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Determinants of the relative abundance of rodents in landscapes dominated by Eucalyptus plantations

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Forestry plantations have increased considerably over recent decades to fulfil human demand for wood, pulp and paper. *Eucalyptus globulus* Labill is one of the most abundant plantation species, particularly in Europe, where its largest presence is in Portugal. Furthermore, plantations in Mediterranean areas such as Portugal frequently suffer from forest fires, and thus it is crucial to understand their impacts on vertebrates. This is especially relevant for some species like small mammals that use landscapes at smaller scales, for which even small changes in forest cover may have a profound effect. In this study, we evaluate the effects of several environmental, disturbance and habitat drivers on the relative abundance of rodents (Muridae) in *Eucalyptus* plantations in Central Portugal. Specimen capture took place across two seasons and at eight study sites representing six different stages of *Eucalyptus* plantations and two native forests from 2019 to 2020. Using a Structural Equation Modeling (SEM) approach, we show that the relative abundance of rodents was promoted by recent wildfire events and was higher in areas where carnivores and wild boar were more abundant. In contrast, abundant deer and increased percentages of herbaceous or litter cover and bare soil limited the abundance of rodents. We did not detect a significant relationship between *Eucalyptus* plantations and the relative abundance of rodents. The presence of other species, either by direct contact (carnivores) or by inducing habitat changes (ungulates), and vegetation structure, likely linked to plantation management or fire regime, are the more important factors dictating the population dynamics of rodents across plantation forests in Central Portugal.

Introduction

Conversion of natural habitats, and specifically native forests, into forestry plantations is increasing worldwide (Calviño-Cancela *et al.*, 2012; FAO 2020; Nahuelhual *et al.*, 2012). Such land conversion is considered an important threat to biodiversity (Millennium Ecosystem Assessment, 2005). The impact of these processes on wildlife can vary according to the type of pre-existing land-cover (Bremer and Farley, 2010; Pawson *et al.*, 2010), management regime (*e.g.* intensive; Carvalho *et al.*, 2010), and the taxa considered (Felton *et al.*, 2010). Currently, forestry plantations account for approximately 3% of the world's forested areas (*i.e.*, approximately 131 million ha; FAO, 2020), aiming to meet the increasing demand for wood and paper pulp (Wack *et al.*, 2003; Deus *et al.*, 2018). *Eucalyptus* is one of the most popular tree genera for plantations, covering nearly 22 million ha outside its native range (Hoogar *et al.*, 2019). *Eucalyptus globulus* Labill is one of the principal species used in plantations due to its rapid growth, coppicing properties, and valuable wood quality (Zerga, 2015). *E. globulus* is the main species planted in European forestry plantations, covering almost 1.5 million ha. Of that, 928,000 ha are located in Portugal, representing 27% of Portugal's forest land-cover (DGT - Direcção Geral do Território, 2018).

Eucalyptus plantations provide less shelter and cover (Teixeira *et al.*, 2017; da Silva *et al.*, 2019) and fewer foraging habitats for some forest-dependent wildlife species (Pina, 1989; Cruz *et al.*, 2015). However, if such plantations are linked to patches of native forest and exhibit some degree of permeability to wildlife (defined as the ability of *Eucalyptus* stands to provide for passage of animals) (Singleton *et al.*, 2002), they can increase habitat connectivity and biodiversity (Rosalino *et al.*, 2014; Piña *et al.*, 2019). Nevertheless, the scale of these impacts (both positive and negative) varies according to plantation size and landscape context, as well as the wildlife species they harbor and the scale of their use (Calviño-Cancela *et al.*, 2012; Cruz *et al.*, 2015).

Wildfires are important determinants of Mediterranean landscapes and frequently occur in forestry plantations (Mirra *et al.*, 2017). These natural or human-caused disturbances can shape the composition and structure of vertebrate communities (*e.g.*, Birtsas *et al.*, 2012, Smith, 2000, Torre and

Díaz, 2004). However, the response of mammal species to fires is often habitat or species-specific (*e.g.*, Puig-Gironès *et al.*, 2018, Puig-Gironès and Pons, 2020; Geary *et al.*, 2020), and depends on the extent and intensity of a given wildfire event (Diffendorfer *et al.*, 2012). In general, such events have a deleterious affect on mammals, especially for small-sized species such as rodents (Puig-Gironès *et al.*, 2018).

Rodents have small home ranges, use the landscape at finer scales relative to larger mammals, and display limited dispersal (Bowman *et al.*, 2002). These species are more sensitive to the negative effects of forestry plantations, especially in plantations composed of smaller stands and where management practices impair the growth of shrubs that are essential for shelter (Teixeira *et al.*, 2017). Shrubs and other herbaceous cover are important for the survival of small mammals because together they provide refuge (*e.g.*, Sabino-Marques and Mira, 2011) and protection against predators (Simonetti, 1989). Furthermore, rodents have short lifecycles, with brief gestation periods that facilitate rapid responses to changing environments (Rosalino *et al.*, 2011a). They also play important ecological roles, including serving as the base of many trophic chains (see review by Verdade *et al.*, 2011), contributing to soil restructuring through fossorial behaviour (Barrett and Peles, 1999), and by being pioneer colonizers (for instance, at the initial stage of forestry plantations) and seed dispersers (Brewer and Rejmánek, 1999; Sunyer *et al.*, 2013). These characteristics, together with the fact that they are easy to capture, mark and track (Barrett and Peles, 1999), make rodents ideal models for assessing how *Eucalyptus* stands can affect wildlife populations.

Although *Eucalyptus* plantations cover an estimated 1.5 million ha in Europe, few studies have assessed how these plantations affect small mammal populations, particularly rodents (*e.g.*, in terms of their presence or relative abundance). Currently published data are limited to local-scale studies (*e.g.*, Carrilho *et al.*, 2017; Teixeira *et al.*, 2017). To bridge this knowledge gap, we implemented a regional-scale study to identify the environmental, disturbance, and habitat factors that determine the relative abundances of rodents in the *Eucalyptus*-dominated landscapes of central Portugal. We specifically wanted to understand the influence of a) type of habitat (native vs non-native), b) habitat structure (*e.g.*, bare soil, herbaceous, shrub and tree cover), c) fire occurrence, d) relative abundances of competitors and predators, and e) season on the relative abundance of rodents (see Figure 1 and Table 1 for predicted influence and reasoning). Moreover, we explored if rodent populations in *Eucalyptus* plantations changed their relative abundance among plantation production phases (see Figure 1 and Table 1 for predicted influence and reasoning).

Methods

Study areas

The study was carried out in an area covering >8,500 km^2 in central Portugal. We targeted eight study locations, six of which consisted of *Eucalyptus* plantations ≥20 km^2 and encompassed three production phases (initial – Pampilhosa; intermediate – Góis, Penamacor and Penha; pre-harvest – Mortágua and Fundão). The remaining two sites corresponded to native forests (Lousã and Malcata) that acted as control areas. The characteristic native vegetation of the control areas consisted of deciduous trees, such as oak (*Quercus* sp.), chestnut (*Castanea sativa* Mill.), poplar (*Populus* spp.) and ash (*Fraxinus angustifolia* Vahl), as well as shrubs mainly *Cistus* sp., *Lavandula* sp., *Ulex* sp., *Rubus* sp., *Erica* sp., *Cytisus* sp., *Daphne gnidium* L. and *Pterospartum tridentatum* (L.) Willk. All sampled areas were at least 10 km apart to ensure their spatial independence. The eight areas were grouped into two sets (western and eastern) with three *Eucalyptus* plantations and a control site in each set (Figure 1).

