart, covering a total area of 1600 m². In all 25 trapping points we set three different live traps, all located in a circle with 1 m radius: two Sherman traps of distinct sizes (38 × 10 × 12 cm and 23 × 8 × 9 cm) and one pitfall trap (plastic bucket; 14 × 14 × 17 cm). The combined use of three types of traps aimed to maximize multi-species trapping efficiency (Gurnell and Flowerdew, 2006), since species with very distinct morphological and ecological characteristics are present in the area (Gonçalves et al., 2012).

Sherman traps were placed at the ground level and covered with vegetation to avoid direct sun exposure. These traps were baited with a mixture of canned sardine in oil and oatmeal, and cotton was added to provide nest material to minimize possible effects of small mammal stress and hypothermia (Gurnell and Flowerdew, 2006). Pitfall traps were buried, and buckets had holes in the bottom to allow drainage of rainwater, and contained a piece of styrofoam to prevent animals from drowning. The traps were placed in the field and kept closed for two nights prior to the sampling period to minimize trap avoidance. After the acclimation period, traps were set active for four consecutive nights and checked every morning. Bait and bedding were checked at each trap visit.

Captured animals were marked individually by fur clipping at predefined areas of the animal's body, following the protocol defined by Gurnell and Flowerdew (2006). These marks allowed

