Propagule pressure and land cover changes as main drivers of red and roe deer expansion in mainland Portugal

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Abstract

Aim: The management of the rapid expansion of wild ungulate populations is a challenging task and a societal priority. Using a progressive database of red (Cervus elaphus) and roe (Capreolus capreolus) deer colonization over the last three decades, we estimate the range expansion rates and the underlying mechanisms involved in the expansion patterns of red and roe deer populations at the south-western edge of its European distribution.

Location: Mainland Portugal.

Methods: We compiled and grouped historical red and roe deer distribution data in three time periods (1981–1990, 1991–2000 and 2001–2010). We used generalized linear mixed models to evaluate how biotic and abiotic drivers determine the expansion patterns of red and roe deer.

Results: We reported a significant expansion of red and roe deer populations during the last three decades. The significant interaction between propagule pressure and land cover suggests that the effects of propagule pressure vary along environmental gradients. We found that the influence of livestock on red and roe deer expansion is idiosyncratic. Contrary to red deer, roe deer expansion was also influenced by climatic conditions. We did not detect any significant effect of human factors on the red and roe deer expansion.

Main conclusions: The synergistic effects between variables should be taken into account when studying the patterns of species expansion. Our study emphasize that policy makers should consider the spatial, temporal, ecological and societal nuances of species expansion in order to prioritize management measures and to allocate management budgets. Although concerted strategies to curtail species spread should mitigate red and roe deer economic and ecological impacts, these effects can be neutralized by a continuous rural exodus and the consequent forest and shrub encroachment.

Keywords
Anthropogenic disturbance, Capreolus capreolus, Cervus elaphus, interspecific interactions, population dynamics, ungulate expansion
Wild ungulates of the Palearctic realm are experiencing an ongoing increase in their geographical distribution. Particularly, the members of the Cervidae family, such as the red deer (Cervus elaphus) and the roe deer (Capreolus capreolus), are increasingly ubiquitous and abundant in most European countries (Apollonio, Andersen, & Putman, 2010). Various factors have been involved in the demographic burgeoning of these species, such as socioeconomic changes (e.g., rural exodus and abandonment of traditional agricultural practices), re-naturalization of the habitats, re-introduction programs for both conservation and hunting purposes, the ongoing decrease in the number of hunters and the common practice of supplemental feeding, especially in hunting managed areas (e.g., Acevedo et al., 2011; Milner, Van Beest, Schmidt, Brook, & Storaas, 2014; Putman, Apollonio, & Andersen, 2011; Valente, Valente, Fonseca, & Torres, 2017). The decline in number and distribution of large terrestrial carnivores due to human persecution is also frequently referred as an important cause for the rise of wild ungulate populations (Jędrezejewski, Apollonio, Jędrezejewska, & Kojola, 2010). Although the human hunting of wild ungulates could control the population size (see Quirós-Fernández, Marcos, Acevedo, & Gortázar, 2017), this activity is not able to reproduce the indirect effects of natural predation on population dynamics (Ordiz, Bischof, & Swenson, 2013). The expansion of wild ungulates comes with a cost, representing a conservation and management challenge, particularly in areas where no measures are implemented to mitigate the increasing human–wildlife conflicts (Bueno, Barrio, García-González, Alados, & Gómez-García, 2010; Cromsigt et al., 2013; Perea, Girardello, & San Miguel, 2014). The negative impacts of ungulate expansion include, among others, damage to forestry and agriculture, increased involvement in vehicle collisions, dissemination of vectorborne and zoonotic diseases, and deleterious effects on the vegetation structure and dynamics (e.g., Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Gortazar, Acevedo, Ruíz-Fons, & Vicente, 2006; Herruzo & Martínez-Jauregui, 2013). In contrast, the recovery of wild ungulate is of paramount importance in promoting the increase in large carnivore populations, in sustaining their populations and in contributing to reduce human–carnivore conflicts (Chapron et al., 2014). The management of wild ungulate populations is therefore a challenging task and makes the understanding of the forces driving ungulate expansion an urgent scientific and societal priority. While a large body of literature documents recolonization by threatened species (e.g., Mateo-Sánchez, Cushman, & Saura, 2014), less attention has been paid to understanding the recolonization processes of common species, even when they have a high socioeconomic and ecologic relevance, such as the Cervidae family (but see Acevedo et al., 2005).

Following the same trend in Europe, wild ungulates have expanded in Portugal since the end of the twentieth century and are already a source of conflict with landowners (Torres, Miranda, Carvalho, & Fonseca, 2015; Vingada, Fonseca, Cancela, Ferreira, & Eira, 2010). The red and the roe deer are both native to Portugal and are currently the most widespread and abundant cervids in the country. While it was almost facing extinction in Portugal just a century ago, the red deer has registered a significant expansion in recent decades (Vingada et al., 2010). The species is now common and widespread throughout Portugal, with the most representative populations located near border areas with Spain (Salazar, 2009). In turn, roe deer populations have always persisted in a few patches on the north of the Douro River, where its presence was restricted to forested mountain areas (Vingada et al., 2010). In the last four decades, roe deer distribution has also expanded in Portugal (Torres et al., 2015). Despite this population increase, roe deer densities have remained low, particularly when compared to central and northern European populations (Valente, Marques, Fonseca, & Torres, 2016; Valente et al., 2014).