Data collection took place during two seasons (wet season: from February to May; dry season: from end June to September) in both 2019 and 2020. The climate of the western set is characterized as having higher annual precipitation (1200–2600 mm) and lower annual mean temperature (10–15 ˚C) relative to the eastern set (annual precipitation 400–1000 mm; and annual mean temperature ~17.5 ˚C). Both areas had an average altitude of ~1000 m, with the average altitude of *Eucalyptus* plantations being 500 m.

Sampling design

We used a capture-recapture approach based on a 40x40-m^2 sampling grid implemented in each of the eight study areas. At every grid node, located 10 m apart, we set two types of Sherman traps (XLF15 Folding Live Capture, 10.2x11.4x38.1 cm, and LFA Folding Live Capture Traps, 7.6x8.9x22.9 cm; H.B. Sherman Traps), representing a total of 50 traps *per* site. These traps have been recommended for studies assessing small mammal community composition (Torre *et al.*, 2016). We used both trap types to ensure that all rodent species could be trapped, ranging from large species (*e.g.*, black rat, *Rattus rattus* L.) more easily captured in the larger traps, to small species (*e.g.*, Western Mediterranean mouse, *Mus spretus* Lataste) that are more likely captured in smaller traps (Torre *et al.*, 2010). Every trap was baited with a mixture of canned sardines, oatmeal and cooking oil, and we added a piece of cotton to each trap to prevent animal hypothermia (Gurnell and Flowerdew, 2006). Traps were active for four consecutive nights *per* season, and each one was checked every morning and re-baited if necessary (Gurnell and Flowerdew, 2006).

Animal capture

For each captured animal, species, age, and gender were determined using morphometric characteristics (weight, tail size, body size, and hind foot size) (Gurnell and Flowerdew, 2006; Bencatel *et al.*, 2017), with weight and measurements recorded using a scale with 0.1 g accuracy and an aluminum ruler with 0.1 cm accuracy, respectively. Each animal was individually marked with color combinations to allow identification in a subsequent trapping event (Gurnell and Flowerdew, 2006). Marking was achieved using small color-coded spots on the tail (red, blue, green, purple, or black; see Figure S1; Supplementary material), tattooed with a 0.45x12-mm syringe, as suggested by Chen *et al.* (2016). Capture and handling procedures followed national and international standards (Gannon and Sikes, 2007), and they were authorized by the Portuguese Institute for Nature Conservation and Forests (ICNF) through capture licenses 138/2019/CAPT, 139/2019/CAPT, 09/2020/CAPT and 10/2020/CAPT.

Data processing

For each sampling grid, we recorded the occurrence of disturbance (*i.e.*, fire) and the dominant environment (native vs plantation), as well as the production phase of the plantations (*i.e.*, initial, intermediate or pre-harvest) (Table 1). All trap sites were characterized *in situ* according to habitat features (*e.g.,* tree species, percentage cover of each vegetation type) (Table 1). The percentage cover *per* trap site was estimated visually as the abundance of each vegetation type (*i.e.*, shrubs, herbaceous and litter cover, and bare soil) within a circular area with a 1-m radius centered on the trap location (Bookhout, 1996) (Table 1). We also recorded all tree species whose main stems were located within this 1-m radius. We used camera-trapping data to estimate the abundances of medium- and large-sized mammals in the eight study areas. We established a 16-km^2 camera-trap grid in each study area (Figure S2 - Supplementary data 1), in which 25 cameras were active for 30 days per season (dry or wet) for the two study years (see Castro (2019) for further detail). Relative abundances of individual species were estimated as the number of independent camera-capture events (*i.e.,* > 30-minute interval between events) for target species in the study areas (*i.e.*, in the 16-km^2 camera-trap grid *per* area) divided by the number of days the cameras were active (representing the RAI: relative abundance index, as per O'Brien *et al.*, 2003). Our camera traps provided data on predators, enabling us to characterize their impact on rodent communities (Norrdahl *et al.*, 2002; Korpimäki *et al.*, 2005). They also provided RAI data on red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), fallow deer (*Dama dama* L.) and wild boars (*Sus scrofa* L.), all of which may reduce the availability of food and shelter to rodents and thus have a negative impact on small mammal communities (Muñoz *et al.*, 2009) (Table 1).

Table 1

We used Pounds' relative abundance index (1) (Pounds, 1981) to estimate the relative abundance of rodents for each sampling season and trapping site:

$$I_{1j} = \frac{N_{1j}}{T_j * R_j - \sum C_j - r_{1j}} * 1000 \tag{1}$$

where I_{1j} is the index of relative abundance of species 1 at site *j*, N_{1j} is the number of different single individuals of species 1 captured at site *j*, T_j is the number of available traps set on site *j*, R_j is the number of daily trap inspections at site *j*, C_j is the number of captures (new and recaptures) of species other than species 1 at site *j*, and r_{1j} is the number of recaptures of species 1 at site *j*.

Due to the low overall capture of *Microtus cabrerae* Thomas and *Erinaceus europaeus* L., we have excluded both these species from our analyses (see Results). Since the orders Rodentia and Eulipotyphla display different feeding habits (granivores/herbivores vs insectivores, respectively), we decided not to pool these species for further analysis. *Crocidura russula* Hermann was not present in some areas for all four sampling periods (*e.g.*, at Lousã and Pampilhosa), or numbers of captured individuals were very low (*e.g.*, only one individual captured at Penamacor and Fundão, respectively, see Table S1; Supplementary material), so we excluded this species from our analysis. Accordingly, our study focused only on the relative abundances of the two primary rodents captured at our study sites, *Apodemus sylvaticus* L. and *Mus spretus* Lataste.

Data analysis

We used the species' ecology, their environmental requirements, and possible interspecific relationships to develop a series of hypothesized direct and indirect causal relationships between the relative density of rodents and the candidate environmental, disturbance, and habitat factors (Table 1). We used a structural equation modeling (SEM; Lefcheck 2016) to formalize and assess the importance of those relationships (Figure 2). Piecewise SEM is a probabilistic modeling approach based on a series of general linear models (GLMs) that combine multiple predictors and response variables in a single causal network (Lefcheck 2016). This type of model enabled us to identify direct and indirect relationships among the different predictors, to assess the relative importance of each variable, and to identify relationships between predictors that were not initially hypothesized.

Our study areas each have different habitats, with distinct structures and different usage intensities, so we tested the direct impact of habitat type and proportion of vegetation types on the relative density of rodents (Table 1). We expected to observe a positive influence of native habitat, presence of deciduous trees, higher percentages of shrubs, herbaceous and litter cover, and occurrence of fire on relative abundances. Inversely, we hypothesized a negative influence of the presence of *Eucalyptus* trees, plantation production phase and higher percentages of bare soil on those abundances (see Table 1 for the underlying reasoning). We also anticipated that the abundance of other sympatric taxa would negatively affect the relative abundance of rodents due to their impacts on soil and vegetation structure (*e.g.*, wild boar and deer) or by increasing predation pressure (*e.g.*, carnivores). Finally, we expected a negative effect of the wet season on the relative abundance of rodents (see Table 1 for the underlying reasoning).