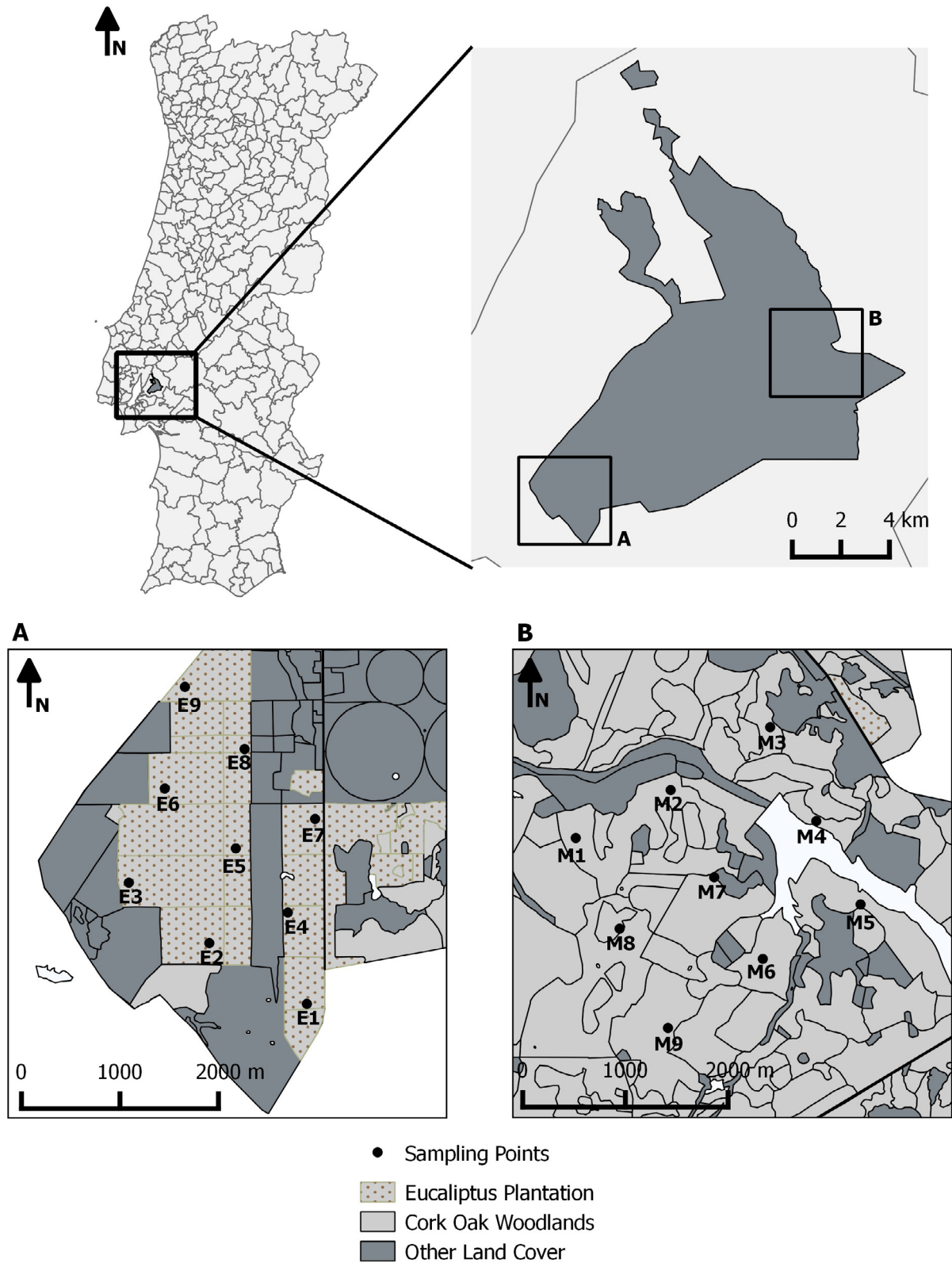


Fig. 1. Location of *Eucalyptus* plantations and cork oak *montado* sampling areas within Companhia das Lezírias farmstead. For each area, sampling point grids (*Eucalyptus* plantations: E1–E9; Cork oak *montado*: M1–M9) are shown.

us to easily identify the animals in subsequent recapture events. All captured animals were identified to the species level (Macdonald and Barrett, 2002), and their gender, age and reproductive condition determined, using the criteria mentioned by

Gurnell and Flowerdew (2006). Body metrics, such as weight (using a Pesola Scale Light Line 50 g, with an accuracy of 0.5 g) and body, tail and hind foot length (using an aluminium ruler, with an accuracy of 0.1 cm), were also registered and used as criteria in

species identification. All individuals were released at their trapping location. Capture and handling processes followed national and international standards (Gannon et al., 2007), according to the capture licenses 151/2014/CAPT and 419/2015/CAPT (ICNF - Nature Conservation Institute and Forestry).

2.3. Vegetation sampling

In each sampling area, vegetation properties were described at both stand and trap levels. At stand-level, vegetation structure and diversity were measured using the point-intercept method (Elzinga et al., 2001; Nunes et al., 2014). At each sampling point we established three parallel transects of 20 m, separated by 10 m. Along each transect, at every 50 cm, a rod was placed perpendicular to the ground and plants, lichens, mosses, litter and bare soil touching the rod were recorded. The proportion of points intercepted by each category along transects was used to calculate the ground cover of each class (% cover), as a surrogate of its abundance. Maximum height of herbaceous and shrub species was also measured at each point. Shrubs were identified to species level and classified according to the type of fruit they produce, fleshy or dry, with the latter sorted in legumes, acorns and other dry fruits. This subdivision was made because each group may impact differently small mammal diets. To analyse a possible effect of different plant functional groups on small mammals, we separated herbaceous species in four groups: grasses (Poaceae), legumes (Fabaceae), composites (Asteraceae), and other. The first three families compose at least 80% of the plant community, and grasses and legumes are known as important for animal nutrition (e.g., Lantová and Lanta, 2009).

At trap-level, understory cover was estimated for each trapping point (i.e. 225 trapping points per sampling area; 25 per sampling point) based on a circle with a 1 m radius around the trap. In each circle the vertical projection of shrubs on the soil was visually estimated, as an indication of the cover surrounding each trap. The average % cover for the 25 trapping points was calculated for each of the nine sampling points by grid. We also determined the distance from the centroid of each sampling point to other habitats and to permanent water points, to assess the possible effects other habitats on small mammal density.