Studies have been conducted to investigate the factors influencing fine scale distribution of red and roe deer populations in Portugal (Alves, Silva, Soares, & Fonseca, 2014; Carvalho, Santos, Torres, Santarém, & Fonseca, 2017; Torres, Santos, & Fonseca, 2014; Torres, Santos, Linnell, & Fonseca, 2011). However, the description of the biotic and abiotic (ecogeographical) drivers promoting species’ expansion is still undetermined, even though this information is pivotal to shift from a reactionary to a proactive approach in order to control the expected impacts, both positive and negative, of red and roe deer expansion. Recent evidence suggests that population abundance and the proximity to the species original range (“propagule pressure,” Simberloff, 2009) create scope for the expansion of wild ungulate populations (Acevedo et al., 2005; Morelle, Fattebert, Mengal, & Lejeune, 2016; Torres, Carvalho, Fonseca, Serrano, & Lopez-Martin, 2016). Interspecific interactions also affect species dispersal processes and, therefore, species’ large-scale distributions (Svenning et al., 2014; Wisz et al., 2013). However, the outcome of these interactions, particularly between red and roe deer, depends on the context (Borkowski & Ukalska, 2008; Latham, Staines, & Gorman, 1997). The interactions between domestic and wild ungulates have attracted attention mainly due to risks associated with the bidirectional transmission of multihost pathogens (Gortazar et al., 2014; Miller, Farnsworth, & Malmberg, 2013); yet, recent works highlight that future research is needed to shed light on how livestock presence and abundance influence the expansion patterns of wild ungulates (see Acevedo, Cassinello, & Gortazar, 2007). The nature, frequency and magnitude of interspecific interactions vary because they are intertwined with dietary overlap, availability of resources and population density (Forsyth & Hickling, 1998; Gebert & Verheyden-Tixier, 2001; Schieltz & Rubenstein, 2016). These factors are partially influenced by structural changes in land cover. Mainland Portugal has a long history of human occupation, but nowadays red and roe deer are exposed to novel conditions arising from the abandonment of the traditional agricultural practices, the loss of landscape multifunctionality due to modern forestry practices (i.e., monocultures) and the development of infrastructure. Despite the noteworthy ability of cervids to occur under different environmental scenarios, studies carried out in Portugal have suggested that red and roe deer avoid agricultural fields (Carvalho et al., 2017; Torres et al., 2011), show a selection
for patches with high shrub cover (Torres et al., 2011, 2014) and tend to occur far from roads and human settlements (Torres et al., 2011). In harsh environments, red and roe deer preferentially occur at low elevation where permanent water sources are found and the carrying capacity of the habitat remains high even during the dry season (San-José, Braza, Aragón, & Delibes, 1997). Therefore, structural changes in land cover, anthropogenic disturbance (e.g., human population density, linear infrastructures), physical barriers (e.g., altimetry, terrain roughness, rivers) and climate may represent important constraints for species movements and expansion (Corlatti, Hackländer, & Frey-Ross, 2009).

In this study, we aimed to estimate the range expansion rates and the underlying mechanisms involved in the expansion patterns of red and roe deer populations in mainland Portugal. Taking advantage of the progressive dates of species colonization over the last three decades, we tested a series of hypotheses regarding how propagule pressure, interspecific interactions, structural changes in land cover, human pressure, topography and climate influenced the colonization sequence of these species at the national scale (Table 1). As our hypotheses are not mutually exclusive, for example relationship between propagule pressure and expansion probability can vary as a function of environmental suitability (Duncan, 2016), we also investigated how the combined effect of these variables influences the expansion of red and roe deer.

2 | METHODS

2.1 | Study area

Our study was carried out in mainland Portugal (Figure 1). Portugal is a complex and heterogeneous territory, with an elevational range between sea level and 1993 m.a.s.l. The country’s topography is characterized by pronounced differences between the north/central regions (high elevations and rough landscapes) and south/coastal regions (plains of low elevation). According to the Köppen–Geiger classification system, mainland Portugal experiences a Mediterranean climate and the north-eastern regions are under Atlantic influences (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006).

2.2 | Distribution data

The historical red and roe deer distribution was compiled from different public and private libraries throughout the country (see Salazar, 2009). We also performed a literature review of relevant studies using search engines such as the ISI Web of Knowledge (https://www.isiknowledge.com/). The information gathered from unpublished internship reports and master theses from Portuguese Universities was used (e.g., Carvalho, 2011, 2013; Salazar, 2009; Santos, 2009). Our bibliographic analysis extends across the whole continental region of Portugal. Several field campaigns were also carried out to update species distribution by means of direct observations and indirect signs. Fieldwork was mainly focused on red and roe deer nuclei and adjacent areas. All the collected information was synthesized and grouped into six periods for red and roe deer (until 1970, 1971–1980, 1981–1990, 1991–2000, 2001–2010 and 2011–2015). Here, we only analysed three time periods (1981–1990, 1991–2000 and 2001–2010) because reliable environmental information is only available from the late 1980s. As the original information referred to parishes, we transformed the presence data into a grid resolution of 10 × 10 km (our territorial units for analytical purposes). We intersected the parishes in which red and roe deer occur with the 10 × 10 km grid and then calculated the parish area for each 10 × 10 km square. The square was denoted as presence whenever overlapped at least 50% of the occupied parishes. The definition of grid resolution was consistent with the mean natal dispersal distance of the studied species (red deer has natal dispersal distances generally lower than 10 km [Jarnemo, 2011; Prévot & Licoppe, 2013], and roe deer has natal dispersal distances of approximately 2–3 km [Wahlström & Liberg, 1995; Gaillard et al., 2008]). All the data were processed in a GIS environment (ESRI, 2011).