Importantly, the relative abundance of rodents may also be influenced by indirect predictor impacts, arising from driver interdependencies (*i.e.*, how drivers influence the variation of other drivers), as illustrated in Figures 2B and 2C. Native habitats (native forest and shrubland cover) promote ungulate and carnivore abundances due to the greater availability of food and shelter offered by such environments relative to forestry plantations (da Silva *et al.*, 2019) and lack of vegetation management (*e.g.*, understory cutting). Cover provided by shrub, herbaceous, and litter layers is typically more abundant in such locations in the wet season, and there is less bare soil in native habitats and in later production phases of plantations (Schultz and Halpert, 1993). The presence of deciduous trees may provide food (*e.g.*, acorns) and shelter (*e.g.*, dens inside tree trunks) that can also benefit ungulates and carnivores, respectively (*e.g.*, Focardi *et al.*, 2000; Carvalho *et al.*, 2014). Conversely, relative abundances of carnivores and ungulates will be lower in the presence of *Eucalyptus* trees and in harvested plantations due to increased disturbance linked to harvesting activities (Timo *et al.*, 2014). Percentage of shrub, herbaceous, and litter cover increases as plantations become older (Bargali *et al.*, 1992). Moreover, fires promote the occurrence of bare soil patches and negatively affect vegetation cover, thereby reducing the relative abundance of ungulates and carnivores (Moreira and Russo 2007). Wildfire events are limited in the wet season, and native deciduous habitats (*e.g.*, oak woodlands) display lower fire hazard relative to highly flammable *Eucalyptus* (Xanthopoulos *et al.*, 2011), albeit fire also negatively impacts native habitats (Moreira and Russo 2007). Deer reduce shrub and herbaceous cover (Bugalho and Milne, 2003; Freschi *et al.*, 2017), and the relative abundances of carnivores and ungulates tend to be lower in the wet season since reproduction occurs in the dry season (MacDonald and Barrett, 1995).

We standardized all variables prior to analysis (*i.e.*, z-scores; Zuur *et al.*, 2007) using the R package “standardize” (Eager 2017). SEM was implemented using the “piecewiseSEM” package (Lefcheck 2016). Model fit was assessed by estimating R^2, a measure of the proportion of variance in the dependent variable explained by the model (Zuur *et al.*, 2007). All analyses were implemented in R Statistical Software version 3.6.3 (R Core Team 2019).

Results

We attained 179 captures of a total of 109 individuals during 6400 trap nights (*i.e.*, 8 sites x 50 traps x 4 survey nights x 4 sampling seasons) across all study areas. We trapped three species of Rodentia [wood mouse *A. sylvaticus* (Number of captures/Ncapt = 72; Number of recaptures/Nrecap = 52); Western Mediterranean mouse *M. spretus* (Ncapt = 18; Nrecap = 16); and Cabrera vole *M. cabrerae* (Ncapt = 1; Nrecap = 0)], as well as two species of Eulipotyphla [white-toothed shrew *C. russula* (Ncapt

= 17; Nrecap = 1) and European hedgehog *E. europaeus* (Ncapt = 1; Nrecap = 1)]. We captured rodents in seven out of eight study areas (*i.e.,* we detected rodents in 87.5% of the monitored sites, see Table S1; Supplementary material).

Our camera-trapping study across the sampling period revealed captures of four ungulate species: 1614 independent events (I.E.) of wild boar, 1474 I.E. of roe deer, 576 I.E. of red deer, and 17 I.E. of fallow deer. Furthermore, we obtained a total of 462 I.E. for five different species of carnivore: red fox (*Vulpes vulpes* L.); common genet (*Genetta genetta* L.); beech marten (*Martes foina* Erxleben); Eurasian badger (*Meles meles* L.); and Egyptian Mongoose (*Herpestes ichneumon* L.) (see Table S2 in Supplementary material for more details).

Our SEM analysis revealed a combined direct effect of several distinct drivers on the relative abundance of rodents. After accounting for interactions between independent variables and their indirect effects on the relative abundance of rodents (Figure 3B and 3C), the model suggested that recent wildfire events and the relative abundance of carnivores and wild boars promoted the relative abundance of rodents in our study sites. In contrast, the relative abundance of rodents was negatively related to deer, percentages of herbaceous, litter and bare soil coverage, and the presence of nearby deciduous trees (Figure 3A; Table S3, Supplementary material). Overall, the most influential factors were wildfire events ($\beta=0.437$, SE=0.144, $p=0.002$) and relative abundance of deer ($\beta=-0.332$, SE=0.045, $p<0.001$). None of the remaining variables significantly influenced rodent abundance (Figure 3A). Our SEM explained a moderate amount of the variance in the relative abundance of rodents across our study sites ($R^2=0.23$).

Discussion

The wood mouse, *A. sylvaticus*, is the most widely distributed and common species in Mediterranean Europe and was the most abundant species across our study sites (Bencatel *et al.*, 2017; Balestrieri *et al.*, 2017). Together with the second most abundant species, *M. spretus,* both appear to be the most common rodents in the *Eucalyptus*-dominated landscapes we studied in central Portugal, as reported previously for other areas of the Iberian Peninsula and in European ecosystems (Bencatel *et al.*, 2017). Our results support past observations that these two species are tolerant to plantation forestry (Gentili *et al.*, 2014; Puig-Gironès *et al.*, 2018; Noguerales *et al.*, 2015). In particular, the SEM suggested that *Eucalyptus* or plantation phase had no effect on the relative abundance of those rodent species. However, the SEM revealed that our rodent populations were mostly affected by recent wildfire events, which promoted their relative abundance, yet were negatively correlated with the relative abundance of deer.

We believe that the positive effect of wildfires on the relative abundance of rodents may arise via two indirect ecological mechanisms: food availability, and predator use of burned areas. Although the majority of vegetation may be destroyed by fire, and plant-based foods become immediately scarce, other resource may still be available (*e.g.*, insects) (Mason Jr. *et al.*, 2021; Palusci *et al.*, 2021). This is especially true in areas where salvage logging does not occur and dead trees and branches remain untouched (Pons *et al.*, 2020). Such conditions help retain forest-dwelling beetle communities (Koivula and Spence 2006), even in *Eucalyptus* plantations (Ulyshen *et al.*, 2018). However, fire also appears to stimulate vegetation regrowth and enhances plant productivity in some areas (Briani *et al.*, 2004), leading to rapid increases in vegetation cover and above-ground biomass (Clemente *et al.*, 1996;

Alhamad *et al.*, 2012) that can be used as food by rodents such as *A. sylvaticus* that also consume plants, stems and leaves (Rogers and Gorman, 1995; Khammes and Aulagnier, 2007).

