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Eucalyptus plantations alter spatiotemporal relationships of wild ungulates

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Abstract

Eucalyptus plantations, the second most economically important exotic tree in Europe, cover *circa* 1,5 million hectares on this continent. However, little is known about their effect on the ecological patterns of widely distributed and increasing populations of wild ungulates. This lack of knowledge jeopardizes our ability to correctly manage these populations in increasingly ubiquitous exotic forests. We aimed to understand how exotic forestry plantations influence ungulates spatial and temporal dimensions of their niche and determine how the species interactions may be changed by these artificial systems. We used roe deer and red deer as wildlife models, the Portuguese *Eucalyptus* plantation as standards for forestry plantations, and camera-trapping, occupancy modeling, and kernel density estimators as tools to fulfill our goals. *Eucalyptus* plantations had a strong effect on roe deer and red deer spatial behavior when compared to areas dominated by native vegetation. Both species seem to avoid disturbed areas such as agricultural land and *Eucalyptus* plantations. Even when using plantations, they shift their activity to reduce human encounters. Furthermore, plantations are not a homogeneous landcover, and thus distinct production phases of *Eucalyptus* plantations affect species interactions and activity patterns differently. Our results show that the pre-harvesting phases seem to be the more critical period for deer. Thus, production forest managers must guarantee that plantation structure encompasses areas with different tree ages to minimize this effect and fulfill deer's food and cover requirements. Forestry activities should avoid dawn and dusk, to minimize disturbance and to reduce the negative interaction between sympatric guild members, by allowing species to be sparsely distributed (and not clustered in the few undisturbed patches). Plantations should include dispersed native patches to which animals may move in search of food and refuge, therefore creating discontinuities within plantations.

Keywords: Eucalyptus plantations, activity patterns, Deer, Mediterranean, production forests, *Capreolus capreolus*, *Cervus elaphus*.

1. Introduction

The world native forest area has been decreasing, with an average net loss of 4.7 million hectares of forests *per year* between 2010–2020 (FAO and UNEP, 2020). While deforestation is occurring at unprecedented rates in many parts of the world, planted and intensely managed forests have increased by over 105 million hectares since the ’90s and was estimated that in 2015, 20% of the global planted forest area consisted of fast-growing exotic species (Payn et al., 2015). Exotic eucalypts, planted to supply the paper, timber, and wood industry, are one of the tree species most used in plantations because of their fast growth, wide ecological adaptability, and economic profitability (Turnbull, 1999). This fast-growing tree species, native to Australia, is an economically important asset for some regions of the world (Águas et al., 2014), such as Brazil, India, and Europe (Gutiérrez-Poch, 2012; Lima-Toivanen, 2012), whose plantations shaped the landscape. It’s projected that *Eucalyptus* plantations currently cover more than *ca*. 20 million hectares, outside the species’ native range (Forrester and Smith, 2012).

Numerous studies have been piling up in the last decades to assess the impacts of the expanding *Eucalyptus* plantations on biodiversity and ecological processes (Brockerhoff et al., 2013; Teixeira et al., 2020). *Eucalyptus* plantations often induce significant environmental impacts such as soil erosion, hydrological cycle disruption (Madeira *et al.*, 2007), biodiversity loss and landscape changes (da Silva *et al.*, 2019), although the management system of plantations has important effects on the magnitude of such impacts (Teixeira *et al.*, 2017). In fact, several studies demonstrate that *Eucalyptus* plantations show lower species diversity of plants (Proença et al., 2010), birds (Proença et al., 2010), and mammals (Ramírez and Simonetti, 2011) when compared to native forests (da Silva *et al.*, 2019). However, not all mammal groups have been equally studied and thus this pattern cannot be empirically generalized. For example, small mammals and carnivores have far more studies assessing their ecological adaptations and challenges in these altered areas (e.g., Teixeira et al., 2017, 2020), than other groups, like ungulates. But the fast-paced changes induced by exotic *Eucalyptus* plantations expansion, linked to an increase in human demand for paper and wood, makes it urgent to understand their ecological impact on native mammals, particularly herbivores, who use forests as food and cover providers (Ramírez and Simonetti, 2011).

Eighty percent of European *Eucalyptus* plantations occur in the Iberian Peninsula (Cerasoli et al., 2016), and in Portugal it corresponds to 26% of all forested areas (ICNF, 2019). The expansion of *Eucalyptus* plantations in the country was mostly exacerbated by the abandonment of traditional agricultural practices, a consequence of rural exodus (Bignal and McCracken, 2000). This exodus did not only benefit *Eucalyptus* plantations, but also some mammal species, such as red deer (*Cervus elaphus* Linnaeus, 1758) and roe deer (*Capreolus capreolus* Linnaeus, 1758) (Carvalho et al., 2018), which are now widely distributed nationwide. To face this drastic landscape transformation, these species will have to adapt to the novel habitats, but to our knowledge, no studies have assessed the effect of the exotic *Eucalyptus* plantations on deer space use, activity patterns, and interspecies interaction. Roe deer and red deer are ecologically flexible species and extensively overlap their geographical ranges (Carvalho et al., 2018), co-existing in the same environments (Torres et al., 2012). The coexistence patterns and their consequences for both species have been the target of several studies, but there is no consensus as to the dynamics of their interaction. In central and western Europe, some studies point out that larger deer species can displace roe deer (Ferretti et al., 2008; Latham et al., 1999). However, Borkowski and Ukalska (2008) did not find evidence of such competition or interference. For north-eastern Portugal, Torres et al. (2012) suggested that in a Mediterranean environment the interspecific interference between these two species is asymmetrical as roe deer seems to be negatively affected by red deer presence, while the opposite cannot be confirmed. However, no information is available on how the establishment of a novel environment (*i.e., Eucalyptus* forestry plantations) can shape the temporal and spatial pattern of those co-occurring mammals and determine their interactions.

To fill this caveat, this study aims to investigate how exotic forestry plantations influence ungulates spatial and temporal dimensions of their niche and determine how these species interactions may be changed by these artificial systems. By using roe and red deer as wildlife models and the Portuguese *Eucalyptus* plantation as standards for forestry plantations we expect that: a) the occupancy pattern of both species is negatively influenced by the *Eucalyptus* plantations due to higher anthropogenic disturbance (Cruz et al., 2015), lower resources availability (*e.g.*, food; Teixeira et al., 2017), higher structural and/or compositional homogeneity of plantations (Carrilho et al., 2017) (Hypothesis 1 to 4; see Table 1 for all the details and reasoning of the tested hypothesis linked to each species spatial occupancy patterns); b) in *Eucalyptus* plantations both species will show higher temporal overlap patterns, since the higher anthropic disturbance typical of this environment (Timo et al., 2015) will induce species to concentrate their activity in the period where humans are absent from plantations; and c) the presence of red deer negatively influences the probability of roe deer occurrence, because red deer presents a higher body size that can displace roe deer through direct competition (Ferretti et al., 2008; *e.g.,* overlapping dietary niches; Storms et al., 2008), which would cause spatial segregation between both ungulates (Richard et al., 2010; Torres et al., 2012).

2. Material and methods

2.1 Study area

Our study was carried out in central Portugal, in eight different study areas (Figure 1). These study areas were grouped in two regions - western and eastern - each one with four study areas: three located within *Eucalyptus* plantations (all with different harvesting phases present, from early plantation to pre-harvesting stands) and one located in a control zone, dominated by native vegetation (*e.g.*, oak or conifer forests). Each study area comprised an area of 20 km^2 and was distant 10 km from the nearest one.

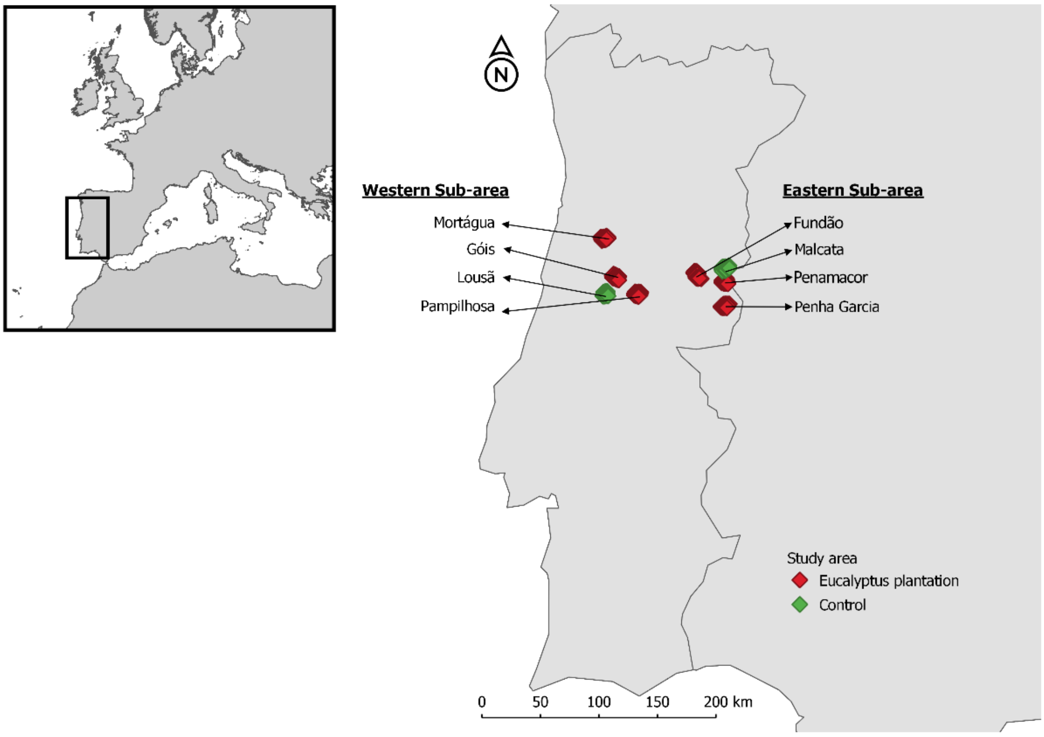

Figure 1 – Location of the eight study areas in Portugal, divided into two regions: western and eastern. Study areas within Eucalyptus plantations are colored in red and the control areas are in green.