2.3 | The predictors

To test our hypotheses, we selected predictor variables known to influence the species’ distribution range (Table 1). We used the number of eight adjacent cells occupied by the species for time t–1 (NCELL) and the presence/absence of red/roe deer species (PRED/PROE) to test the effect of propagule pressure and interspecific interactions on species’ expansion, respectively. The number of domestic ungulates (ruminants, swine and equines) per grid cell was also used to explore the potential effect of interspecific interactions between domestic and wild ungulates in the range expansion patterns of red and roe deer populations. This information was collected from the Instituto Nacional de Estatística (Instituto Nacional de Estatística, 2016) and compiled for three periods (1989, 1999 and 2009). The land use/land cover information was gathered from the Corine Land Cover database (CLC, http://www.eea.europa.eu/data-and-maps/data). CLC database was selected due to its high spatial resolution (250 m), partial temporal coverage of the studied periods and to standardize land cover classification for the three periods (1990, 2000 and 2012). We considered five different classes of vegetation: (1) homogeneous agricultural areas (HMAGR, e.g., arable land, permanent crops and pastures), (2) heterogeneous agricultural areas (HTAGR, e.g., agro-forestry areas), (3) forests (FORES, e.g., broad-leaved, coniferous and mixed forests), (4) shrubs and herbaceous associations (SHBS, e.g., moors, heathland, sclerophyllous vegetation and transitional woodland shrub), and v) open areas (OPEN, e.g., bare rock, natural grassland and sparsely vegetated areas). The percentage of each class was calculated for each territorial unit. To evaluate the influence of landscape structure on red and roe deer expansion, we calculated four landscape indices (patch density, PATCH; edge density, EDGE; aggregation index, AGGREG; and Shannon’s diversity index, SHADI) for the five different land use/land cover classes (HMAGR, HTAGR, FORES, SHBS and OPEN). These classes were selected because HMAGR, HTAGR and SHBS provide food resources, and FORES offers mainly protection,
| Hypothesis                                      | Rationale                                                                 | Prediction                                                                 | Variables                                                                 | Code |
|------------------------------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|------|
| H1 (Propagule pressure)                        | The spread and establishment of an ungulate is more likely to occur in the adjacent areas of the original range (Acevedo et al., 2005) and is influenced by the population size (Torres et al., 2016). | High levels of propagule pressure, that is higher number of cells occupied in the period 𝑡, boosted red and roe deer expansion. | Number of adjacent cells occupied | NCELL^a |
| H2 (Interspecific competition)                 | Strong interactions between wild ungulate species are expected to be more significant only when one or more species reach high densities (Forsyth & Hickling, 1998). | Red and roe deer may coexist without competitively excluding each other because are morphophysiological distinct and are expected to occur at low densities in the front of expansion. | The presence/absence of red/roe deer (binary) | PRED/PROE^a |
| H3 (Structural changes in land cover)          | Domestic and wild ungulates live in sympathy in many rural areas; therefore, they potentially compete for space and resources (Schieltz & Rubenstein, 2016). | As wild ungulates response to livestock depends on several factors such as diet type and body size, we expected that red and roe deer are affected differently by livestock abundance. | Number of domestic ungulates (ruminants, swine and equines) | NDUNG^a |
| H4 (Anthropogenic pressure)                    | Landscape structure and the amount of suitable habitat influence the occurrence (Torres et al., 2011), abundance (Acevedo et al., 2011), movement (Allen, Mannson, Jamero, & Bunnefeld, 2014) and dispersal (Pérez-Espona et al., 2008) of wild ungulates. | Habitats re-naturalization in the last decades favoured the spread of red and roe deer populations into new territories. The influence of land cover is expected to be idiosyncratic. | Homogeneous agricultural areas (%) | HMAGR |
|                                                |                                                                           |                                                                           | Heterogeneous agricultural areas (%) | HTAGR^a |
|                                                |                                                                           |                                                                           | Forest stands (%) | FORESa |
|                                                |                                                                           |                                                                           | Shrub and herbaceous associations (%) | SHBS^a |
|                                                |                                                                           |                                                                           | Open areas (%) | OPEN^a |
|                                                |                                                                           |                                                                           | Patch density (patches/km²) | PATCH |
|                                                |                                                                           |                                                                           | Edge density (m/ha) | EDGE^a |
|                                                |                                                                           |                                                                           | Aggregation index (%) | AGGREG |
|                                                |                                                                           |                                                                           | Shannon's diversity index | SHADI |
| H5 (Natural barriers)                          | Anthropogenic and natural barriers are important constraints for species movements (Corlatti et al., 2009). Water availability may represent a physiological and behavioural constraint for ungulates (Wallach et al., 2007). | Red and roe deer expansion mainly occur along regions with low human pressure. | Human population density (inhab/km²) | HPOP^b |
|                                                |                                                                           |                                                                           | Artificial surfaces (%) | ASUR |
|                                                |                                                                           |                                                                           | Asphalted roads density (km/km²) | ASPHAL^a |
|                                                |                                                                           |                                                                           | Wild Ungulate Land Avoidance Index | WULAI |
| H6 (Climatic conditions)                       | Landscape structure and the amount of suitable habitat influence the occurrence (Torres et al., 2011), abundance (Acevedo et al., 2011), movement (Allen, Mannson, Jamero, & Bunnefeld, 2014) and dispersal (Pérez-Espona et al., 2008) of wild ungulates. | Habitats re-naturalization in the last decades favoured the spread of red and roe deer populations into new territories. The influence of land cover is expected to be idiosyncratic. | Homogeneous agricultural areas (%) | HMAGR |
|                                                |                                                                           |                                                                           | Heterogeneous agricultural areas (%) | HTAGR^a |
|                                                |                                                                           |                                                                           | Forest stands (%) | FORESa |
|                                                |                                                                           |                                                                           | Shrub and herbaceous associations (%) | SHBS^a |
|                                                |                                                                           |                                                                           | Open areas (%) | OPEN^a |
|                                                |                                                                           |                                                                           | Patch density (patches/km²) | PATCH |
|                                                |                                                                           |                                                                           | Edge density (m/ha) | EDGE^a |
|                                                |                                                                           |                                                                           | Aggregation index (%) | AGGREG |
|                                                |                                                                           |                                                                           | Shannon's diversity index | SHADI |
|                                                |                                                                           |                                                                           | Human population density (inhab/km²) | HPOP^b |
|                                                |                                                                           |                                                                           | Artificial surfaces (%) | ASUR |
|                                                |                                                                           |                                                                           | Asphalted roads density (km/km²) | ASPHAL^a |
|                                                |                                                                           |                                                                           | Wild Ungulate Land Avoidance Index | WULAI |
|                                                |                                                                           |                                                                           | Altimetry (m) | ALTIM |
|                                                |                                                                           |                                                                           | Slope (°) | SLOPE |
|                                                |                                                                           |                                                                           | Terrain roughness | TRNESS^a |
|                                                |                                                                           |                                                                           | Stream density (km/km²) | STREAM^a |
|                                                |                                                                           |                                                                           | Mean temperature in spring and summer (°C) | TMEANSS^a |
|                                                |                                                                           |                                                                           | Cumulative rainfall in spring and summer (mm) | PCUMSS^a |