There is likely little direct correlation between the mortality of small mammals and wildfires (Vieira and Briani, 2013), (Puig-Gironès *et al.*, 2018), especially in environments where fires are not uncommon and small mammals have developed associated survival strategies (*e.g.*, hiding in underground burrows or retreating to patches that have escaped the fire) (Vieira and Marinho-Filho, 1998). Rapid recolonization of burned areas can then occur, either by individuals that survived the fire or those inhabiting neighboring unburned areas, taking advantage of the food available after fires and lower competition for food and refuge (Puig-Gironès *et al.*, 2018). Moreover, larger mammal species, such as many carnivores, are not as resilient to wildfire events, and are more likely to suffer or die as a direct effect from forest fires (Smith 2000; personal observation) and fire-associated habitat changes (Birtsas *et al.*, 2012; Lino *et al.*, 2019). Although the ecological responses of predators to fires may be site-, habitat- and/or guild-specific (Geary *et al.*, 2020), the avoidance of burned areas by certain predatory species, especially after high-intensity fires, may result in reduced predatory pressures on their prey in post-fire areas (Torre and Díaz 2004).

The presence and abundance of ungulates may negatively impact rodent populations by reducing the availability of food and shelter (Muñoz *et al.*, 2009). The most common deer species in our study area are browsers (roe deer) or browsers/grazers (red deer) (Spitzer *et al.*, 2020). Accordingly, they may compete with small mammals (especially grazers) for food. Furthermore, by consuming or trampling plants to modify vegetation structure (Sabo *et al.*, 2017), deer also limit the amount of vegetation available to small mammals as cover (Flowerdew and Ellwood, 2001).

Other factors proved less significant, with no apparent relationship between the cover of bare soil, litter and herbaceous vegetation and the relative abundances of rodents. In areas dominated by herbaceous vegetation (especially when composed of plants of lower height), litter, or bare soil rodents lack sufficient cover to provide secure routes for travel or to act as refugia (Rosalino *et al.*, 2011a, 2011b). Therefore, rodents likely reduce predation risk by avoiding open areas (Galantino *et al.*, 2020), giving rise to lower relative abundance in those habitats. The presence of nearby deciduous trees also seems to negatively impact the distribution of rodents. Deciduous trees frequently act as refugia for rodent predators, for instance as roost sites for tawny owls (Yatsiuk and Wesołowski, 2020) or latrine sites for common genets (Espírito-Santo *et al.*, 2007). Thus, rodents are likely to avoid areas where predators are more frequently present (Díaz *et al.*, 2005).

Finally, we detected that the presence of carnivorous species and wild boar had a positive effect on rodents. That result seems counterintuitive considering that rodents in our study area avoided areas of presumed higher predation risk (e.g., deciduous trees). The majority of mesocarnivores we detected (see Supplementary material) have a generalist diet, though many prey mostly on rodents (Loureiro *et al.*, 2012). Several studies have shown that mesocarnivore abundance is often driven by prey abundance (*e.g.*, Vilella *et al.*, 2020), even in areas prone to wildfires (Puig-Gironès and Pons, 2020; Birtsas *et al.*, 2012). Thus, mesocarnivores may adapt their spatial behavior to extend their hunting activity into areas where rodents may be more abundant. The positive effect of carnivore abundance on rodents could have arisen from predators targeting areas in which the rodent population was greater. Thus, predators were attracted to greater densities of rodents, and the rodent population did not avoid those predators.

Initially, we predicted a negative effect of wild boar on rodents, as the feeding behaviors of these ungulates alter habitat structure through rooting activity that removes vegetation and disturbs the soil (Barrios-Garcia and Ballari, 2012). Surprisingly, our data revealed the opposite pattern. Rooting activity changes vegetation structure and composition in the short to medium term and to varying degrees (Burrascano *et al.*, 2015). Areas with lower rooting frequency (*i.e.*, where wild boar abundance was lower) often displayed a dominance of thorny vegetation and underground storage organs, with a concomitant reduction in the extent of herbaceous layers (Burrascano *et al.*, 2015). However, herbaceous plants recovered quickly after wild boar rooting activity (Brunet *et al.*, 2016), providing food and protection (when dense layers develop) for some rodents, promoting their abundance in areas frequented by wild boars.

Overall, our modeling results did not reveal any significant effect of *Eucalyptus* plantations on the relative abundance of rodents. To date, published studies on the effect of *Eucalyptus* stands on mammal populations have generated contradictory results. Some studies have shown that such forest patches exert a damaging effect as they offer less usable habitat, providing low amounts of food and shelter (Mangas *et al.*, 2008; Pereira *et al.*, 2012). Other studies have indicated that *Eucalyptus* patches may provide habitat for wildlife, acting like more developed forest matrixes, increasing habitat heterogeneity, and sometimes contributing to landscape connectivity (Brockerhoff *et al.*, 2008; Calviño-Cancela *et al.*, 2012). Some studies even report that *Eucalyptus* plantations provide no advantages or disadvantages to mammal populations (Martin *et al.*, 2012). However, plantation age appears to be the most important factor for explaining the distribution or abundance of mammals, not stand type (Timo *et al.*, 2014). Thus, our study reinforces the need to assess the effect of plantations regionally, as landscape context, community and guild may give rise to different responses over time.

We must stress that despite trapping across four sampling seasons over two years, we captured a relatively small number of rodents. Thus, our results may be limited by the small sample size in terms of the number of sites and trapped animals. This low abundance of small mammals in *Eucalyptus* plantations is a common pattern (e.g., Martin *et al.*, 2012; da Silva *et al.*, 2019). Therefore, a good sampling strategy to increase small mammal trapping probability and generate more data in low abundance landscapes might be to: 1) use a higher number of traps (double the number of traps used here, from 50 to 100); and 2) increase the number of trap nights (increase from four to five trap-nights *per* session) (Conard *et al.* 2008). We also acknowledge a mismatch between the scale used to assess the abundance of rodents ($40m^2$) and the scale used to estimate the abundance of large mammals ($16km^2$). However, since the later taxa use the landscape at larger scales, the combined use of data from several camera-traps (N=25) minimizes any bias from data collected in a single camera trap. Finally, although the goodness of fit of our model is not high (R^2=0.23), it is higher than that achieved in many ecology and evolutionary studies (see Møller and Jennions 2002 review) and, according to Chin (1998; criterion R^2>0.19), can be considered moderate.

Conclusion

Our study reveals the significant impact of wildfires and relative abundance of deer on rodent communities, but also highlights the contribution of vegetation structure. However, those factors are not independent of plantation management, including vegetation age that is linked to deer abundance. Together, our findings indicate that preserving some understory may be pivotal to promoting rodent abundance. Despite wildfires apparently enhancing rodent abundance, we must emphasize that it is likely only generalist and resilient species, such as those targeted in our study, that benefit from fires (Briani *et al.*, 2004; Puig-Gironès *et al.*, 2018). Of course, the beneficial effects will be dependent on the extent and intensity of wildfire events (Diffendorfer *et al.*, 2012) and the spatial distribution of unburned habitat patches (Shaw *et al.*, 2021).

Despite the limitations of those data, we identified significant influential drivers of the relative abundance of rodents in these anthropogenic landscapes. These findings help to increase our knowledge of the biodiversity that inhabits *Eucalyptus* plantations, particularly in Mediterranean ecosystems. Although planted species such as *Eucalyptus* are typically described as having some negative influence on various wildlife species (Calviño-Cancela *et al.*, 2012; Martin *et al.*, 2012; Gheler-Costa *et al.*, 2013), our findings do not support such a claim, as we detected no effect of *Eucalyptus* plantations or production phases on the relative abundance of rodents. Instead, our results are in line with the few other results available from Iberian studies (*e.g.*, Carrilho *et al.*, (2017); Teixeira *et al.*, (2017)), and thus they contribute to the ongoing debate of the impact of *Eucalyptus* plantations on native wildlife.