Both regions have a Mediterranean climate, characterized by hot and dry summers and cold and wet winters, with a mean annual temperature and mean annual rainfall reaching 16ºC and 750mm, respectively (data from the Portuguese Institute for Sea and Atmosphere – IPMA – collected from 1971 to 2000). Although some variations can be observed between the eastern and western regions' flora composition, both landscapes are globally dominated by *Eucalyptus globulus* Labill. and *Pinus* spp. plantations, with interspersed native woodlands, mainly composed of oak woodlands (*e.g., Quercus robur* L. and *Quercus suber* L.) and Mediterranean shrublands dominated by strawberry tree shrublands (*Arbutus unedo* L.) and *Cistus ladanifer* L. *Eucalyptus* plantations are temporally heterogeneous (Table S1) Several production stages in plantations can be identified, from the seedling establishment to full-grown tree, prior to harvesting (Table S2; Figure S1), which succeed each other in time, over 9-12 years harvesting cycles.

2.2 Study design

In each study area, 25 camera traps (Cuddeback 20 Megapixel IR H-1453 white series) were set, based on a 1 km grid (Figure S2), to ensure camera site independence, thus decreasing the possibility of detecting the same individual in multiple sites (Rovero and Zimmermann, 2016). The cameras were active 24 hours a day for 30 consecutive days (30 trap-nights), *per* sampling period. No bait was used, and four survey periods were considered: February-May and June-September of 2019, and January-May and July-September of 2020, corresponding to the wet and dry seasons of each year, respectively. Cameras were set at 40-60 cm from the ground, attached to trees or, when trees were absent or could not provide stable support for the camera, to wooden stakes (Figure S3). Cameras were set to take three photos at each detection, with a 30-seconds time interval between any subsequent detection event.

2.3 Candidate drivers of landscape use patterns

2.3.1 Field collected data

While setting up the camera traps in the field, we collected *in situ* environmental data at a microscale. We defined a 100 m radius buffer around each camera trap, where data was collected. To test our hypotheses, we selected predictor variables within that buffer, known to influence the species' distribution range: a) type of habitat where the camera was set; b) percentage of the ground surface covered by tree, shrub, herbaceous, rocky soil, and exotic species; c) shrub vegetation mean height; d) number of landscape units; e) dominant *Eucalyptus* harvesting phase; and f) presence of watercourses (see Table 1 for the variable's rationale). The habitat type and the *Eucalyptus* harvesting phase were observed at the site where the cameras were installed and the entire 100m buffer was surveyed to detect the presence of any watercourse and register the number of different landscape units. The percentage of cover of each type of vegetation was visually estimated by applying a mapping method (Baker, 2001), where we draw the boundaries of each vegetation type and estimate the overall percentage of cover, by assigning each vegetation type to one category [1 (0%); 2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]. In each area dominated by shrub vegetation, we visually estimated the mean height by assigning the height dominant category [1 (<0.5m); 2 (0.5m-1.5m); 3 (>1.5m)].

We also registered the season (*i.e.*, dry or wet season), when the sampling was implemented. The 100m radius was defined to encompass the core-area of the smallest species (roe deer; core-area in Mediterranean areas = ±2ha; Cimino and Lovari, 2003), and allow researchers to visually estimate vegetation cover accurately, as well as assess the other micro-habitat variables within the buffer, in both open and closed environments. This characterization was done by the same persons minimizing inter-observer variations.

2.3.2 Remotely collected data

We included in our set of spatial drivers' covariates collected remotely using a GIS, produced with the software QGIS (QGIS Development Team, 2016). We measured the distance to the nearest artificial land, agricultural patch, unpaved roads, and paved roads (Table 1 and Table S3). We also defined a buffer with a 200 m radius around each camera trap to estimate the number of different habitat types present, the habitat's Shannon-Wiener diversity index, and the density of habitat edges (Table 1 and Table S3). The 200m radius (buffer's area *ca*. 12 ha) was defined based on the median size of the roe deer's home range (the small cervid targeted), which is around 10 ha (Melis et al., 2005; Torres et al., 2011). Previous studies have identified the roe deer and red deer preferred habitats within Mediterranean landscapes (Alves et al. 2014; Torres et al., 2011; Torres et al., 2012; Torres et al., 2014;). Therefore, to uncover if those patterns of habitat selection were also applicable to the monitored populations, two extra variables were considered, and estimated within the 200m buffer: proportion of roe deer [conifer forests and Pyrenean oak forests; (Torres et al., 2011; Virgós and Tellería, 1998)] and red deer's preferred habitat [shrublands; (Alves et al., 2014; Torres et al., 2014)] (Table 1 and Table S3).

Table 1 – Variables used in the single-species occupancy modeling procedure (as candidate drivers of occupancy), grouped by working hypothesis. The acronym and the underlying rationale used for each selection are presented.

Variables (acronym)	**Rationale**
H1 - Anthropogenic disturbance	
Distance (m) from the camera to the nearest artificial land (*e.g.,* settlements, houses) - Dist_artificial	Anthropogenic disturbances may alter animals' behaviour and activity patterns (Reimoser, 2012). Human activity associated with infrastructures (*e.g.*, settlements, houses) and to unpaved and paved (that represent different levels of disturbance and collision risks that can result in mortality hazards (Torres *et al.*, 2014). are major disturbance factors (Hewison et al., 2001) that may affect deer.
Distance (m) from the camera to the nearest road: paved (Dist_paved) and unpaved (Dist_unpaved)	
H2 – Food and Water resources	
Distance (m) from the camera to the nearest agricultural land (Dist_agricultural)	Agricultural land patches can provide food for deer all year round (Putman, 1986; Szemethy et al., 2003). Food and water are basic survival resources, and their availability may change throughout the annual cycle. The Mediterranean summer is hot and dry. During summer both plants and animals have little water available (which influences food availability). Herbivores, such as roe and red deer, must feed on plants that can withstand such hydric stress or that exist in spaces where water is available (Storms et al., 2008).
Presence of watercourse within a 100m buffer around cameras (Watercourse)	
H3 - Habitat composition	
Main habitat of camera site (Habitat)	Roe and red deer habitat selection may not be dependent solely on food availability. Other characteristics like cover can be relevant for protection against adverse weather conditions and predatory and hunting pressures (Mysterud and Østbye, 1999). Thus, habitat composition (e.g., habitat type, specific habitats that are known to be preferred by roe and red deer; Alves et al., 2014; Torres et al., 2014; Virgós and Tellería, 1998) and structure (Eucalyptus, tree, shrub, herbaceous cover, and shrub vegetation height) may affect deer occupancy patterns.
Percentage of area covered by vegetation strata within a 100m buffer (Exotic; Tree_cover; Shrub_cover; Herbaceous_cover)	
Shrub vegetation mean height within a 100m buffer (Shrub_height)	
Proportion of roe deer preferred habitat (conifer forests and Pyrenean oak forests) in a 200m buffer (Pref_roe_hab)	
Proportion of red deer preferred habitat (shrublands) in a 200m buffer (Pref_red_hab)	
H4 - Habitat Heterogeneity	
Number of different habitats observed within a 200 m radius (Heterogeneity_200)	Heterogeneous landscapes are known to positively influence deer spatial behavior by reducing individuals' home range (Kie et al., 2002), which increases the site-occupancy probability. It also increases the number of habitats and of edges (open-close), and therefore ecotones, that may provide different resources available in distinct periods, but also various disturbance degrees.
Habitat's Shannon-Wiener index within 200m buffer (Shannon)	
Density of habitat edge in a 200m buffer (m/m^2) (Edge_density)	
Number of different habitats observed within a 100m buffer (Heterogeneity_100)	

2.4 Statistical analysis

2.4.1 Data manipulation

To ensure temporal independence between each species detection, we only included photos that were separated by a minimum time interval of 30 minutes from a previous detection of the same species. All the detections of each target species were grouped into 5 days occasions. In each of these 5 days' occasions groups, we register if the targeted species was detected (1) or non-detected (0). Data manipulation was conducted using R Statistical Software (R Core Team, 2020) using the packages "camtrapR" (Niedballa et al., 2016).