The symbol a indicates the variables included in both red and roe deer models, and the symbol b indicates the variables included in the roe deer model of expansion.
shelter and serve as important ecological corridors for species range expansion. The landscape indices were computed using the software Fragstats 4.2 (McGarigal, Cushman, & Ene, 2012).

To analyse anthropogenic pressure, we used four variables: (1) the human population density (HPOP), collected from the Instituto Nacional de Estatística (Instituto Nacional de Estatística, 2016), (2) the percentage of grid cell occupied by artificial surfaces (ASUR, e.g., urban settlements, construction sites and non-agricultural vegetated areas), compiled from the CLC database, (3) the density of asphalted roads (ASPHAL) per grid cell, compiled from the Centro de Informação Geoespacial do Exército (https://www.igeoe.pt/), and (4) the wild ungulate land avoidance index (WULAI, see Cassinello, Acevedo, & Hortal, 2006). The average altitude (ALTIM) of each sampling cell was recorded, whereas the slope (SLOPE) and the terrain roughness (RNESS) were used as indicators of topographic heterogeneity. These variables were computed from the ASTER Global Digital Elevation Model platform (https://asterweb.jpl.nasa.gov/gdem.asp). The stream density (STREAM) per grid cell was computed from the cartographic information available in Sistema Nacional de Informação de Recursos Hídricos (http://snirh.apambiente.pt/). The mean temperature (TMEANSS) and the cumulative rainfall (PCUMSS) in spring and summer were spatially computed from WorldClim (http://www.worldclim.org/bioclim) at 30 arc-second resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to take into account the climate effects on species range expansion. We used the temperature and rainfall values of April, May, June, July, August and September to perform these calculations. All variables were handled and processed in a GIS environment (ESRI, 2011).
2.4 | Range expansion rates

We calculated the increase in occupied area of red and roe deer populations and the average rate of species expansion. The first was quantified by adding the area of the newly occupied grid cells (10 × 10 km) to the species range at period t (cumulative occupied area). The second was determined by computing the distance between the centroids of colonization front at the period t + 1 and the centroids of the species range at period t (i.e. $t_{1981–1990} - t_{1970–1980}$, $t_{1991–2000} - t_{1981–1990}$, $t_{2001–2010} - t_{1991–2000}$). As the expansion rate varies between nuclei, we performed these calculations per nucleus.

2.5 | Statistical analysis

Before building the statistical models, an exploratory analysis was carried out to assess the properties of our data and the explanatory variables were examined to control for collinearity (Zuur, Ieno, & Elphick, 2010). We started by identifying highly collinear explanatory variables by means of pairwise correlations using Spearman’s rank correlation test. The explanatory variable with lower ecological relevance was dropped whenever a strong correlation was recorded ($r_s > 0.5$; Booth, Niccolucci, & Schuster, 1994). The explanatory variables were split and analysed by hypothesis to avoid flawed comparisons. As anthropogenic processes that influence the amount of available habitat are often the same that lead to landscape fragmentation (Fahrig, 2003), we assigned the predictors of land cover change and landscape structure to the same group. Next, we looked for associations among the explanatory variables using variance inflation factors (VIFs). We assumed no multicollinearity between explanatory variables when all VIF values were below 5 (Rogerson, 2001).