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Conflict of interest statement

None declared.

Data availability statement

The datasets generated during the current study are available from the corresponding author on reasonable request.

Supplementary Material

The following supplementary material is available at Forestry online: Figure S1 - photos illustrating small mammals with tattoo marks; Figure S2 – Location of the small mammal sampling grids ($40m^2$) within the camera-trap grids ($16km^2$); Table S1 - numbers of small mammals captured in each season *per* area, the species identified and their corresponding relative abundances; Table S2 – numbers of independent capture events of medium/large mammal species registered in camera-traps for each area; Table S3 – Structural Equation Modeling (SEM) results.

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Table and Figure captions

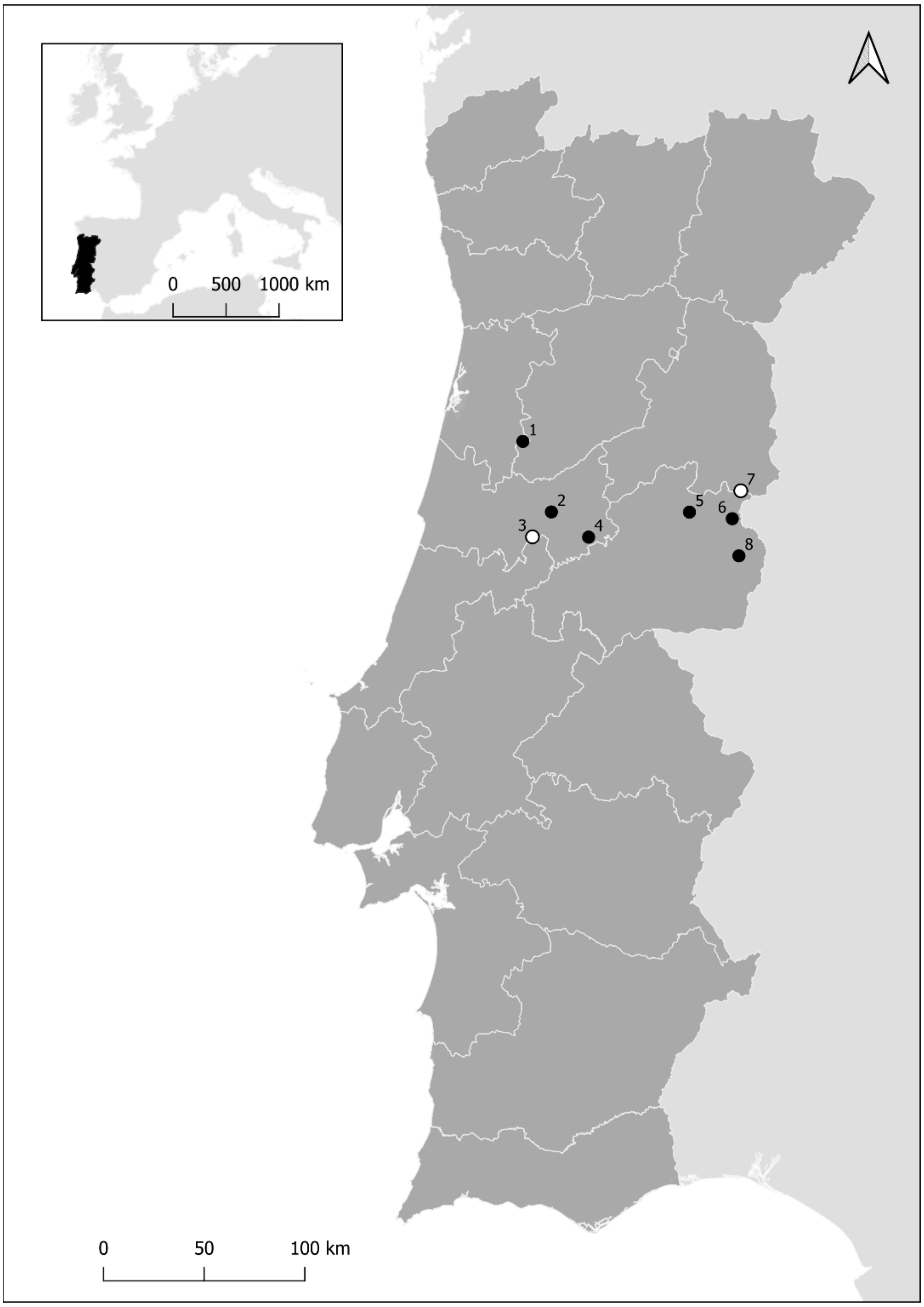

Figure 1 Location of the study areas in central Portugal where each grid for sampling the relative abundance of small mammals was implemented: 1- Mortágua; 2- Góis; 3- Serra da Lousã (native); 4- Pampilhosa da Serra; 5- Fundão; 6- Penamacor; 7- Serra da Malcata (native); 8- Penha-Garcia. This figure was produced using QGis 3.4.3 Madeira software (QGIS Development Team 2019).