2.4.2 Single-species occupancy modelling

Sampling sites were treated as pseudoreplicates because multi-season occupancy models are overparameterized and we had no interest in local colonization or extinction probabilities (Hines et al., 2014). Therefore, our sampling points were organized in a camera*season combination. Occupancy models were built using single-season occupancy models (MacKenzie et al., 2002). Species occupancy was estimated under a maximum likelihood-based approach, accounting for imperfect detection. For the occupancy model analysis, we grouped the candidate environmental covariates in the four occupancy hypotheses defined previously, linked to different mechanistic processed that may shape occupancy patterns of both species: (1) anthropogenic disturbance; (2) food and water resources; (3) habitat composition; and (4) habitat heterogeneity (see Table 1). For each hypothesis, all the covariates were tested for collinearity by calculating the Variance Inflation Factors (VIF) (Zuur et al., 2009). Variables were considered collinear if VIF > 3 (Zuur et al., 2009) and were excluded. First, we tested what variables were deemed more relevant to influence animals' detection. We built a group of candidate models in which the detection probability varied as a function of four environmental covariates (tree cover, shrub cover, shrub vegetation mean height, and season) while maintaining the occupancy constant (MacKenzie et al., 2006). We produced models corresponding to all the possible combinations of the four candidate covariates that may influence detectability. All produced models were ranked by their Akaike Information Criterion, corrected for small samples (AICc) (Burnham and

Anderson, 2002), and the one that reached a lower AICc value was considered that most fit to explain detectability variations. Then, we produced occupancy models for all the hypotheses, by including: 1) in the detectability section of the model the variable(s) identified as influential for detectability in the previous modelling phase, and; 2) in the occupancy section those covariates grouped in each hypothesis. For each hypothesis, we produced models corresponding to all combinations of the candidate variable and selected the top-ranked model (*i.e.* lowest AICc and with a ΔAICc=0) as the best model for each hypothesis (Burnham and Anderson, 2002). The effects of covariates on detection and occupancy probability were treated as well-supported when the 95% unconditional Confidence Interval (CI) of averaged β estimates did not include zero (MacKenzie et al., 2017). Well-supported covariates that were included in the top-ranked models of each hypothesis (H1-H4) were used as candidate covariates to test a fifth hypothesis (named "combined"), whose reasoning was to understand if the combination of variables linked to distinct mechanistic processes would better explain the occupancy probability variation for our model species. These combined hypothesis models were built using the strategy described earlier. The model with the lowest AICc among all the hypotheses, for each species, was deemed the best overall model and therefore, the more supported hypothesis. The goodness of fit of the best model was tested using Pearson's chi-square, and the overdispersion parameter ($\hat{c}$) was estimated using 500 bootstrap samples (Mackenzie and Bailey, 2004). For the species best models with $\hat{c} > 1$ (*i.e.*, with an important overdispersion; Mackenzie and Bailey, 2004), we reanalyzed the data and used a quasi-likelihood approach in model selection, quasi-AICc (QAICc), a commonly used approach to modelling overdispersed data (MacKenzie et al., 2006). The $\hat{c}$ used in this procedure was estimated for the global model, with 500 bootstrap samples (Mackenzie and Bailey, 2004). Then we repeated the model's selection process but using QAICc instead of AICc. The final bet model selected was the overall top-ranked model of all the hypotheses.

Data analysis was conducted using R Statistical Software (R Core Team, 2020) using the packages "unmarked" (Fiske and Chandler, 2011), "MuMIn" (Barton, 2020), and "AICcmodavg" (Mazerolle, 2020).

2.4.3 Activity pattern

The independent detection records for each target species were regarded as a random sample, assuming an underlying continuous temporal distribution, meaning that an animal is equally likely to be photographed when the cameras are active. The probability density function was estimated nonparametrically using a kernel density estimator (Ridout and Linkie, 2009). The time data was converted from local to solar time, to standardize the temporal data. After correction, the time was scaled into a 0-1 range and then transformed into radians (time*2π). Then, to visualize the daily activity patterns of *C. capreolus* and *C. elaphus,* we created probability density function plots for the global data set, but also for different subsets of our data to uncover pattern variation between locations (*i.e.,* native vegetation and *Eucalyptus* plantation areas) and season. Comparisons between activity patterns estimations were made by estimating the coefficient of overlap Δ_4 (Linkie and Ridout, 2011), which is recommended for relatively large sample sizes (Ridout and Linkie, 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap). The precision of this estimator was achieved by computing a standard deviation from 999 bootstrap samples (Linkie and Ridout, 2011). The Mardia-Watson-Wheeler's test (W) (Batschelet, 1981) was used to compare the detections' distribution across the diel cycle for all the previous combinations of data between *C. capreolus* and *C. elaphus*.

The activity pattern analysis was conducted using R Statistical Software (R Core Team, 2020) using the packages "circular" (Agostinelli and Lund, 2007), "overlap" (Ridout and Linkie, 2009), and "solaR" (Perpiñán, 2012), "CircStats" (Lund and Agostinelli, 2018) and "suncalc" (Thieurmel and Elmarhraoui, 2019).

2.4.4 Co-occurrence between roe and red deer

Co-occurrence patterns between roe deer and red deer were based on a conditional two-species occupancy model, composed of a hierarchical tree of conditional occupancy and detection probabilities, where species A is established to be dominant and species B subordinate (Richmond et al., 2010). The model provides the unconditional probability of species A occupancy (ψ^{A}), the conditional probability of occupancy of species B when species A is present (ψ^{BA}) and the conditional probability of occupancy of species B when species A is absent (ψ^{Ba}). Furthermore, it also estimates the probability of dominant species being detected when the subordinate species is present (r^{A}), the probability of dominant species being detected when the subordinate species is absent (p^{A}), the probability of subordinate species being detected when the dominant species is not present (p^{B}), the probability of subordinate species being detected when the dominant species is present and detected (r^{BA}) and the probability of subordinate species being detected when the dominant species is present, but not detected (r^{Ba}) (Richmond et al., 2010). We also estimated the Species Interaction Factor (SIF), which is a metric that allows us to infer if the species are avoiding themselves or co-occurring. The SIF was calculated using the following formula from Nagy-Reis et al. (2017):

$$SIF = \frac{\mathrm{r}^{A}\mathrm{r}^{BA}}{\mathrm{r}^{A}(\mathrm{r}^{A}\mathrm{r}^{BA} + (1 - \mathrm{r}^{A})\mathrm{r}^{Ba})}$$

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

Data analysis was conducted using R Statistical Software (R Core Team, 2020) using the packages “wiqid” (Meredith, 2020).

3 Results

From the projected 800 cameras (25 cameras in each eight study areas, in four seasons), we were only able to install 798 cameras due to a wildfire that prevented the installation of two cameras in the planned grids. Of those installed, only 765 were fully functional during the entire survey period, because 33 had mechanical problems or were stolen. The full survey period comprised 26706 active trap days. Roe deer was detected in seven study areas, with a total of 1476 events, while red deer in six areas, with a total of 576 events. The study site Mortágua was removed from the dataset because neither species occurred in this area.

3.1 Single-species occupancy models

The variables "Habitat" (H3) and "Shannon-Wienner Index" (H4) were removed after being tested for collinearity (VIF > 3). Both roe deer and red deer occupancy patterns were best described by the combined occupancy hypothesis (Tables 3; see Table S4 and S5 for the AICc ranked list of all produced models), highlighting that in our study areas both species' occupancy probabilities are not related with only one set of environmental characteristics (and, therefore, mechanistic process).

Roe deer's best occupancy model (see Table S6) presented a $\hat{c} > 1$, and therefore, as mentioned in methods, we repeated the model selection process, but now using a quasi-likelihood approach (QAICc), with a $\hat{c}$ value of 2.28, obtained from the full model, without the correlated variables. In these new model sets, roe deer detectability was negatively influenced by shrub vegetation mean height higher than 1.5 meters (Shrub_height.3) and wet season (Table 2). Occupancy probability was higher in sites with lower habitat edge density, higher heterogeneity of habitat types, within habitats preferred by roe deer, and far away from agricultural land cover (Table 3). A higher percentage of exotic plantations decreased occupancy probability (Table 3).

Table 2 - Average coefficients (Coef) of variables included on roe and red deer top-ranked models for detectability (shaded rows correspond to variables whose coefficients 95% Confidence Intervals (CI 95%) do

not include 0). Variable's acronyms are described in Table 1 (SE – Standard Error; z-value - standard score; Pr (>|z|)– p-value).