We used generalized linear mixed models (GLMMs; McCullagh & Nelder, 1989) to understand the expansion dynamics of red and roe deer populations in mainland Portugal over the last three decades (1981–1990, 1991–2000 and 2001–2010). GLMMs are particularly useful for analysing hierarchically structured datasets and constitute a flexible approach for quantifying the variation among multiple measured sample units (Bolker et al., 2009). In our study, for each period $t + 1$, newly occupied grid cells in relation to the period $t$ were denoted as 1 (presence data). In turn, unoccupied grid cells in the vicinity of the already colonized area $t$ were denoted as 0 (absence data). Grid cells already colonized in the period $t$ were excluded from the analysis. All explanatory variables were standardized because it improves the convergence of the fitting models and allows an easier comparison of effects sizes (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). As spatial auto-correlation was expected in our data, for example species home range may overlap two or more grid cells, and grid cells were repeatedly considered (“sampled”) in the models until a red and/or roe deer population become established, we considered grid ID as a random factor. Further, as the drivers underlying species range expansion may vary between geographical areas and each population nucleus was represented by a variable number of grid cells, the population nucleus was also included as a random factor. As grid ID and population nucleus are hierarchically structured, that is each 10 × 10 grid was assigned to the respective population nucleus, we implemented the GLMMs with nested random effects. The population nucleus was not considered in roe deer models as a random factor due to insufficient replication ($n = 4$); in this case, it was considered as fixed factor. The temporal structure (three decades) was included as a fixed factor in each model. As intentional releases or reintroduction programs may introduce an unintended bias in our analysis, we added a binary variable in our models to control for the occurrence of these initiatives (0: the presence of the species did not result from a reintroduction program carried out during the study period and 1: the presence of the species resulted from a reintroduction program carried out during the study period). Our models were implemented using a Laplace approximation, to reduce model bias and use of likelihood-based methods for inference. We tested the significance of random factors using the likelihood ratio test (LRT). The GLMM analysis was carried out using the lme4 package in the R software (Bates, Maechler, Bolker, & Walker, 2014). We performed a multiple model comparison using an information-theoretic approach to select the most parsimonious model. This approach was implemented by fitting a series of alternative models per hypothesis and by combining interactively the explanatory variables of each hypothesis (Table 1). The second-order Akaike Information Criterion (AICc; Akaike, 1974) was used as the parsimony criterion. A model is selected over another whenever it reduces the AICc by two units (Burnham & Anderson, 2002). When this criterion was not met, a model averaging approach based on AICc and Akaike weight was applied using the MuMIn package (Barton, 2015). Akaike weights are particularly useful because they allow us to evaluate quantitatively the fitted models and to calculate the relative importance of each variable (Burnham & Anderson, 2002). The amount of variation explained by each mixed model (pseudo-$R^2$) was calculated following the recommendations of Nakagawa and Schielzeth (2013). We calculated the marginal $R^2$ and the conditional $R^2$. The first is associated with model fixed effects, while the second considered the fixed and the random effects.

All statistical analyses were performed using the statistical software R 3.3.0 (R Development Core Team, 2016).

3 | RESULTS

3.1 | Range expansion rates

Overall, we reported a significant expansion of red and roe deer populations during the last three decades, that is red and roe deer currently occupies an area of approximately 14 and 5 times the species range, respectively, in the early 80s (Figure 2). Red and roe deer were spotted in 517 and 1589 parishes, respectively (see Appendix S1), which means that both species occur permanently in one-third of mainland Portugal (Figure 3). The total area of mainland Portugal with a permanent presence of at least one of these two species is 53,300 km$^2$, roughly 60% of the country. Portugal hosts several population nuclei increasingly large and ubiquitous (Figure 3). Although we did not detect a clear geographical pattern on red deer expansion, we reported a slightly southward trend on roe deer spread.
The average rate to which it occurs was, however, contingent on the geographical area and time period. For instance, we recorded a faster roe deer expansion between 1990 and 2000 in the nucleus located along the eastern border with Spain (nucleus 1: 7.3 km/year). Regarding the red deer nucleus, the expansion rate was relatively constant between the three periods but varied between population nuclei (range: 1.0–2.8 km/year). The average expansion rates for red deer were 1.9 km/year during 1980–1990, 1.6 km/year during 1991–2000, and 1.7 km/year during 2001–2010, and for roe deer were 1.1 km/year during 1980–1990, 4.2 km/year during 1991–2000 and 2.7 km/year during 2001–2010.

3.2 | Drivers of range expansion

From the initial set of 22 predictors, we retained 14 variables to explain red deer expansion and 15 variables to explain roe deer expansion. The variables HMAGR, PATCH, AGGREG, SHADI, ASUR, WULAI, ALTIM, SLOPE (for red and roe deer) and HPOP (for roe deer) were excluded due to collinearity. At least one variable per hypothesis was retained (Table 1). For red deer, the most parsimonious model included seven variables and two interaction terms (Table 2). For roe deer, the most parsimonious model included ten variables and one interaction term (Table 3). The models with the lowest AICc resulted from the combination of several variables, which indicates that our hypotheses are not mutually exclusive. The variables representing anthropogenic pressure, natural barriers and climatic conditions did not enter the most parsimonious red deer expansion model. For roe deer, the variable of anthropogenic pressure (ASPHAL) was
excluded from the most parsimonious models. For red deer, the percentage of variance explained by the most parsimonious model was 58.1% (marginal $R^2$) and 63.7% (conditional $R^2$). For roe deer, the percentage of variance explained by the most parsimonious model was 78.3% (marginal $R^2$) and 80.1% (conditional $R^2$). LRT demonstrated that random factors, both grid ID and nucleus, were significant for red deer (LRT between the full and the null model = 4.01, $df = 11$, $p < .05$) and that grid ID was significant for roe deer (LRT between the full and the null model = 0.18, $df = 14$, $p < .05$). Model coefficients indicate that propagule pressure was positively associated with the expansion probability of both red ($\beta_{NCELL} = 1.62$, SE = 0.19, $z = 8.51$, $p < .001$) and roe deer ($\beta_{NCELL} = 3.38$, SE = 1.58, $z = 2.14$, $p < .05$) populations. The presence of roe deer did not enter in the most parsimonious red deer model; however, the presence of red deer was marginally significant for roe deer expansion ($\beta_{PRED} = 2.91$, SE = 1.63, $z = 1.79$, $p = .07$). Contrary to roe deer ($\beta_{CATTLE} = 0.77$, SE = 0.39, $z = 1.94$, $p = .05$), livestock abundance could limit red deer expansion ($\beta_{CATTLE} = -0.27$, SE = 0.17, $z = -1.63$, $p = .10$). The influence of land cover on species’ expansion was supported by our results (see land cover transition maps in the Appendix S2).