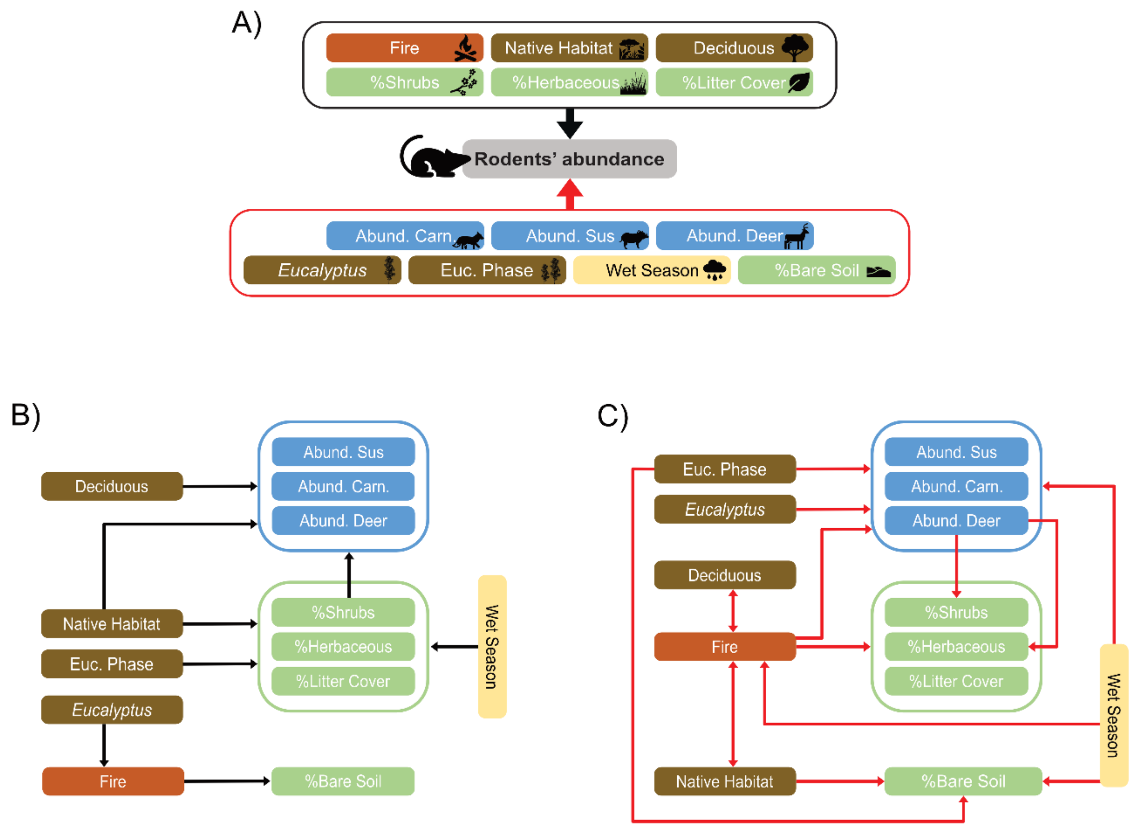

Figure 2 Conceptual model showing the direct causal relationships between environmental, disturbance and habitat drivers of relative abundance of rodents (A), as well as the indirect positive (B) and negative (C) causal relationships between drivers: 1) environmental characteristics linked to season (yellow box); 2) promoters of disturbance, such as fire (orange box) and interspecific relationships (blue boxes); and 3) habitat type (brown) and structure (green boxes). Arrows indicate the directionality of the influence and colors reflect the type of influence, *i.e.*, black = positive and red = negative.

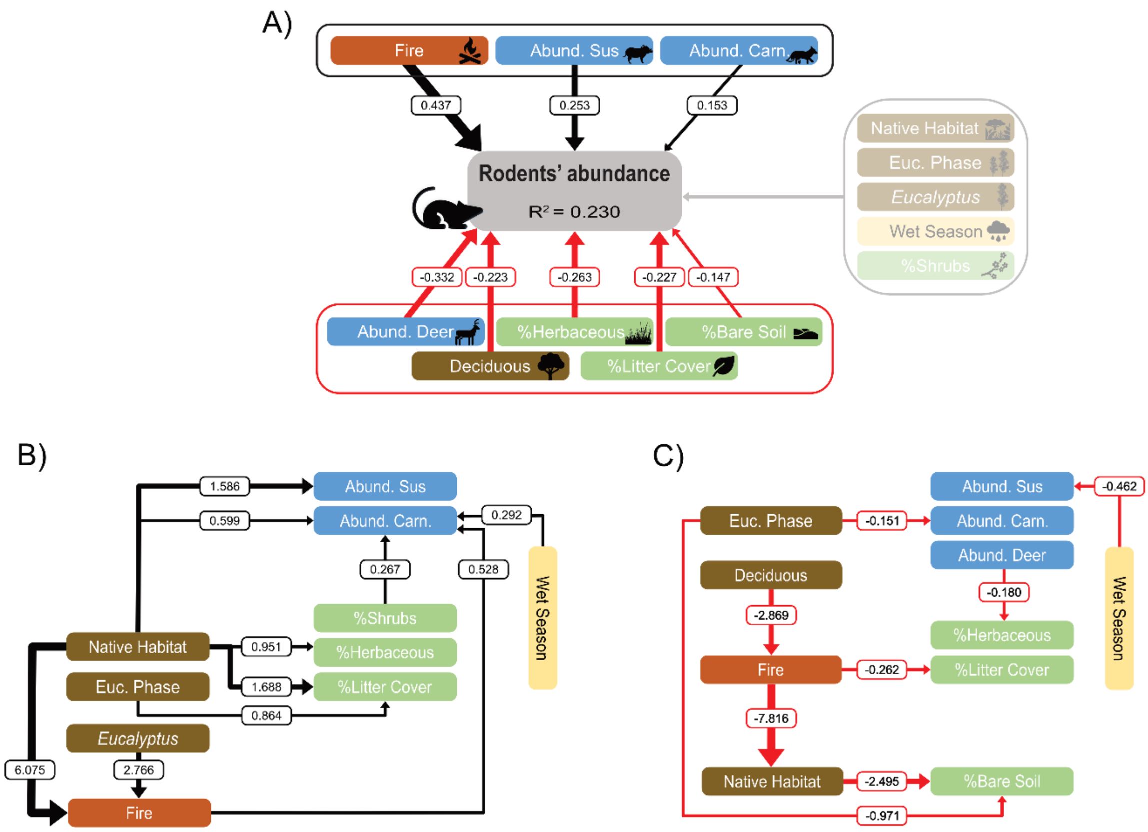

Figure 3 Results of structural equation modeling (SEM) highlighting the direct relationships between the relative abundance of rodents and the tested factors (A), as well as the positive (B) and negative (C) interrelationships between the tested factors: 1) environmental characteristics linked to season (yellow box); 2) promoters of disturbance, such as fire (orange box) and interspecific relationships (blue boxes); and 3) habitat type (brown) and structure (green boxes). Arrows indicate the directionality of the influence, with arrow thickness representing the relative size of the effect and colors reflecting the type of influence, *i.e.*, black = positive and red = negative, grey = non-significant.

Table 1. Explanatory variables used in the modeling procedure to assess the determinants of the relative abundance of rodents, their units and the rationale for selecting them (RAI – Relative Abundance Index).

Variable acronym	Description	Units (range)	Reasoning	Data type
Deciduous	Presence of deciduous trees stems within the 1 m radius	Absence / Presence [0–1]	Areas dominated by *Eucalyptus* plantations and with impoverished understory vegetation are known to have lower species richness and relative abundance, as they may provide lower availability of food or shelter (Rosalino *et al.*, 2009; Carrilho *et al.*, 2017). Thus, local land-cover composition and structure can be important community drivers. Areas dominated by native habitat (or with deciduous trees nearby traps), with greater % cover of shrubs, herbaceous plants and litter likely host higher relative abundance of rodents, and those dominated by bare soil may display lower rodent abundance (Carrilho *et al.*, 2017; Teixeira *et al.*, 2017). Furthermore, later production phases of	Field observations
Eucalyptus	Presence of *Eucalyptus* trees within the 1 m radius			

Euc. Phase	*Eucalyptus* production phase	Categories: 1 – Initial (≤ 1.5 m); 2 – Intermediate (> 1.5 - < 10 m); 3 – Pre-harvest (≥ 10m)	*Eucalyptus* (*i.e.* pre-harvesting) may host a higher relative abundance of rodents since mechanical trimmings and trail-cleaning are more frequent and there are higher levels of anthropogenic disturbance (from humans and machinery), leading to lower use of these older stands by carnivores (Timo *et al.*, 2015). Plantation understory soil cover is often higher at the end of the production cycle (Carneiro *et al.*, 2007), thus providing more refuge opportunities to small mammals. Deciduous trees are often used as roost or latrine sites by flying and terrestrial predators, respectively (Yatsiuk and Wesołowski, 2020; Espírito-Santo *et al.*, 2007). Thus, rodents are likely to avoid areas where predators are more frequently present (Díaz *et al.*, 2005).
%Shrubs	Percentage of all types of shrub cover within the 1 m radius	Categories: 1 - 0–35%; 2 - 36–70%;	
%Herbaceous	Percentage of herbaceous cover within the 1 m radius		
%Litter_Cover	Percentage of litter cover within the 1 m radius		