Detection (Roe deer)						
Model-averaged coefficients	Coef	SE	z-value	Pr (>|z|)	CI 95%	
Intercept	**-0.634**	**0.087**	**-7.296**	**<0.001**	**-0.804**	**-0.464**
Shrub_height.2	-0.026	0.121	-0.216	0.829	-0.264	0.212
Shrub_height.3	**-0.339**	**0.092**	**-3.703**	**<0.001**	**-0.519**	**-0.160**
Season (wet)	**-0.324**	**0.111**	**-2.917**	**0.004**	**-0.542**	**-0.106**
Detection (Red deer)						
Intercept	**-0.610**	**0.133**	**-4.595**	**<0.001**	**-0.871**	**-0.350**
Shrub_height.2	**-1.271**	**0.182**	**-6.996**	**<0.001**	**-1.627**	**-0.915**
Shrub_height.3	0.072	0.150	0.482	0.630	-0.222	0.366
Tree_cover.3	**-0.631**	**0.280**	**-2.257**	**0.024**	**-1.180**	**-0.083**
Tree_cover.4	-0.085	0.225	-0.376	0.707	-0.525	0.356
Tree_cover.5	-0.203	0.179	-1.138	0.255	-0.553	0.147
Season (wet)	**-0.958**	**0.178**	**-5.367**	**<0.001**	**-1.308**	**-0.608**

Table 3 - Average model of roe and red deer top-ranked occupancy models (shaded rows correspond to variables whose coefficients Confidence Intervals (CI 95%) do not include 0). Acronyms are described in Table 1 (Coef – Coefficients; SE – Standard Error; z-value - standard score; Pr (>|z|)– p-value; CI 95% - Coefficient 95% confident interval).

Occupancy (Roe deer)						
Model-averaged coefficients	Coef	SE	z-value	Pr (>|z|)	CI 95%	
Intercept	-0.017	0.107	-0.159	0.874	-0.227	0.193
Dist_agricultural	**0.480**	**0.128**	**3.756**	**<0.001**	**0.230**	**0.731**
Edge Density	**-0.845**	**0.184**	**-4.591**	**<0.001**	**-1.206**	**-0.485**
Exotic	**-0.496**	**0.129**	**-3.850**	**<0.001**	**-0.748**	**-0.243**
Heterogeneity_200	**0.787**	**0.174**	**4.515**	**<0.001**	**0.445**	**1.129**
Pref_roe_hab	**0.378**	**0.123**	**3.083**	**0.002**	**0.138**	**0.618**
Occupancy (Red deer)						
Intercept	**-1.063**	**0.132**	**-8.050**	**<0.001**	**-1.322**	**-0.804**
Dist_agricultural	**0.350**	**0.141**	**2.480**	**0.013**	**0.073**	**0.627**
Dist_unpaved	-0.277	0.155	-1.790	0.074	-0.581	0.027
Exotic	**-0.555**	**0.116**	**-4.770**	**<0.001**	**-0.784**	**-0.327**

Red deer detectability decreased with shrub vegetation mean height [between 0.5 and 1.5 meters] (Shrub_height.2), tree cover between 26-50% (Tree_cover.3), and wet season (Table 2). Red deer site-occupancy probability occupancy was lower in areas near agricultural lands, as well as in regions with higher *Eucalyptus* plantation cover (Table 3). This best model showed a good model fit (χ^2=204.08; p-value=0.724; ĉ=0.756).

3.2 Roe and red deer diel activity patterns and overlap

Roe deer and red deer showed an overall bimodal activity pattern, with peaks at dawn and dusk, but they were also active throughout the day and night. The activity overlap between these species is quite high (Δ_4=0.870; Table 6), even with different peak activity distributions (W = 22.842; p-value <0.001; Table 6): red deer activity peaks had similar density values (*i.e.*, similar activity levels), while roe deer activity peak at dawn had a much higher density than at dusk (*i.e.*, higher activity levels at dawn; Figure 2).

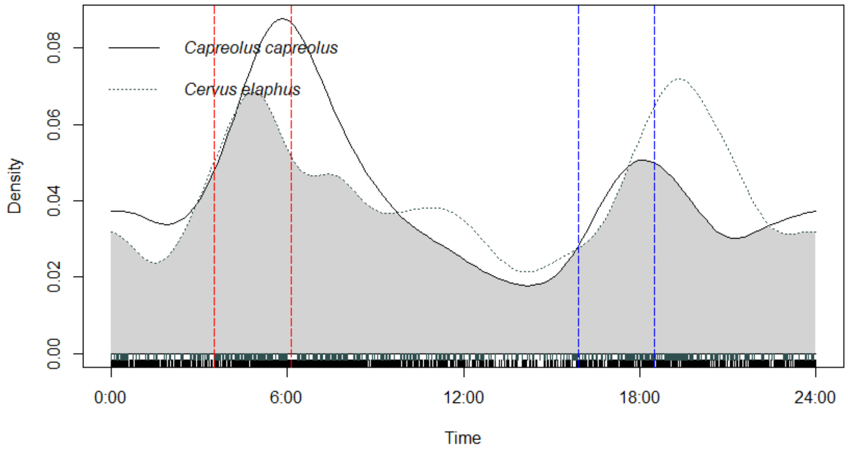

Figure 2 - Overall daily activity patterns and overlap between roe and red deer. Blackline and dotted line represent roe deer and red deer activity densities, respectively. The shaded area is the overlapped activity, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue) periods, throughout the year.

Overlap in *Eucalyptus* plantations was clearly higher (Δ_4=0.949; Table S7), and the Mardia-Watson-

Wheeler test revealed a high match between the daily activity patterns between both deer species (W=0.080, p=0.961; Figure 3a), indicating a similar temporal behavior within *Eucalyptus* plantations. During the wet season, red deer are more active till 12:00, while roe deer decreased sharply its activity just after dawn, a pattern evidenced by both species in the dry season (although this decrease is sharper) (Figure 3c; Table S7). In the dry season, red deer and roe deer seem to reduce activity during daylight hours (Figure 3d; Table S7). In native vegetation areas, both species seem to present distinct activity patterns with red deer showing an activity peak at dusk while roe deer seem to be more active at dawn, a pattern corroborated by the Mardia-Watson-Wheeler test, which detected a heterogeneity in the activity patterns of both species (Figure 3b; Table S7: W = 23.159; p-value <0.001).

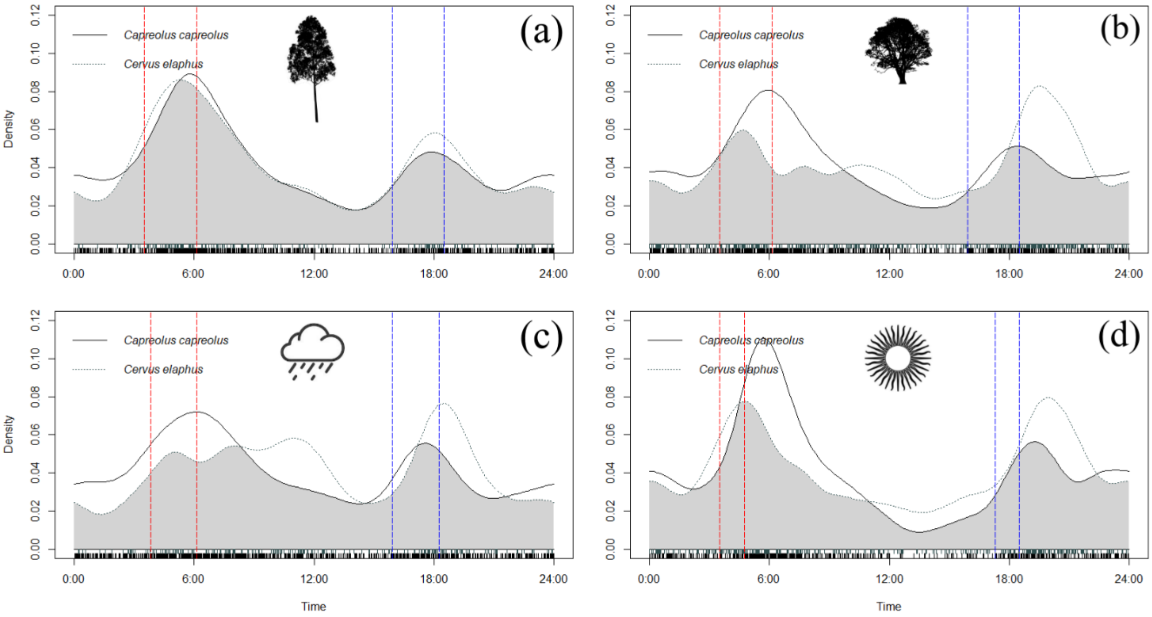

Figure 3 - Daily activity patterns of roe and red deer, and corresponding overlap, for Eucalyptus plantation areas (a), native vegetation areas (b), wet season (c), and dry season (d). Black and dotted lines represent roe deer and red deer activity density patterns, respectively. The shaded area illustrates the overlapped activity period, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue) periods, throughout the year.