### TABLE 2 Parameter estimates for the most parsimonious red deer ($Cervus elaphus$) expansion model

| Hypothesis | Predictor | $\beta$ | Std. error | z-value | p-value |
|------------|-----------|---------|------------|---------|---------|
| –          | Intercept | 0.36    | 0.51       | 0.71    | 0.48    |
| H1         | NCELL     | 1.62    | 0.19       | 8.51    | <0.001  |
| H2         | CATTLE    | -0.27   | 0.17       | -1.63   | 0.10*   |
| H3         | HTAGR     | 0.53    | 0.16       | 3.28    | <0.05   |
|            | FORES     | 0.57    | 0.17       | 3.40    | <0.001  |
|            | SHBS      | -1.28   | 0.59       | -2.18   | <0.05   |
|            | OPEN      | 0.35    | 0.15       | 2.43    | <0.05   |
| –          | PERIOD2000| 0.03    | 0.49       | 0.06    | 0.95$^a$ |
|            | PERIOD2010| -1.95   | 0.55       | -3.53   | <0.001$^a$ |
| H7         | SHBS*PERIOD2000 | 1.51 | 0.60 | 2.51 | <0.05 |
|            | SHBS*PERIOD2010 | 2.43 | 0.64 | 3.80 | <0.001 |
|            | NCELL*FORES | -0.49 | 0.16 | -3.04 | <0.05 |

The effects of variables related to propagule pressure, interspecific competition, land cover changes, period and their interaction were analysed. Significant results are highlighted in bold, and marginal significance is indicated by a superscript "*".

$^a$Please note that the original presence of the red deer in the period 1981–1990 was used as the temporal reference.

### TABLE 3 Parameter estimates for the most parsimonious roe deer ($Capreolus capreolus$) expansion model

| Hypothesis | Predictor | $\beta$ | Std. error | z-value | p-value |
|------------|-----------|---------|------------|---------|---------|
| –          | Intercept | 0.90    | 0.71       | 1.28    | 0.20    |
| H1         | NCELL     | 3.38    | 1.58       | 2.14    | <0.05   |
| H2         | PRED      | 2.91    | 1.63       | 1.79    | 0.07*   |
|            | CATTLE    | 0.77    | 0.39       | 1.94    | 0.05*   |
| H3         | FORES     | -0.25   | 0.30       | -0.84   | 0.40    |
|            | SHBS      | 1.22    | 0.46       | 2.62    | <0.05   |
|            | EDGE      | -0.33   | 0.23       | -1.42   | 0.16    |
| H5         | TRNESS    | -0.50   | 0.32       | -1.57   | 0.12    |
|            | STREAM    | 0.51    | 0.27       | 1.59    | 0.06*   |
| H6         | PCUMSS    | -0.72   | 0.37       | -1.98   | <0.05   |
| –          | PERIOD2000| 0.29    | 0.75       | 0.39    | 0.70$^a$ |
|            | PERIOD2010| 1.08    | 0.83       | 1.30    | 0.20$^a$ |
| H7         | NCELL*PERIOD2000 | -1.91 | 1.31 | -1.45 | 0.15 |
|            | NCELL*PERIOD2010 | -1.16 | 1.33 | -0.87 | 0.38 |

The effects of variables related to propagule pressure, interspecific competition, land cover changes, natural barriers, climate, period and their interaction were analyzed. Significant results are highlighted in bold, and marginal significance is indicated by a superscript "*".

$^a$Please note that the original presence of the red deer in the period 1981–1990 was used as the temporal reference.
Red deer colonization probability was positively and significantly associated with heterogeneous agricultural patches ($\beta_{\text{HAGAR}} = 0.53$, SE = 0.16, $z = 3.28$, $p < .05$), forest cover ($\beta_{\text{FOREST}} = 0.57$, SE = 0.17, $z = 3.40$, $p < .001$), open areas ($\beta_{\text{OPEN}} = 0.35$, SE = 0.15, $z = 2.43$, $p < .05$) and negatively with shrub cover ($\beta_{\text{SHBS}} = -1.28$, SE = 0.59, $z = -2.18$, $p < .05$). In turn, shrub cover was positively correlated with roe deer colonization ($\beta_{\text{SHBS}} = 1.22$, SE = 0.46, $z = 2.62$, $p < .05$). Neither forest cover nor edge density, however, played a significant role in roe deer expansion. A significant interaction was detected between propogule pressure and forest cover ($\beta_{\text{PCOPRESS}} = -0.49$, SE = 0.16, $z = -3.04$, $p < .05$), and between shrub cover and period ($\beta_{\text{SHBSPERIOD2000}} = 1.51$, SE = 0.60, $z = 2.51$, $p < .05$; $\beta_{\text{SHBSPERIOD2010}} = 2.43$, SE = 0.64, $z = 3.80$, $p < .001$) in the red deer expansion model. Roe deer expansion was negatively and significantly correlated with cumulative rainfall in spring and summer periods ($\beta_{\text{PCURASS}} = -0.72$, SE = 0.37, $z = -1.98$, $p < .05$). Higher stream densities promoted the roe deer expansion ($\beta_{\text{PSTREAM}} = 0.51$, SE = 0.27, $z = 1.59$, $p < .06$). Finally, the period had no significant effect on red and roe deer expansion, except the last decade, which was negatively correlated with the red deer colonization probability ($\beta_{\text{PERIOD2010}} = -1.95$, SE = 0.55, $z = -3.53$, $p < .001$).