%Bare_Soil	Percentage of bare soil within the 1 m radius	3 - 71–100%		
Native Habitat	Sampling grid located on native habitat	Absence / Presence [0–1]		
Season	Wet or dry season in 2019 and 2020	Wet / Dry	Relative abundance of rodents is higher after the reproductive season (end of spring and beginning of summer; dry season), with juveniles already exploring their environment as food availability increases (Carrilho *et al.*, 2017; Bronson and Perrigo, 1987). Such seasonal fluctuations in abundance are a common phenomenon among small mammals (*e.g.*, Torre *et al.*, 2018).	-
Fire	Occurrence of fire in 2019 and 2020 in each sampling grid (confirmed in loco by the presence of ashed and burned trees/shrubs)	Absence / Presence [0–1]	Post-fire habitats, especially several months after fire events, tend to host more diverse and abundant prey communities. This pattern arises due to lower predation risk, with certain predators (*e.g.*, stone marten; Birtsas *et al.*, 2012) taking longer to recolonize burned and consequently fragmented habitats (Torre and Díaz, 2004; Lino *et al.*, 2019), and coverage of herbaceous vegetation increasing after fires (Kazanis and Arianoutsou, 1996), promoting cover and food availability, *e.g.*, *Apodemus sylvaticus* is considered a granivore (Khammes and Aulagnier, 2007) and *Mus spretus* feed mainly on grass seeds, plants and insects (Palomo *et al.*, 2009).	Field observations
Abund.Carn.	Relative abundance of mammalian carnivores *per* camera-trap grid	RAI (Nº Photo/ Nº Day)	Areas with more predators display a lower probability of harboring rodents (or at least lower abundance) due to predation pressure (Norrdahl *et al.*, 2002; Korpimäki *et al.*, 2005). Furthermore, ungulates can induce a decrease in habitat quality by reducing the availability of	Camera trapping study

Abund. Sus	Relative abundance of wild boar *per* camera-trap grid	[0–24]	food and shelter, by trampling vegetation (all species), through competition for food (especially grazers such as deer), and by changing habitat structure (for instance, rooting activity by wild boars leads to vegetation removal and disturbed soil) (Barrios-Garcia and Ballari, 2012). All these processes affect the presence and relative abundance of rodents (Muñoz *et al.*, 2009).	(Castro 2019)
Abund. Deer	Relative abundance of red deer, roe deer and fallow deer *per* camera-trap grid			

Supplementary data - Forestry

Figure S1 – Small mammals with tattooed marks

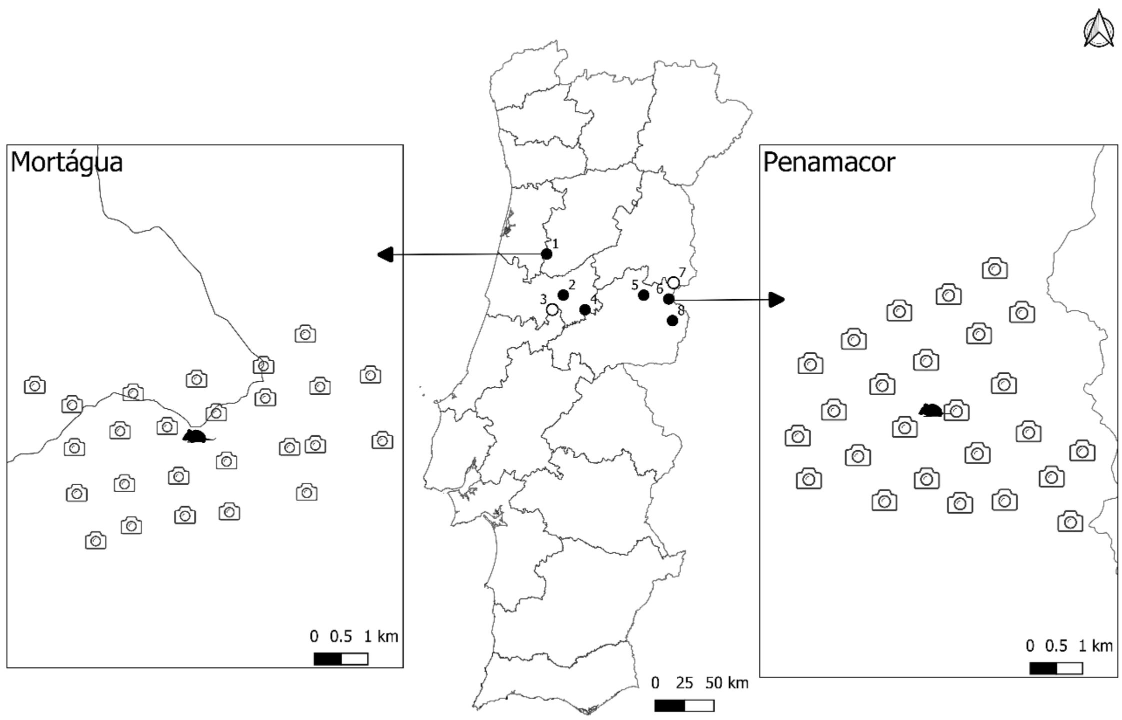

Figure S2 – Example of the location of two small mammal sampling grids (1 – Mortágua; 6 - Penamacor) within camera-trap grids () established to monitor medium-large sized mammals in *Eucalyptus* plantations (2 – Gois; 3 – Lousã; 4 – Pampilhosa; 5 – Fundão; 7 – Malcata; 8 - Penha-Garcia)

Table S1 – Number of small mammals captured in each season, *per* area and species. Relative abundance values for each species are in brackets.

		Western areas				Eastern areas				
		Native	*Eucalyptus* plantations			Native	*Eucalyptus* plantations			
Season	Species	Lousã	Pampilhosa	Góis	Mortágua	Malcata	Penamacor	Penha	Fundão	TOTAL
1st	*Apodemus sylvaticus*	2 (10.20)	4 (21.16)	5 (25.25)	0 (0)	4 (20.62)	4 (20.94)	4 (20.31)	0 (0)	23
	Microtus cabrerae	0 (0)	0 (0)	0 (0)	0 (0)	1 NA	0 (0)	0 (0)	0 (0)	1
	Crocidura russula	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (15.31)	0 (0)	3
	Mus spretus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (5.32)	0 (0)	0 (0)	1
	Total Nº	2	4	5	0	5	5	7	0	28
2nd	*Apodemus sylvaticus*	1 (5.13)	8 (44.94)	4 (20.41)	0 (0)	2 (10.70)	0 (0)	0 (0)	0 (0)	15
	Crocidura russula	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	0 (0)	1 (5.13)	1 (5)	3
	Mus spretus	0 (0)	9 (50.28)	0 (0)	0 (0)	0 (0)	2 (10.26)	0 (0)	0 (0)	11
	Total Nº	1	17	4	1	2	2	1	1	29
3rd	*Apodemus sylvaticus*	1 (5.08)	6 (31.92)	1 (5.05)	5 (26.60)	3 (15.31)	1 (5.35)	0 (0)	0 (0)	17
	Crocidura russula	0 (0)	0 (0)	0 (0)	1 (5.44)	0 (0)	1 (5.35)	6 (30.77)	0 (0)	13
	Mus spretus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (21.05)	0 (0)	0 (0)	4
	Total Nº	1	6	1	6	3	6	6	0	29
4th	*Apodemus sylvaticus*	0 (0)	3 (15.79)	3 (15.38)	0 (0)	8 (42.33)	2 (10.31)	1 (5.32)	0 (0)	17
	Mus spretus	0 (0)	1 (5.32)	0 (0)	0 (0)	0 (0)	1 (5.18)	0 (0)	0 (0)	1
	Crocidura russula	0 (0)	0 (0)	2 (10.31)	1 (5.05)	0 (0)	0 (0)	0 (0)	0 (0)	3
	Erinaceus europaeus	1 (6.37)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1
	Total Nº	1	4	5	1	8	2	1	0	22