We also tested the combined effects of location and season on the activity patterns (Figure 4; Table S7). Red deer in native vegetation areas, during the wet season, maintained higher activity density during daylight hours (Figure 4a), a pattern not adopted in *Eucalyptus* plantation areas nor in the native area in the dry season (Figures 4b and 4d). Inversely, roe deer showed a more constant activity throughout a 24h period in native areas in the wet season, which resulted in a significant lower overlap (Δ_4=0.747; Table S7; Figure 4a), while in the dry season in both area types and in *Eucalyptus* plantations in the wet period, these ungulates seem to be more active at dawn (Figures 4b, 4c and 4d), although the red deer is also more active just after dusk in native areas. Finally, the red deer also seem to concentrate its activity more sharply at dawn in *Eucalyptus* plantation areas during the dry season (Figure 4d), a pattern not evident in the remaining contexts.

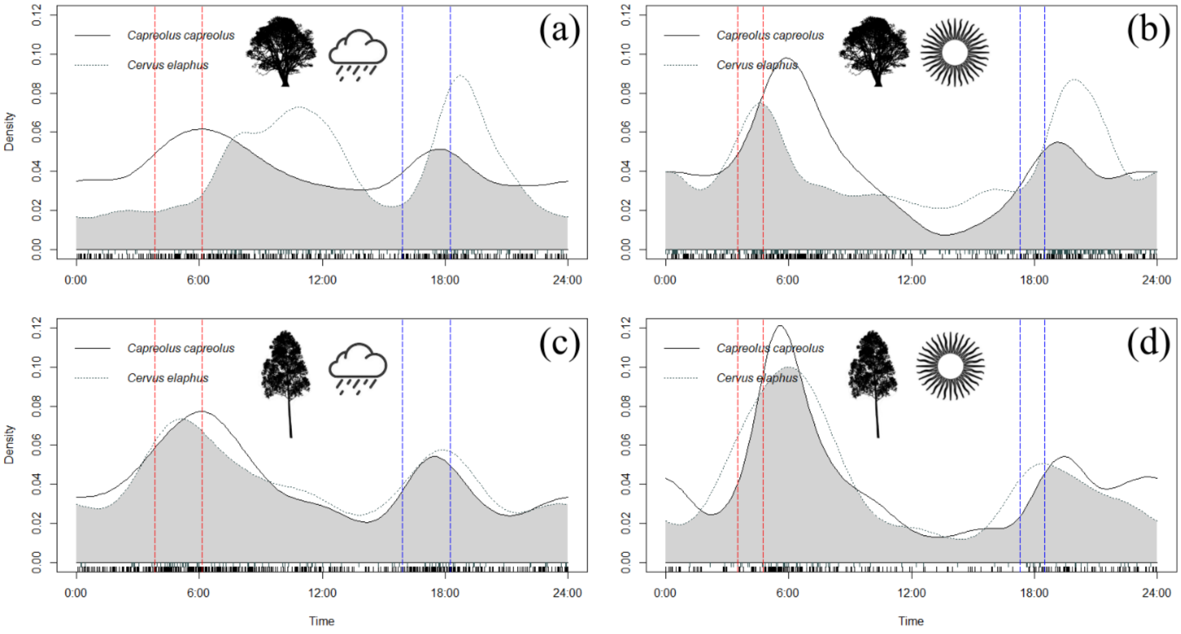

Figure 4 - Daily activity overlap of roe and red deer in native vegetation areas during wet (a) and dry season (b), and in Eucalyptus plantation areas during wet (c) and dry season (d). Black and dotted lines represent roe deer and red deer activity densities patterns, respectively. The shaded area illustrates the overlapped activity period, and the vertical lines mark the beginning and end of dawn (red) and dusk (blue) periods, throughout the year.

3.3 Roe deer and red deer spatial overlap

In our study area, roe deer (B) occupancy probability is generally higher when red deer is present (ψ^{BA}=0.579), although this pattern was not observed for native vegetation sites (Table S8). Roe deer and red deer showed a rather weak overall tendency for aggregation within the study areas (SIF=1.278), demonstrating a low variation between *Eucalyptus* plantations (SIF=1.193) and native areas (SIF=1.259) (Table S8). However, different harvesting phases, within *Eucalyptus* plantations, showed an increasing aggregation tendency towards the older harvesting phase. Although it was not possible to obtain the confidence intervals for the 1st development stage, because data convergence wasn't reached due to the low number of patches on this condition, we were able to estimate the SIF value (SIF=0.954). For the 2nd stage, the estimated SIF value implies a similar aggregation tendency to that of the native areas (SIF=1.250) and the 3rd stage implies a stronger aggregation tendency, reaching the highest value (SIF=1.737; Table S8). Regarding the species detection probability, red deer detectability in the plantation is lower when roe deer is present ($r^A < p^A$), while roe deer's detectability is lower when red deer is absent ($p^B<r^{BA}$; $p^B<r^{Ba}$) (Table S8). For the overall data and native vegetation, the pattern is not as clear.

4. Discussion

Our results show that *Eucalyptus* plantations influence both roe deer and red deer spatial and temporal behavior, and this effect (and its scale) varies between the different harvesting phases of *Eucalyptus* plantations. Consequently, those changes linked to the implementation of plantations also change the patterns of species interactions.

4.1 Roe and red deer occupancy patterns

The occupancy patterns of red and roe deer were mostly driven by a combination of factors with different underlying mechanistic processes (i.e. combined hypothesis). As expected, the multi-origin drivers that affected both species' occupancy were related to human disturbance and habitat structure (habitat composition and habitat heterogeneity), which were already described as drivers for these species in Portugal (Torres et al., 2011, 2014).

Agricultural land can be a food source for roe and red deer (as predicted by H2 – Food and Water resources). However, these areas can also have a high frequency of disturbance due to human presence and machinery activities (*e.g.,* tractors) (Frid and Dill, 2002; Szemethy et al., 2003), which can constrain their use by wildlife. Our results highlight that roe and red deer might tend to view agricultural areas as disturbed areas, to be avoided, and therefore the disturbance effect of these anthropic areas seems to overcome the food opportunities they provide.

Habitat composition is also an influential driver of both deer species populations. Both deer occupancy probabilities are negatively associated with the percentage of exotic plant species land cover, namely *Eucalyptus* plantations. This pattern was somehow expected and corroborates the negative impact of exotic land covers in ungulates, especially if these patches represent exotic plantations (Torres-Porras et al., 2015). Anti-herbivory strategies presented by some exotic species can deter herbivore species, like roe and red deer, from being able to feed on these plants (e.g., terpenes found in *Eucalyptus* leaves; Vavra et al., 2007; Moore et al., 2004). Due to this biological limitation, deer could decrease their occupancy of areas where exotic plant species are dominant, especially if management implies the removal of native vegetation inside plantations. But this habitat seems to provide cover for these species, both from human disturbance, but also of adverse climatic conditions (Mysterud and Østbye, 1999), which from our data seems not to be enough to allow species to use plantations more often.

While red deer populations seemed to be ecologically less demanding, by only being affected by agricultural land and exotic plantations, roe deer occupancy seemed to be also dependent on other landscape composition features. Habitat heterogeneity can be a promoter of cervids occupancy (Kie et al., 2002), namely for roe deer, a relationship that was not observed for red deer, which is a species with a larger home range. As roe deer are considered income breeders (Andersen et al. 1998), they have a browsing feeding pattern and are very selective regarding its food, choosing quality over quantity (Latham et al., 1997). Red deer, on the other hand, can fulfill its nutritional needs with low-quality food, by increasing the quantity of matter ingested (Demment and Van Soest, 1985). As a higher number of habitats (*i.e*., heterogeneity) increases the ecotone zone, roe deer chooses sites with more types of habitats available to be able to select the more nutritious food from various sources available throughout the year cycle (Latham et al., 1999). However, habitat edge density negatively influences roe deer occupancy, which might seem contradictory to the previously described pattern of habitat heterogeneity. However, we think that areas where the borders between different habitats are more sinuous (high interpenetration) are also more fragmented, which enhances the contact area between different habitats, thus facilitating habitat disturbance that reduces their quality (Hargis et al., 1998). In such a context, habitats become less adequate for roe deer. Finally, the positive effect of roe deer's preferred habitat (*i.e.*, conifer forests and Pyrenean oak forests) on occupancy reinforces the ecological importance of these native forests for roe deer as high-quality habitats, demonstrating that the population inhabiting Central Portugal shows similar preference patterns as those found on native Atlantic landscapes with less disturbed habitat cover (Virgós and Tellería, 1998).