4 | DISCUSSION

We tested seven complementary hypotheses to shed light on the ecological and anthropogenic mechanisms underlying the rapid expansion of red and roe deer populations in mainland Portugal. Our results showed that the range expansion patterns differed slightly between the two species. For red deer, the area of the newly occupied range for each decade reduced with time suggesting that the dispersal process will probably reach a steady state in the upcoming years. Contrary to roe deer, we do not expect a significant increase in red deer distribution in the near future.

Our results suggested that the expansion of red and roe deer populations is positively associated with the propogule pressure hypothesis (H1). This evidence corroborates our first hypothesis and is in agreement with previously reported results for roe deer in Iberian mountains (Acevedo et al., 2005) and Catalonia (Torres et al., 2016), north-western Spain, and for other ungulate species, such as the wild boar Sus scrofa in Belgium (Morelle et al., 2016). A distinctive feature of our study shows that propogule pressure does not operate independently from land cover. The significant interaction between propogule pressure and forest cover detected in the red deer model suggests that colonization probability is driven by propogule-environment interactions. This result suggests that the effect of propogule pressure may vary along environmental gradients. Although several lines of evidence suggested that propogule pressure, and all their multiple facets (e.g., propogule abundance, propogule frequency and propogule richness), is the most important factor for the establishment success and species expansion (Simberloff, 2009), we acknowledge that a holistic view is necessary to quantify as precise as possible how propogule pressure interacts with other biotic and/or abiotic variables.

We showed that potential interspecific interactions between red and roe deer had no significant influence on the dispersal patterns of both species (H2). Albeit it corroborates our expectations, we believe this result is only suggestive and must be interpreted with caution as a marginally significant association was found. First, our analyses were based on the presence/absence data because reliable density estimates are lacking for most of the study area. Second, we studied the front of species expansion where population densities are expected to be low, which made interspecific interactions less likely to occur (see Forsyth & Hickling, 1998). Other studies where the significance of red and roe deer interactions was assessed reported divergent conclusions. While Latham et al. (1997) showed that red deer density negatively influences roe deer populations inhabiting Scottish forests, Borkowski and Ukalska (2008) did not detect any evidence of interspecific interactions between these two species in south-western Poland. In the south-eastern part of the Czech Republic, spatial interference between red and roe deer was not observed even at high population densities (Prokesová, Baranceková, & Homolka, 2006). An interesting study carried out in the Dobris Forest, Czech Republic, showed that interactions between red and roe deer were rare and suggested that interspecific cooperative behaviour rules the interactions among sympatric ungulates under predation risk (Bartos, Vankova, Miller, & Siler, 2002). These results could be explained by the fact that red and roe deer are morphophysiological distinct, have different rates of food consumption and are partly segregated at habitat scale (San José et al., 1997). However, we do not disregard the possibility of roe deer being negatively affected and displaced to suboptimal habitats by the presence of red deer (see Richard, Gaillard, Sád, Hamman, & Klein, 2010). We advocate that the role of such interactions in influencing dispersal patterns of wild ungulates requires further analysis at finer scales to control for confounding effects such as climatic conditions and population density. Our results show that red and roe deer are affected differently by livestock abundance (H2). Some factors such as differences in diet type, body size and habitat use have been pointed out as important to explain the wide variety of ungulate responses to livestock presence (Schietz & Rubenstein, 2016). Livestock abundance had a negative marginally significant effect on red deer expansion, which is in agreement with our expectations. The responses of red deer to livestock pressure are further analysis at finer scales to control for confounding effects such as climatic conditions and population density. Our results show that red and roe deer are affected differently by livestock abundance (H2). Some factors such as differences in diet type, body size and habitat use have been pointed out as important to explain the wide variety of ungulate responses to livestock presence (Schietz & Rubenstein, 2016). Livestock abundance had a negative marginally significant effect on red deer expansion, which is in agreement with our expectations. The responses of red deer to livestock presence include, for example, the switch of habitat preferences (Kuiters, Bruinderink, & Lammertsma, 2005). This avoidance behaviour was also reported for other Iberian ungulate species, such as the Iberian ibex (Capra pyrenaica, Acevedo et al., 2007). Roe deer expansion seems to be favoured by livestock abundance, which supports some plausible hypothesis. For instance, the diet overlap between roe deer, a typical browser and domestic grazers is very small, except under specific conditions (Abbas et al., 2013). We realize that our results need further examination to assess how wild ungulates responses to livestock pressure are influenced by variable environmental conditions. Studies conducted at small spatial scales and using data that span a long time frame are increasingly necessary because broad scale analyses, such as ours, may dilute the influence of interspecific interactions on the range expansion patterns of wild populations.
Collectively, our findings corroborate empirical evidences on the significant role of land cover in the colonization sequence of red and roe deer (H3). We emphasize the positive and significant effect of heterogeneous agricultural patches, forest stands and open natural areas on red deer expansion, and the importance of shrub cover for roe deer spread. These results are partially in agreement with fine-scale studies carried out in Portugal (red deer: Alves et al., 2014; Torres et al., 2014; Carvalho et al., 2017; roe deer: Torres et al., 2014). Forests associated with a well-developed understory provide food and shelter for red deer. These areas form important ecological corridors for red deer movements through human-modified landscapes. Even when fragmented and scattered, the forest patches might promote species dispersal and range expansion through consecutive stepping-stone movements (Saura, Bodin, & Fortin, 2014). The positive effect of agricultural and open areas on red deer presence has already been documented for several populations inhabiting Mediterranean ecosystems (Alves et al., 2014; Lovari et al., 2007). The availability of food resources in cultivated landscapes increases both the amount and quality of food supply, probably favouring the red deer settlement and range expansion. The concurrent significance of forests and open areas (heterogeneous agricultural patches and open natural areas) suggests that ecoregions have a noticeable influence on red deer presence and expansion. The use and preference for these transitional areas of vegetation may represent an energetic adaptation, where the travel costs between feeding and shelter areas are minimized (Thomas & Taylor, 2006). The preference for edge habitats is also justified by the need of red deer males to rub and communicate (Ramos, Bugalho, Cortez, & Jason, 2006). The results regarding the influence of shrub cover on red and roe deer expansion were contingent on species and may reflect the species ability to cope with human disturbance and predation risk (Jiang, Zhang, & Ma, 2008). Although considered a forest-dwelling species, roe deer is characterized by a high ecological plasticity and seems to cope with human disturbance better than red deer (Borkowski, 2004; Jiang et al., 2008). The positive and significant association between shrub cover and roe deer expansion, together with the reported conversion of agricultural fields in scrubland (Beilin et al., 2014), corroborate the idea that the species is widely favoured by the re-naturalization of habitats.