2.4. Data analysis and statistical procedure

2.4.1. Species richness, diversity and sex-ratio

For each sampling point in the *Eucalyptus* plantation and in the cork oak *montado* we calculated species richness (i.e. number of different species captured), as well as diversity through the Shannon-Wiener (H') index (Zar, 2010). We tested whether H' was on average different per forest type using a t -test, after verifying normality assumptions with the Shapiro-Wilk Normality test (Zar, 2010). We also assessed whether sex-ratio between both forest types differed using a proportion test (Armitage, 1966).

2.4.2. Density estimation

For each sampling point and period (i.e. fall and spring), we estimated the total density of small mammals and that of species with a sufficient number of captures and recaptures (in this case it was only wood mice, *Apodemus sylvaticus*). We used “Spatially Explicit Capture-Recapture Models” (SECR models; Borchers, 2010), which estimate density based on the number of capture/recapture events and the trap location. For each sampling point, season and taxa, we produced four types of density models: (1) g_0-1 , where g_0 is constant as it assumes no influence of trap day or animal behaviour on density; (2) g_0-t a model that accounts for the influence of the trapping day, i.e. the probability of capture may change with the trapping day; (3) g_0-b is a model that accounts for a variation in

animal behaviour, i.e. it allows for a change in animal's behaviour towards the trap after the first capture event (e.g. after the first capture an animal may have a higher or lower probability of being captured a second time); and (4) g_0-bk , a model that accounts for both the influence of variations in behaviour and trapping day.

The four models produced for each analysis were compared using AICc – Akaike's Information Criteria (Burnham and Anderson, 2002), corrected for small samples, to determine which model better expresses the variability present in our data. Best models were considered those that had lower AICc values. All models with $\Delta AICc$ (i.e. difference between the lowest AICc value and the AICc value for each model) less than two were considered as equally suitable (Burnham and Anderson, 2002). Using the best fitted model, we estimated the total density of small mammals and of wood mouse at each sampling point ($N = 18$) per area (*Eucalyptus* and cork oak *montado*) and season (fall and spring). Spatially Explicit Capture-Recapture Models were built using “secr” package (Efford, 2015) in R (R Core Team, 2015). When the number of captures and recaptures were too low or even 0 models were not produced. For these cases we used the number of animals per sampling area (ind/ha), where the sampling area encompassed the sampling grid plus a buffer of 10 m to account for the inter-trap distance. Density estimates and the surrogate of density were used in the subsequent modelling procedures to assess the factors influencing variation in density (see Section 2.4.2 and Supplementary Material 3). One sampling point (E3) at the *Eucalyptus* plantation was harvested in spring, prior to sampling, and therefore excluded from the analysis.

2.4.3. Factors influencing variation in density

We tested density for homogeneity of variance with the Levene's test (Glass, 1966) and normality with the Shapiro-Wilk test (Zuur et al., 2009). According to the results, we used either the t -test or the Mann-Whitney U test (Zar, 2010) to evaluate whether density varied significantly between *Eucalyptus* and cork oak *montado*, and sampling periods.

Due to the high number of vegetation-related variables (see Supplementary Material 1), we first applied a Principal Component Analysis to reduce data dimensionality (PCA; Zuur et al., 2007). We selected the first four components of each PCA data set (i.e. small mammal and wood mouse) using the scree or elbow test as criterion for components selection (Abdi and Williams, 2010) as independent variables in the following modeling procedures. We used the Moran's I index (Dormann et al., 2007) to test whether there was significant spatial autocorrelation and the Spearman correlation coefficient (r) to assess the correlation (or multicollinearity) between the continuous variables “Distance to the nearest water point” and “Distance to the nearest different habitat”. When spatial autocorrelation was significant, we used Generalized Linear Mixed Models (GLMM) with a Gaussian distribution family, to test the influence of the independent variables [PCA1, PCA2, PCA3, PCA4, Habitat (*Eucalyptus* plantations vs cork oak *montado*), sampling period (fall vs spring), distance to other habitats and distance to water points] on small mammal density (i.e. dependent variable). To incorporate spatial autocorrelation in the analysis, we used the sampling point as random factor. If the autocorrelation was not significant, we used Generalized Linear Models (GLM), i.e. models without random factors in the model.