4.2 Roe and Red deer activity patterns and overlap

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

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

Dry season affects both species' activity patterns by inducing a reduction of activity during daylight hours (Rivrud et al., 2010), an increase at dawn, or after dusk (red deer in native environments and dry season) – which are the milder periods of the day - and a slight increase at night. These species reduce their activity, by resting during high-temperature daily hours, as a thermal strategy (Mysterud and Østbye, 1995) in low food quality, but high temperatures periods, such as those found in the Mediterranean dry season (Bugalho and Milne, 2003). This strategy seems to optimize feeding periods and thermal regulation energetic costs (Belovsky, 1981).

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

Interestingly, both species' coexistence pattern seems to differ in natural and anthropogenic areas. In northeastern Portugal, red deer has a negative effect on roe deer presence, while roe deer presence had a positive effect on red deer occurrence (Torres et a*l*., 2012). Our results indicate a similar interaction between these species in native vegetation areas since roe deer occupancy probability decreases when red deer is present. However, in *Eucalyptus* plantations, both species tend to aggregate more, as roe deer occupancy is promoted by red deer presence. In plantations, the reduction of available resources, *e.g.*, food and cover, (Hobbs et al., 2003) seems to allow for easing the potential interference between species and to induce the need for these species to co-occur in the sites/patches where resources are locally more abundant. Such resource availability spatial patterns will induce species to use more of those resource-rich patches, leading to a higher overlap of occupation in these environments. Similarly, different harvesting phases of the *Eucalyptus* plantation induce different spatial overlap between deer species, as aggregation between species increases towards the older harvest phase. *Eucalyptus* plantations in the intermediate development stage (stage 2) and pre-cut development stage (stage 3) have structural contrasts, such as leaf structure (James and Bell, 2001), tree canopy height, and cover due to spacing between trees and thinning (Neilsen and Gerrand, 1999). Older

Eucalyptus stands have narrower leaves, higher canopies, and, due to thinning regimes, fewer lateral branches (Ferraz-Filho et al., 2018). Therefore, in pre-cut development stage sites, the cover provided by trees at ground level is scarce, increasing animals' visibility and making them more vulnerable to disturbance. Thus, roe deer and red deer occupancy probabilities are lower in these older stands, and roe deer occupancy probability increases where red deer are present, which means these animals need to share the few sites in the older stands that have better habitat conditions. Contrasting with the pre-cut development stage sites, in intermediate development stage sites red and roe deer showed virtually the same aggregation tendency as in native vegetation areas. This pattern could be linked to the higher cover provided by trees that creates more suitable areas to be exploited by the animals (*i.e.*, more cover), allowing these populations to interact in a similar way to those registered in native vegetation areas. A similar pattern was described in gray brocket deer (*Mazama gouazoubira* Fischer, 1814), where initial, as well as the pre-cutting, phases of the *Eucalyptus*, are largely avoided (Timo et al., 2015) and animals tend to use the few higher cover areas.

5. Conclusions and implications for management

Our study clearly shows that the landscape changes occurring during the last decades (*i.e.* the implantation of exotic tree plantations) are shaping how species use temporally and spatially the current ecosystems, and how co-occurring species interact. However, they also undoubtedly highlight that due to the plantation's structural temporal heterogeneity (Verdade et al., 2014), we cannot assume that plantations have a homogeneous effect on the ecological patterns of species that can use these modified systems (*e.g.*, Timo et al., 2015). Both results have strong impacts on how these anthropic ecosystems should be managed to achieve biodiversity preservation and functionality, while still maintaining economical profitability, thus fulfilling forestry certification goals (Gutierrez-Garzon et al., 2020). Pre-harvesting phases seem to be the more critical period for deer and thus managers must guarantee that plantation structure encompasses areas with different tree ages so animals may take shelter in unharvested stands, while others are subject to higher disturbance levels linked to harvesting. Furthermore, forestry activities should avoid dawn and dusk, to minimize disturbance. Finally, to minimize negative interaction between sympatric guild members, by allowing species to be sparsely distributed (and not clustered in the few undisturbed patches), plantation should include dispersed native patches to which animals may move in search of food and refuge, creating discontinuities within plantations.

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SUPPLEMENTARY INFORMATION
for

Eucalyptus plantations alter spatiotemporal relationships of wild ungulates

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This PDF file includes:

Fig. S1 | Eucalyptus stands structure in different development stages.

Fig. S2 | | Example of camera-traps distribution in Penha Garcia study area, showing the 1 km grid to help perceive the distance between each adjacent camera site

Fig. S3 | Example of camera traps

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Tables S8 | Occupancy probability of dominant species (ψ^{A}), *C. elaphus*, of *C. capreolus* when red deer is absent (ψ^{Ba}) or present (ψ^{BA}), detection probability of *C. elaphus* when the subordinate species is absent (p^{A}), detection probability of *C. capreolus* when dominant species is absent (p^{B}), probability of dominant species being detected when the subordinate species is present (r^{A}), probability of subordinate species being detected when the dominant species is present but not detected (r^{Ba}), probability of subordinate species being detected when the dominant species is present and detected (r^{BA}), and Species Interaction Factor (SIF) value for each subset of our data

Supplementary Figures

Fig. S1 | Eucalyptus stands structure in different development stages. Initial development stage on the left, intermediate on the center and pre-harvesting stage on the right.

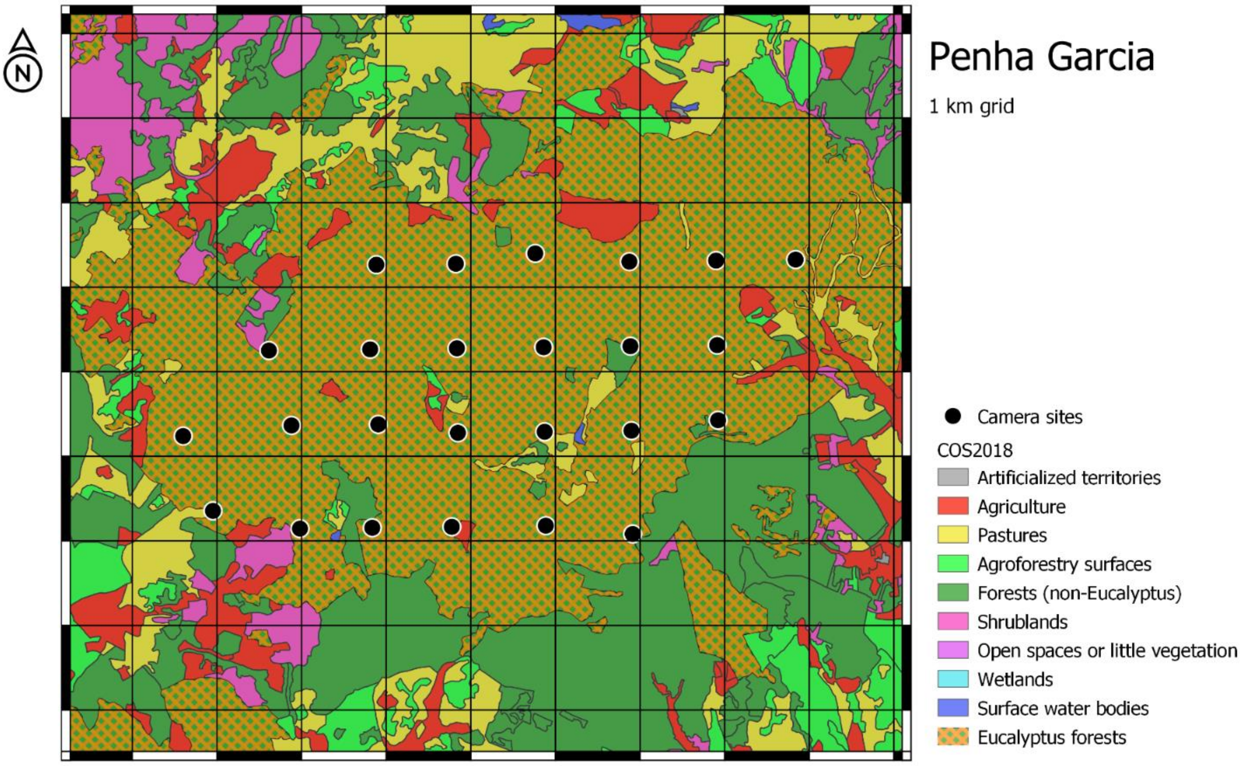

Fig. S2 | Example of camera-traps distribution in Penha Garcia study area, showing the 1 km grid to help perceive the distance between each adjacent camera site. The camera sites are represented by black dots. The land cover, extracted from COS2018 (DGT, 2018), is represented by the coloured areas indicated in the legend.

Fig. S3 | Example of camera traps attached to a tree (left) and to a wooden stake (right).

Supplementary Tables

Table S1 | Percentage of each land cover per study area.