Contrary to our predictions, we did not detect any significant effect of human factors (H4), natural barriers (H5) and climatic conditions (H6) on the red deer dispersal patterns. Human presence and topography had also no apparent effect on roe deer expansion. The low human population density that characterizes the interior of mainland Portugal and the cryptic behaviour this species may adopt are possible explanations for this finding. Even though we did not include additional drivers of anthropogenic disturbance (e.g., hunting pressure) or management practices (e.g., number of fenced populations and number of populations artificially fed) due to a lack of reliable baseline data, we acknowledge that these variables can affect the expansion of wild ungulates. Recent research has begun to analyse behavioural responses of wild ungulates to hunting pressure (Benhaiem et al., 2008; Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015; Thurfjell, Spong, & Ericsson, 2013) and management practices (Ossi et al., 2017). The disturbance caused by the hunting practices is highly seasonal, which triggers temporary behavioural and spatial responses (Tolon et al., 2009). A priority for the future is to quantify, at small spatial scales, how hunting and management strategies affect the spatial behaviour of red and roe deer populations. This information will provide new clues about the home range shifts and expansion patterns of wild populations exposed to different levels of hunting pressure.

With regard to stream density, we reported that roe deer dispersal occurs preferentially over areas with high density of streams. Particularly in dry regions, the water availability is a physiological and behavioural constraint for the species (Wallach, Inbar, Scantlebury, Speakman, & Shanas, 2007). These results probably reveal a higher sensitivity of roe deer to water supply in comparison with red deer. Contrary to what we expected, we detected a significant and negative influence of cumulative rainfall in spring on the expansion patterns of roe deer. This result must be interpreted with caution considering that the few areas where the species were restricted up until recently (e.g., Peneda-Gerês National Park, nucleus 1) are among the wettest regions of mainland Portugal. The southward and hinterland expansion of roe deer during the last three decades has implications on the altitudinal parameters. Therefore, while roe deer expand, reach areas with lower altitudes and far from the coast, where the cumulative rainfall is typically lower. This confounding factor must be accounted for when analysing the role of climate conditions.

## 5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our study shows that it could be naïve to assume that species will simply benefit from higher propagule pressure. A take-home message is that synergistic effects between biotic and abiotic variables should be taken into account when studying the patterns of species expansion. Our findings allow us to understand the potential impacts of forest and shrub encroachment and to forecast the influence of possible changes in the Common Agriculture Policy on the range dynamics of ungulate populations. Despite some limitations, our results have an important practical application for prioritizing management actions. If, on the one hand, the expansion of ungulate populations may have beneficial effects such as the increase in genetic diversity, hunting harvest opportunities and also the recovery of large carnivore populations, on the other, may cause harmful ecological and economic impacts. Bearing in mind that ungulate impacts are contingent on the region, policy makers should consider the spatial, temporal, ecological and societal nuances of species expansion in order to prioritize management measures and to allocate management budgets. Concerted strategies to curtail species spread should focus along the front of expansion. Fencing croplands and management culls could be important to prevent damage to agriculture and forestry. The reduction in the effectiveness of stepping stones and the attractiveness of ecological corridors that connect disjunct populations is essential in regions where the dissemination of vectorborne and zoonotic diseases is the main concern. If the objective is to foster ungulate expansion,
habitat interventions aimed at creating edge and opening areas of high vegetation richness may be very effective and, at the same time, may alleviate the problems of overpopulation. Despite some potential unintended consequences (Champagnon, Elmberg, Guillemain, Gauthier-Clerc, & Lebreton, 2012), reintroductions and translocations of individuals into suitable habitats allowed the ungulate reestablishment in previously extirpated areas and the restoration of ecosystem functioning. We, however, advocate that stakeholders’ interests cannot be set aside because the success of management measures is largely dependent of their prior acceptance. The implementation of a planning scheme should be preceded by a public consultation not only because public perceptions are context-dependent, but also because the tools used to control or regulate ungulate populations could be controversial. An open debate among researchers, managers and policy makers is needed, and specific questions should be asked to increase the effectiveness of management strategies.

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DATA AVAILABILITY

Data available upon request.

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BIOSKETCHES

The team research is mainly focused on the ecology and management of wild ungulates. Based on a multidisciplinary framework, the team seeks to understand the range and population dynamics of ungulate species, to assess the impacts of environmental changes on the life history traits of individuals and ungulate populations and to shed light on their role as reservoirs of infectious diseases at the human–livestock–wildlife interface under the One Health paradigm.

Author contributions: JC and RTT conceived the study. JC, RTT, JPVS, TB and CF collected and compiled the data. JC, PA and ES analysed the data. JC and RTT wrote the manuscript. All authors contributed to the development of ideas and approved the final version of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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