We produced a set of models representing all possible combinations of the independent variables. Model selection procedures were similar to those described for Spatially Explicit Capture-Recapture Models (Burnham and Anderson, 2002). When more than one model fitted the $\Delta AICc < 2$ criterion, we applied a model averaging procedure (Burnham and Anderson, 2002). Finally, we used the confidence intervals of the coefficients for variables included in the best models (95% CI), to determine the direction

(positive or negative) of its influence on small mammal density, i.e., those whose confidence intervals (CI) do not cross the 0. Model validation was based on the analysis of the dispersion of the residuals versus the adjusted values for each best model to detect heteroskedasticity (Zuur et al., 2009). Models were built in R (R Core Team, 2015) using the packages “lme4” (Bates et al., 2015) and “MuMIn” (Barton, 2016).

3. Results

We captured 681 individuals in a total of 1299 capture/recapture events, 53% (N = 363) of which in the cork oak *montado* (called *montado* hereafter) and 47% (N = 318) in the *Eucalyptus* plantation (*Eucalyptus* hereafter). These individuals belong to five species of rodents [wood mouse, *Apodemus sylvaticus* (N = 527), Algerian mouse, *Mus spretus* (N = 67), Cabrera vole, *Microtus cabreriae* (N = 8), Lusitanian pine vole, *Microtus lusitanicus* (N = 2), and black rat, *Rattus rattus* (N = 1); [Supplementary Material 2](#)] and one species of insectivores [greater white-toothed shrew, *Crocidura russula* (N = 76)]. Three of these species (*A. sylvaticus*, *M. spretus* and *C. russula*) were captured in *Eucalyptus* while all five were trapped in *montado*. However, the average diversity in *Eucalyptus* was similar to that registered for *montado* (*Eucalyptus* plantation: $H' = 0.629 \pm 0.153$; *montado*: $H' = 0.461 \pm 0.134$; Shapiro-Wilk = 0.964, p-value = 0.671, t = 0.567, p = 0.579). The community was largely dominated by wood mouse in both habitats (*Eucalyptus*: N = 241 and 76%, *montado*: N = 286 and 78%). We found no differences in sex ratio between *Eucalyptus* and *montado* (Small mammals: Sex-ratio_{*Eucalyptus*} = 1.12; Sex-ratio_{*montado*} = 0.99; $\chi^2 = 0.436$ p = 0.509; *Apodemus sylvaticus*: Sex-ratio_{*Eucalyptus*} = 1.28; Sex-ratio_{*montado*} = 1.02; $\chi^2 = 1.399$, p = 0.237), with a dominance of males (i.e. sex ratio >1).

The type of SECR models that better fitted the density estimations varied according to the sampling point (see [Supplementary Material 3](#)). Small mammal density averaged 50 ind/ha (st.dev. = 44 ind/ha) and that of wood mice averaged 42 ind/ha (st.dev. = 45 ind/ha). We detected no significant difference between sampling seasons and habitats (all p > 0.05; [Fig. 2](#)), but this result may be associated with the high standard deviation around the density estimates. Nevertheless, some trends were detected. In *Eucalyptus* small mammal and wood mouse densities decreased from fall to spring, the opposite occurring in *montado* ([Fig. 2](#)). Overall density of both mammalian groups decreased from fall to spring, with *montado* areas reaching higher densities when data from the entire study period is included ([Fig. 2](#)).

The first four Principal Components accounted for 0.734 of the cumulative proportion of variance of all vegetation data, and were used in the subsequent analysis. Distance to other habitats and distance to water points were not correlated ($r = -0.002$, $p > 0.05$), and thus were also used as candidate variables for model building. We detected a significant spatial autocorrelation for wood mouse ($I = 0.101$, $p < 0.001$), but not for total small mammals ($I = 0.042$, $p = 0.053$); therefore, we used a GLMM for wood mouse and a GLM for overall small mammal data.