Table S2 – Number of independent events of medium/large mammal species registered in camera traps, in each area

	Western areas				Eastern areas				
	Native	*Eucalyptus* plantations			Native	*Eucalyptus* plantations			
Species	**Lousã**	**Pampilhosa**	**Góis**	**Mortágua**	**Malcata**	**Penamacor**	**Penha**	**Fundão**	**Total Nº**
Capreolus capreolus	150	12	61		553	284	46	368	1474
Cervus elaphus	410		10		6	65	82	3	576
Dama dama						9	8		17
Genetta genetta	1	4	6	4	1	8	1	1	26
Herpestes ichneumon			1			1	1		3
Martes foina	7	1		11	16	3	1	2	41
Meles meles	1	1	6		15		1	4	28
Sus scrofa	430	44	40	29	537	330	40	164	1614
Vulpes vulpes	58	37	50	27	85	56	16	35	364
Total Nº	**1057**	**99**	**174**	**71**	**1213**	**756**	**196**	**577**	**4143**

Table S3 – Structural Equation modelling (SEM) results. Models are separated according to the dependent variable considered (see table 1 for variables description). In bold are highlighted variables whose influence is significant (i.e. p<0.05).

	Estimate	**Std.Err**	**z-value**	**P(>|z|)**	**Std.lv**	**Std.all**
Rodents' relative abundance						
%Shrubs	0.010	0.056	0.173	0.863	0.010	0.006
% Herbaceous	-0.263	0.076	-3.460	0.001	-0.263	-0.129
%Bare Soil	-0.147	0.050	-2.964	0.003	-0.147	-0.187
%Litter Cover	-0.227	0.047	-4.813	0.000	-0.227	-0.254
Eucalyptus	-0.118	0.107	-1.105	0.269	-0.118	-0.053
Deciduous	-0.223	0.109	-2.042	0.041	-0.223	-0.076
Wet Season	0.121	0.072	1.684	0.092	0.121	0.056
Fire	0.437	0.144	3.044	0.002	0.437	0.097
Abund. Carn	0.153	0.039	3.968	0.000	0.153	0.136
Abund. Sus	0.253	0.046	5.468	0.000	0.253	0.225
Abund. Deer	-0.332	0.045	-7.420	0.000	-0.332	-0.303
Native Habitat	-0.244	0.231	-1.056	0.291	-0.244	-0.087
Euc. Phase	-0.142	0.074	-1.903	0.057	-0.142	-0.145
%Shrubs						
Fire	-2.684	12.052	-0.223	0.824	-2.684	-0.970
Native Habitat	-60.161	263.964	-0.228	0.820	-60.161	-34.785
Wet Season	-1.215	5.895	-0.206	0.837	-1.215	-0.912
Abund. Deer	37.688	165.024	0.228	0.819	37.688	55.736
Euc. Phase	-2.879	13.147	-0.219	0.827	-2.879	-4.802
% Herbaceous						
Fire	-0.012	0.065	-0.190	0.850	-0.012	-0.006
Native Habitat	0.951	0.054	17.775	0.000	0.951	0.691
Abund. Deer	-0.180	0.020	-9.081	0.000	-0.180	-0.335
Wet Season	-0.007	0.031	-0.208	0.835	-0.007	-0.006
Euc. Phase	0.016	0.015	1.064	0.287	0.016	0.033
%Litter Cover						
Fire	-0.262	0.105	-2.489	0.013	-0.262	-0.052
Native Habitat	1.688	0.069	24.397	0.000	1.688	0.538
Wet Season	0.095	0.050	1.888	0.059	0.095	0.039

Euc. Phase	0.864	0.024	36.217	0.000	0.864	0.794
%Bare Soil						
Fire	0.077	0.100	0.765	0.445	0.077	0.013
Native Habitat	-2.495	0.066	-37.899	0.000	-2.495	-0.699
Wet Season	-0.055	0.048	-1.149	0.251	-0.055	-0.020
Euc. Phase	-0.971	0.023	-42.767	0.000	-0.971	-0.785
Native Habitat						
Fire	-7.816	2.358	-3.315	0.001	-7.816	-4.885
Deciduous						
Fire	-0.036	0.069	-0.519	0.603	-0.036	-0.023
Fire						
Native Habitat	6.075	2.350	2.585	0.010	6.075	9.721
Wet Season	0.088	0.121	0.728	0.467	0.088	0.182
Eucalyptus	2.766	1.055	2.623	0.009	2.766	5.626
Deciduous	-2.869	1.083	-2.649	0.008	-2.869	-4.382
Abund. Deer						
Fire	-2.606	8.142	-0.320	0.749	-2.606	-0.637
Native Habitat	-6.679	23.110	-0.289	0.773	-6.679	-2.611
Wet Season	1.762	5.049	0.349	0.727	1.762	0.894
%Shrubs	-37.140	102.923	-0.361	0.718	-37.140	-25.114
Eucalyptus	-24.715	68.484	-0.361	0.718	-24.715	-12.283
Deciduous	-1.879	5.813	-0.323	0.746	-1.879	-0.701
Euc. Phase	8.989	24.696	0.364	0.716	8.989	10.136
Abund. Carn						
Fire	0.528	0.130	4.067	0.000	0.528	0.132
Native Habitat	0.599	0.116	5.174	0.000	0.599	0.239
Wet Season	0.292	0.062	4.735	0.000	0.292	0.152
%Shrubs	0.267	0.051	5.280	0.000	0.267	0.185
Eucalyptus	-0.002	0.098	-0.016	0.987	-0.002	-0.001
Deciduous	0.186	0.100	1.865	0.062	0.186	0.071
Euc. Phase	-0.151	0.036	-4.264	0.000	-0.151	-0.175
Abund. Sus						
Fire	0.116	0.108	1.074	0.283	0.116	0.029

Native Habitat	1.586	0.096	16.443	0.000	1.586	0.634
Wet Season	-0.462	0.051	-8.986	0.000	-0.462	-0.240
%Shrubs	0.013	0.042	0.308	0.758	0.013	0.009
Eucalyptus	0.104	0.081	1.271	0.204	0.104	0.053
Deciduous	0.024	0.083	0.284	0.776	0.024	0.009
Euc. Phase	0.005	0.030	0.169	0.866	0.005	0.006