		Native mixed forests	Eucalyptus plantations	Conifer forests	Shrublands	Native broadleaf forests	Mosaic
Eastern	Penamacor	3%	97%				
	Penha Garcia		99%		1%		
	Malcata	2%		92%	3%	3%	
	Fundão		100%				
Western	Góis		96%		1%		3%
	Pampilhosa		100%				
	Lousã	11%		67%	10%	12%	
	Mortágua		100%				

Table S2 | Percentage of cover of each Eucalyptus production stage per plantation study area (1 correspond to a young plantation and 3 to a pre-harvesting stage).

		***Eucalyptus* production stage 1**	***Eucalyptus* production stage 2**	***Eucalyptus* production stage 3**
Eastern	Penamacor	2.06%	90.72%	7.22%
	Penha Garcia	7.07%	82.83%	10.10%
	Fundão	5.10%	83.67%	11.22%
Western	Góis	12.50%	57.29%	30.21%
	Pampilhosa	23.00%	77.00%	
	Mortágua	5.00%	78.00%	17.00%

Table S3 | Variables used in the single-species occupancy modeling procedure (as candidate drivers of occupancy), grouped by working hypothesis. The acronym, description, range, expected influence, and data source are presented.

Variable acronym	Description	Mean [range]	Expected Influence	Data Source
H1 - Anthropogenic disturbance				
Dist_artificial	Distance (m) from the camera to the nearest artificial land (*e.g.*, settlements, houses)	1979 [93-5947]	+	COS2018 (DGT, 2018)
Dist_unpaved	Distance (m) from the camera to the nearest road (paved and unpaved)	126.5 [0-1020]	+	OpenStreetMap Data Extracts (OSM, n.d.)
Dist_paved		1144 [4-4928]	+	
H2 – Food and Water resources				
Dist_agricultural	Distance (m) from the camera to the nearest agricultural land	985.6 [0-4216]	-	COS2018 (DGT, 2018)
Watercourse	Presence of watercourse within a 100m buffer around cameras	Binary [0-absent; 1-present]	+	Field Observation
H3 - Habitat composition				
Habitat	Main habitat of camera site	Nominal [*Eucalyptus* plantations; Conifer forests; Mosaic; Native broadleaf forests; Native mixed forests; Shrublands]	*Eucalyptus* plantations will have a negative influence (-)	Field Observation
Exotic	Percentage of area covered within a 100m buffer	63.36 [0-100]	-	
Tree_cover		Categorical ordinal [1 (0%); 2 (1%-25%); 3 (26%-50%); 4 (51%-75%); 5 (76%-100%)]	+	
Shrub_cover			+	
Herbaceous_cover			+	
Shrub_height	Shrub vegetation mean height within a 100m buffer	Categorical ordinal [1 (<0.5m); 2 (0.5m-1.5m); 3 (>1.5m)]	+	
Pref_roe_hab	Proportion of roe deer preferred habitat (conifer forests and	0.244 [0-0.986]	+ (for roe deer)	COS2018 (DGT, 2018)

	Pyrenean oak forests) in a 200m buffer			
Pref_red_hab	Proportion of red deer preferred habitat (shrublands) in a 200m buffer	0.058 [0-0.881]	**+ (**for red deer)	
H4 - Habitat Heterogeneity				
Heterogeneity_200	Number of different habitats observed within a 200 m radius	2.278 [1-7]	+	COS2018 (DGT, 2018)
Shannon	Habitat’s Shannon-Wiener index within 200m buffer	0.447 [0-1.511]	+	
Edge_density	Density of habitat edge in a 200m buffer (m/m^2)	0.004 [0-0.015]	+	
Heterogeneity_100	Number of different habitats observed within a 100m buffer	1.945 [1-5]	+	Field Observation

Table S4 | Roe deer occupancy models ranked by AICc value for each hypothesis. Model's variables are linked to occupancy (ψ) and detection (p). Only models that fulfilled the criterion ΔAICc <2, per hypothesis, are presented (AICc – Akaike Information Criterion corrected for small samples; ΔAICc – difference between the lowest AICc in the set and the models; Akaike Weight – probability of each model being the best among the set of generated models; Overall ΔAICc – difference between the lowest AICc and the models).

Hypothesis	**Model**	**Df**	**AICc**	**ΔAICc**	**Akaike weight**	**Overall ΔAICc**
Null Model	p(.), ψ(.)	2	3227			127,305
Constant Occupancy Hypothesis *[16 models]*	p(Shrub_height + Tree_cover + Season), ψ(.)	8	3204,37	0,000	0,772	104,677
Occupancy Hypothesis 1 (Anthropogenic disturbance) *[64 models]*	p(Shrub_height + Tree_cover + Season), ψ(Dist_paved + Dist_artificial)	10	3152,37	0,000	0,567	52,676
	p(Shrub_height + Tree_cover + Season), ψ(Dist_paved + Dist_artificial + Dist_unpaved)	11	3154,09	1,718	0,240	54,394
Occupancy Hypothesis 2 (Food and water resources) *[32 models]*	p(Shrub_height + Tree_cover + Season), ψ(Dist_agricultural)	9	3165,87	0,000	0,432	66,177
	p(Shrub_height + Tree_cover + Season), ψ(Dist_agricultural + Watercourse)	10	3165,89	0,021	0,427	66,198
Occupancy Hypothesis 3 (Habitat composition) *[512 models]*	p(Shrub_height + Tree_cover + Season), ψ(Shrub_height + Shrub_cover + Herbaceous_cover + Exotic + Pref_roe_hab)	20	3127,74	0,000	0,246	28,041
	p(Shrub_height + Tree_cover + Season), ψ(Shrub_height + Herbaceous_cover + Exotic + Pref_roe_hab)	16	3129,19	1,453	0,119	29,493
	p(Shrub_height + Tree_cover + Season), ψ(Shrub_cover + Herbaceous_cover + Exotic + Pref_roe_hab)	18	3129,69	1,957	0,092	29,997
Occupancy Hypothesis 4 (Habitat heterogeneity) *[64 models]*	p(Shrub_height + Tree_cover + Season), ψ(Edge_density + Heterogeneity_200)	10	3197,76	0,000	0,514	98,061
	p(Shrub_height + Tree_cover + Season), ψ(Edge_density + Heterogeneity_200 + Heterogeneity_100)	11	3199,28	1,521	0,240	99,582

Occupancy Combined Hypothesis *[2048 models]*	p(Shrub_height + Tree_cover + Season), ψ(Shrub_cover + Herbaceous_cover + Dist_agricultural + Edge_density + Exotic + Heterogeneity_200 + Pref_roe_hab)	21	3099,7	0,000	0,274	0,000
	p(Shrub_height + Tree_cover + Season), ψ(Herbaceous_cover + Dist_agricultural + Edge_density + Exotic + Heterogeneity_200 + Pref_roe_hab)	17	3099,92	0,228	0,244	0,228

Table S5 | Red deer occupancy models ranked by AICc value for each hypothesis. Model's variables are linked to occupancy (ψ) and detection (p). Only models that fulfilled the criterion ΔAICc <2, per hypothesis, are presented (AICc – Akaike Information Criterion corrected for small samples; ΔAICc – difference between the lowest AICc in the set and the models; Akaike Weight – probability of each model being the best among the set of generated models; Overall ΔAICc – difference between the lowest AICc and the models).

Hypothesis	**Model**	**Df**	**AICc**	**ΔAICc**	**Akaike weight**	**Overall ΔAICc**
Null Model	p(.), ψ(.)	2	1801,611			109,841
Constant Occupancy Hypothesis [16 models]	p(Shrub_height + Tree_cover + Season), ψ(.)	8	1743,609	0,000	0,760	51,839
Occupancy Hypothesis 1 (Anthropogenic disturbance) [64 models]	p(Shrub_height + Tree_cover + Season), ψ(Dist_unpaved)	9	1731,367	0,000	0,335	39,597
	p(Shrub_height + Tree_cover + Season), ψ(Dist_paved + Dist_unpaved)	10	1731,61	0,243	0,297	39,840
	p(Shrub_height + Tree_cover + Season), ψ(Dist_artificial + Dist_unpaved)	10	1732,619	1,252	0,179	40,849
Occupancy Hypothesis 2 (Food and water resources) [32 models]	p(Shrub_height + Tree_cover + Season), ψ(Dist_agricultural + Watercourse)	10	1717,781	0,000	0,561	26,011
	p(Shrub_height + Tree_cover + Season), ψ(Dist_agricultural)	9	1718,372	0,591	0,417	26,602
Occupancy Hypothesis 3 (Habitat composition) [512 models]	p(Shrub_height + Tree_cover + Season), ψ(Exotic)	9	1701,885	0,000	0,363	10,115
	p(Shrub_height + Tree_cover + Season), ψ(Exotic + Pref_red_hab)	10	1703,78	1,895	0,141	12,010
Occupancy Hypothesis 4 (Habitat heterogeneity) [64 models]	p(Shrub_height + Tree_cover + Season), ψ(Edge_density)	9	1743,426	0,000	0,211	51,656
	p(Shrub_height + Tree_cover + Season), ψ(.)	8	1743,609	0,184	0,192	51,839
	p(Shrub_height + Tree_cover + Season), ψ(Heterogeneity_200)	9	1743,752	0,326	0,179	51,982
	p(Shrub_height + Tree_cover + Season), ψ(Heterogeneity_100)	9	1745,154	1,728	0,089	53,384
	p(Shrub_height + Tree_cover + Season), ψ(Edge_density + Heterogeneity_200)	10	1745,373	1,947	0,080	53,603

	p(Shrub_height + Tree_cover + Season), ψ(Edge_density + Heterogeneity_100)	10	1745,42	1,994	0,078	53,650
Occupancy Combined Hypothesis *[8192 models]*	p(Shrub_height + Tree_cover + Season), ψ(Dist_unpaved + Dist_agricultural + Exotic)	11	1691,77	0,000	0,603	0,000
	p(Shrub_height + Tree_cover + Season), ψ(Dist_agricultural + Exotic)	10	1693,4	1,630	0,267	1,630