3.1. Small mammal density

Only two models were considered the best models ($\Delta AICc < 2$), which included two variables: PC2 and season ([Table 1](#)). However, only PC2 did not cross the 95% CI and we were confident on its positive influence on small mammal density ([Table 1](#)). Dispersion of the residuals versus the adjusted values showed that the produced average model showed a good fit ([Supplementary Material 4](#)). Given the PC2 loadings ([Supplementary Material 1](#)), small mammal density seems to be higher in areas with higher shrub cover and abundance, height of herbs and shrubs, abundance of litter, lichens, and woody species that produce fleshy and dry fruits, especially acorns; but with lower abundance of woody species that produce legume fruits, total herbaceous species, leguminous and composite species, moss and bare soil.

3.2. Wood mouse density

Three models were considered best models, and included six variables: PC1, PC2, season, habitat, distance to the nearest water point, and distance to other habitats ([Table 2](#)). The average model showed a good fit ([Supplementary Material 4](#)). Wood mouse density increased with PC2 and decreased with spring, *Eucalyptus* plantations and at higher distances to other habitats (variables whose CI95% did not cross 0; [Table 2](#)). PC2 loadings are as described above for the total small mammal density ([Supplementary Material 1](#)).

4. Discussion

Our results indicate that small mammal density at the studied *Eucalyptus* plantation was similar to that found in the native cork oak *montado*, not supporting the initial prediction that *Eucalyptus* plantations would withheld lower densities of small mammals. This pattern is similar to that detected for the body condition of small mammals, as we only found an effect of gender on body

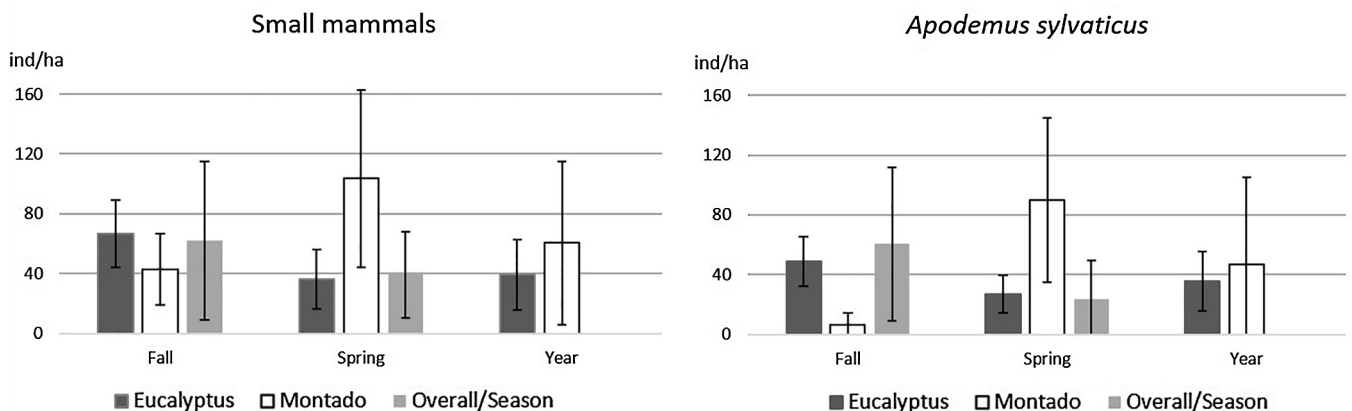


Fig. 2. Average density estimation (ind/ha \pm SD) for small mammals and wood mouse in *Eucalyptus* plantations, cork oak “montado”, fall and spring (Overall/season represents the average density for all sampling points – *Eucalyptus* and “montado”; Year represents the average density per forest type during the entire study period).

Table 1
First five GLM with the lowest AICc, ranked by the Δ AICc values, and Coefficients (Coef), standard error (SE), z-value and correspondent significance [Pr (>|z|)] and 95% confidence intervals (CI 95%) of the variables included in the best models explaining the variability in small mammals' density. Shaded model are considered the best models (Δ AIC < 2) and variables in bold have CI 95% that do not cross 0.

Model	df	AICc	Δ AICc	Akaike weight
PC2	3	335.84	0.00	0.388
Season+PC2	4	337.78	1.93	0.148
PC1+PC2	4	338.07	2.23	0.127
PC2+Habitat	4	338.25	2.41	0.116
Dist_water+PC2	4	338.3	2.46	0.113

Variable	Coef	SE	z-value	Pr (> z)	CI 95%
Intercept	62.369	9.147	6.566	<0.001	43.751/80.987
PC2	10.588	4.224	2.404	0.016	1.957/ 19.218
Season	3.353	9.699	0.336	0.737	-19.126/ 43.466

PC1 and PC2 – First and second principal component of vegetation variables (see Supplementary Material 1); Season - fall vs spring; Habitat - *Eucalyptus* vs Cork oak woodland; Dist_water – Distance to the nearest water point.

condition (Teixeira, 2015). We think that the possible deleterious effects that *Eucalyptus* plantations might have on small mammals described in the literature (e.g. Umetsu and Pardini, 2007; Gheler-Costa et al., 2012), may be overruled by stronger influences from other landscape characteristics, such as understory.

Small mammal density is affected by the structure and composition of the vegetation, suggesting that food and refuge affect density. Due to the small scale at which these species use the habitat (e.g., Rosalino et al., 2011), the presence of a developed understory with high shrub cover, tall herbs and shrubs, and higher surface cover by litter and lichens (mainly fruticose species) may allow animals to move sheltered and with a reduced probability of being spotted by predators. Small mammals are at the basis of many Mediterranean food webs, being preyed by terrestrial (e.g. Lataste's viper *Vipera latastei* - Santos et al., 2007; common genet, *Genetta genetta* - Rosalino and Santos-Reis, 2002) and flying (e.g. tawny owl, *Strix aluco*; Capizzi, 2000) predators. To avoid this predation pressure, it is likely that small mammals seek protective cover when patrolling their territory, searching for mate or food (Tattersall et al., 2001). This behaviour might be driving the selection of areas with higher plant cover to avoid predation (Tew and Macdonald, 1993), especially in regions, as our study area, where mesopredator's richness is high (Gonçalves et al., 2012).

Food availability also seems to be contributing for higher small mammal density, as areas with higher abundance of shrub species have a greater probability of supporting higher small mammal densities. This could be because these shrubs produce fruits (e.g. *Myrtus* sp), which are often used by rodents as food (Khammes and Aulagnier, 2007; Bauduin et al., 2013). Moreover, the presence of shrub species such as *Cistus* spp. and *Lavandula* spp. may be particularly attractive to pollinators (Herrera, 1992; Silva, 2007), and this may increase the abundance of insect species that can be preyed by either insectivores (e.g. greater white-toothed shrew, *Crocidura russula*; Brahmí et al., 2012) or rodents (e.g. *Mus spretus*; Palomo et al., 2009).

For the wood mouse we found a similar pattern to that of the overall community, but also that *Eucalyptus* plantations negatively affected density. This negative effect may be due to a preference for

consuming acorns (Khammes and Aulagnier, 2007), a fruit only present in the cork oak *montado*. Alternatively, wood mice often nest in hollow trees (*pers. obs.*), which are relatively common in cork oak *montado* but absent in *Eucalyptus* plantations as these trees never reach old ages (in Europe *Eucalyptus* are harvested before reaching 10 years of age; Alves et al., 2012). We also found higher wood mouse densities in areas closer to other habitats (ecotone regions) and in the fall. Ecotones have higher beta diversity than core habitats (Kark and van Rensburg, 2006), and because of this they may offer more foraging opportunities as the transition to another ecosystem may bring about different and complementary foods. In addition, and specifically in our study area, *Eucalyptus* plantations are often adjacent to cork oak *montado*, where wood mice may find acorns.