Table S6 | Roe deer occupancy models ranked by QAICc value estimated by ĉ value of 2,28 for each hypothesis. Model's variables are linked to occupancy (ψ) and detection (p). Only models that fulfilled the criterion ΔQAICc <2, per hypothesis, are presented (QAICc –Akaike Information Criterion corrected for overdispersed count data corrected for small samples; ΔQAICc – difference between the lowest QAICc in the set and the models; Akaike Weight – probability of each model being the best among the set of generated models; Overall ΔQAICc – difference between the lowest QAICc and the models).

Hypothesis	**Model (ĉ=2,28)**	**Df**	**QAICc**	**ΔAICc**	**Akaike weight**	**Overall ΔQAICc**
Null Model	p(.), ψ(.)	2	1419,625			40,656
Constant Occupancy Hypothesis *[16 models]*	p(Shrub_height + Season), ψ(.)	5	1415,955	0,000	0,264	36,986
	p(Shrub_height + Tree_cover + Season), ψ(.)	8	1416,587	0,631	0,192	37,618
	p(Shrub_height + Tree_cover), ψ(.)	7	1417,282	1,327	0,136	38,313
	p(Shrub_height), ψ(.)	4	1417,845	1,890	0,102	38,876
Occupancy Hypothesis 1 (Anthropogenic disturbance) *[32 models]*	p(Shrub_height + Season), ψ(Dist_paved + Dist_artificial)	7	1394,817	0,000	0,326	15,848
	p(Season), ψ(Dist_paved + Dist_artificial)	5	1396,214	1,397	0,162	17,245
	p(Shrub_height), ψ(Dist_paved + Dist_artificial)	6	1396,411	1,594	0,147	17,442
	p(Shrub_height + Season), ψ(Dist_paved + Dist_artificial + Dist_unpaved)	8	1396,765	1,949	0,123	17,796
Occupancy Hypothesis 2 (Food and water resources) *[16 models]*	p(Shrub_height + Season), ψ(Dist_agricultural)	6	1399,845	0,000	0,357	20,876
	p(Shrub_height + Season), ψ(Dist_agricultural + Watercourse)	7	1401,07	1,225	0,194	22,101
Occupancy Hypothesis 3 (Habitat composition) *[256 models]*	p(Shrub_height + Season), ψ(Exotic + Pref_roe_hab)	7	1389,483	0,000	0,185	10,514
	p(Season), ψ(Shrub_height + Exotic + Pref_roe_hab)	7	1390,853	1,370	0,093	11,884
	p(Shrub_height + Season), ψ(Shrub_height + Exotic + Pref_roe_hab)	9	1390,922	1,439	0,090	11,953
	p(Shrub_height), ψ(Exotic + Pref_roe_hab)	6	1391,185	1,701	0,079	12,216
	p(Season), ψ(Exotic + Pref_roe_hab)	5	1391,46	1,977	0,069	12,491
Occupancy Hypothesis 4 (Habitat heterogeneity) *[32 models]*	p(Shrub_height + Season), ψ(Edge_density + Heterogeneity_200)	7	1414,922	0,000	0,167	35,953
	p(Shrub_height + Season), ψ(.)	5	1415,955	1,033	0,099	36,986

	p(Shrub_height), ψ(Edge_density + Heterogeneity_200)	6	1416,77	1,848	0,066	37,801
	p(Season), ψ(Edge_density + Heterogeneity_200)	5	1416,771	1,849	0,066	37,802
	p(Shrub_height + Season), ψ(Edge_density + Heterogeneity_200 + Heterogeneity_100)	8	1416,826	1,904	0,064	37,857
	p(Shrub_height + Season), ψ(Heterogeneity_200)	6	1416,853	1,931	0,063	37,884
Occupancy Combined Hypothesis *[256 models]*	p(Shrub_height + Season), ψ(Dist_agricultural + Exotic + Heterogeneity_200 + Edge_density + Pref_roe_hab)	10	1378,969	0,000	0,238	0,000
	p(Shrub_height), ψ(Dist_agricultural + Exotic + Heterogeneity_200 + Edge_density + Pref_roe_hab)	9	1380,622	1,653	0,104	1,653

Table S7 | Roe and red deer activity overlap, represented by the Δ_4 value, and confidence interval (95%) for each respective subset of our data, and the correspondent Mardia-Watson-Wheeler's W statistic value and p-value for homogeneity in activity.

	Δ_4	**CI 95%**		**W statistic**	**p-value**
Global	0.870	0.832	0.909	22.842	<0.001
Native areas	0.837	0.791	0.884	23.159	<0.001
Plantation areas	0.949	0.902	0.996	0.080	0.961
Wet season	0.836	0.776	0.897	11.690	0.003
Dry season	0.831	0.780	0.882	19.366	<0.001
Native areas during Wet season	0.747	0.668	0.826	12.399	0.002
Native areas during Dry season	0.810	0.748	0.872	20.339	<0.001
Plantation areas during Wet season	0.942	0.880	1.004	0.390	0.823
Plantation areas during Dry season	0.872	0.801	0.943	0.452	0.798

Table S8 | Occupancy probability of dominant species (ψ^A), *C. elaphus*, of *C. capreolus* when red deer is absent (ψ^{Ba}) or present (ψ^{BA}), detection probability of *C. elaphus* when the subordinate species is absent (p^A), detection probability of *C. capreolus* when dominant species is absent (p^B), probability of dominant species being detected when the subordinate species is present (r^A), probability of subordinate species being detected when the dominant species is present but not detected (r^{Ba}), probability of subordinate species being detected when the dominant species is present and detected (r^{BA}), and Species Interaction Factor (SIF) value for each subset of our data.

	ψ^A (95%CI)	**ψ^{Ba} (95%CI)**	**ψ^{BA} (95%CI)**	**p^A (95%CI)**	**p^B (95%CI)**	**r^A (95%CI)**	**r^{Ba} (95%CI)**	**r^{BA} (95%CI)**	**SIF**
All data	0.236	0.445	0.579	0.286	0.333	0.350	0.272	0.409	1.278
	(0.203-0.274)	(0.396-0.494)	(0.479-0.673)	(0.223-0.358)	(0.305-0.363)	(0.300-0.403)	(0.221-0.330)	(0.333-0.489)	
Native vegetation sites	0.418	0.771	0.658	0.467	0.381	0.477	0.236	0.390	1.259
	(0.348-0.490)	(0.667-0.849)	(0.515-0.776)	(0.371-0.566)	(0.336-0.429)	(0.412-0.542)	(0.170-0.319)	(0.305-0.482)	
Plantation sites	0.368	0.484	0.625	0.103	0.078	0.065	0.400	0.483	1.193
	(0.257-0.495)	(0.075-0.916)	(0.441-0.779)	(0.057-0.178)	(0.008-0.472)	(0.040-0.105)	(0.333-0.471)	(0.341-0.629)	
***Euc.* development stage 1 sites**	0.973	0.892	0.322	0.005	0.803	0.074	0.182	0.163	0.954
	(NA-NA)	(NA-NA)	(NA-NA)	(NA-NA)	(NA-NA)	(NA-NA)	(NA-NA)	(NA-NA)	
***Euc.* development stage 2 sites**	0.415	0.999	0.606	0.095	0.034	0.061	0.403	0.512	1.250
	(0.313-0.525)	(0.000-1.000)	(0.436-0.753)	(0.049-0.174)	(0.022-0.054)	(0.043-0.086)	(0.349-0.459)	(0.352-0.669)	
***Euc.* development stage 3 sites**	0.097	0.326	0.592	0.303	0.299	0.165	0.316	0.643	1.737
	(0.030-0.270)	(0.190-0.500)	(0.116-0.941)	(0.087-0.664)	(0.196-0.428)	(0.027-0.589)	(0.084-0.700)	(0.135-0.954)	

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