We did not detect any significant variation in small mammal and wood mouse density between seasons and habitat, but some trends emerged. In *Eucalyptus* plantation (and for the total data) there is a decrease in density from fall to spring, while in *montado* areas the opposite pattern was detected. The higher density of wood mouse in the fall contradicts what is usually described for this species in Mediterranean environments, i.e. density peaks in April-May (Rosário and Mathias, 2004). A plausible explanation could be the combined effect of local plant phenology (we observed high acorn productivity in fall; Jensen, 1982), predator dynamics (higher hunting pressure on some mesopredators that are hunted in the game season from October to February; Red fox *Vulpes vulpes* and Egyptian mongoose *Herpestes ichneumon*), and weather conditions (a milder fall; *pers. obs.*), that may have allowed for a higher wood mice survival in fall. Moreover, this higher density in *Eucalyptus* plantations in the fall may indicate that small mammal populations may contain immigrants in that season. These immigrants may be using this habitat while searching for territory, but are unable to establish it and were not present in the area in the next spring. Inversely, the reverse pattern registered in *montado* areas, may indicate a higher stability in population and spatial structure, since a disruptive demographic and spatial population structure induces animals to emigrate (Ehrlich et al., 2009), a mechanism that we think is not acting in *montado*.

Table 2

First five GLMM with the lowest AICc, ranked by the Δ AICc values, and Coefficients (Coef), standard error (SE), z-value and correspondent significance [Pr (>|z|)] and 95% confidence intervals (CI 95%) of the variables included in the best models explaining the variability in wood mice density. Shaded model are considered the best models (Δ AIC < 2) and variables in bold have CI 95% that do not cross 0.

Model	df	AICc	Δ AICc	Akaike weight
Season+Habitat+ Dist_water+ Dist_habitat+PC2	8	211.49	0.00	0.342
Season+Habitat+ Dist_water+ Dist_habitat+PC1+PC2	9	212.72	1.23	0.186
Season+Habitat+ Dist_habitat+PC2	7	213.36	1.87	0.134
Season+Habitat+ Dist_habitat+PC1+PC2	8	214.25	2.76	0.086
Season++Habitat+Dist_waterDist_ habitat+PC1	8	215.22	3.73	0.053

Variable	Coef	SE	z-value	Pr (> z)	CI 95%
Intercept	75.614	9.581	7.362	<0.001	58.999/92.229
Season (spring)	-12.129	6.514	1.737	0.082	-23.427/-0.832
Habitat (<i>Eucalyptus</i>)	-34.039	12.161	2.613	0.009	-55.118/-12.960
Dist_water	-4.160	4.418	0.891	0.373	-12.776/2.342
Dist_habitat	-14.930	5.428	2.565	0.010	-24.344/-5.516
PC1	-0.357	1.167	0.289	0.773	-4.616/2.070
PC2	6.323	3.030	1.949	0.051	1.073/11.574

PC1 and PC2 – First and second principal component of vegetation variables (see Supplementary Material 1); Season (fall vs spring); Habitat – *Eucalyptus* vs Cork oak woodland; Dist_water – Distance to the nearest water point; Dist_habitat – Distance to the nearest different habitat.

This hypothesis is reinforced by a higher, but not significant, overall density in *montado*.

The wood mouse dominated the small mammal community in both forest types. This dominance was already mentioned for many areas of the Mediterranean region (e.g., Spain: García et al., 1998; Pons and Pausas, 2007; Italy: Cagnin et al., 1998; Portugal: Pita et al., 2003) and is commonly associated with the species' use of widespread food resources, such as acorns and other seeds, and with preference for areas with some understory (Pita et al., 2003). The estimated overall density of wood mouse reached intermediate values between those reported for Southern Mediterranean ecosystems (Doñana, southern Spain = ca. 5 ind/ha; Moreno and Kufner, 1988) and those for temperate ecosystems (UK = ca. 50 ind/ha; Wilson et al., 1993). These density estimates are probably related to environmental productivity, with our study region showing intermediate productivity values between highly productive temperate systems and less productive Mediterranean ecosystems (Chen et al., 2012).

The absence of a detectable effect of *Eucalyptus* production forests on small mammal density is corroborated by species diversity values. Diversity in *Eucalyptus* plantations and *montado* was not significantly different, as the high proportion of wood mice in *montado* may counterbalance the higher number of species, leading to a

lower diversity. The two extra rodent species detected in *montado* were the Lusitanian pine vole and black rat. These species were only seldom captured in *montado*; however, their ecological characteristics may constrain the use of *Eucalyptus* plantations. The Lusitanian pine vole is a fossorial species that uses a system of tunnels to move and feed and prefer soils with some humidity (Mira and Mathias, 2002). *Eucalyptus* usually exhaust groundwater (Calder et al., 1997), making the soil drier and more difficult to excavate than in *montado*. The black rat, although a generalist species, commonly nests on tree trunks and foliage, away from the soil surface, or in underground galleries around tree roots (Zamorano and Palomo, 2002). The difficulty to build tunnels in a plantation, together with absence of secondary trunks in *Eucalyptus* trees (the main trunk is often vertical and without branching), may prevent black rats to use *Eucalyptus* plantations often. Corroborating the above mentioned pattern, also the sex-ratio did not differ significantly between the studied environments, with a male dominated community in both. Our described male bias is in line with what has been observed in other small mammals, and specifically the wood mice population of Iberia (e.g. Abad, 1991; Rosário and Mathias, 2004). We believe this is in accordance with Trivers and Willard hypothesis that mothers in good condition will invest more in the gender with higher variation in survival and

reproductive success (Trivers and Willard, 1973; Koskela et al., 2009). Males, due to their lengthier movements for territory patrolling and search for females, are more exposed to predation, leading to a higher variation in their survival and reproductive success, which may induce a male sex-ratio bias.

SECR models are highly sensible to variations in the number of recaptures and cannot estimate densities if recapture events are extremely low (Marques et al., 2011). Thus, although we managed to estimate density for the great majority of sampling points, we had to exclude some because we did not have sufficient recaptures. This reduction in sample size may result in less reliable average results (with high standard deviations) but suggests a patchy distribution of small mammals. Sampling should be repeated in other *Eucalyptus* plantations in other regions and with different management regimes, so that we can test if the results we obtained might represent a general pattern or are more specific to our study *Eucalyptus* plantation and small mammal community.

5. Conclusions

Our results do not support the often described negative influence of *Eucalyptus* plantations on small mammal density (e.g. neotropics; Martin et al., 2012), as they clearly illustrate that the impact of *Eucalyptus* plantations on vertebrates' density is variable and species-specific. Density seems to be driven not by the type of tree but by the characteristics of the understory layer that promotes food and refuge for small mammals. Thus, management regimes that allow for the development of a complex vegetation structure within the *Eucalyptus* plantation may contribute to maintaining vertebrate populations. In this way, production forests may contribute to the maintenance of regional biodiversity (Faith et al., 1996).

The maintenance of a complex vegetation structure, which does not highly contrast with the nearby native vegetation patches, can have benefits by enhancing habitat opportunities, decreasing edge effects, and improving landscape connectivity (Fischer et al., 2006). But for some species, however, it is not possible to consider *Eucalyptus* plantations as a good habitat, as seen from our results for the wood mouse, the dominant species in the area. The ecological requirements of specialist species (e.g., acorn food preference by the wood mouse) may not be fulfilled by *Eucalyptus* plantations (Felton et al., 2010). Thus, to increase the ecological function within *Eucalyptus* plantations, managers should consider improving the structural complexity of the plantation and implement “stepping stones” or corridor patches of native vegetation that may allow for more specialist species to survive (e.g. wood mice; Fischer et al., 2006). It is however important to recognize that actions promoting understory development alone may also have other consequences (e.g. increase fire risk), which might jeopardize any beneficial effects on small mammal populations. Thus, management action plans should also consider side effects of population enhancement actions and assess trade-offs. To conclude, *Eucalyptus* plantations value as habitat for wildlife depends on its composition and understory structure, which is mostly determined by management actions, but also the focal taxa and the context in which these plantations are embedded.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.11.009>.

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