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Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula

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ABSTRACT

In the Iberian Peninsula, Oak Decline (hereafter, **OD**) is becoming a serious and frequently occurring disease in Mediterranean oaks. Decline processes seem to involve multiple biotic and abiotic factors, which combine to reduce the vigour of oak trees often causing death. However, the exact causes of its extension are still unknown and therefore, given the ecological, economic and social relevance of these trees in Mediterranean countries it is crucial to develop tools that allow us to anticipate its occurrence and to reduce its expansion. In this sense, the present work aims to (i) unravel the relative role of environmental factors on the distribution of one of the most important phenomena that threat the biodiversity of the Iberian oaks, and (ii) to produce a spatially explicit model of **OD** risk, to assist conservation managers dealing with this phenomenon. To this, we have used a dataset of **OD** foci gathered during the period 2015–2017 by the program "Methodology for the inventory and monitoring of oak masses affected by the decline of oak in the southwest of Castilla y Leon" (this region is beginning to suffer the damages of this disease). In total, 68 locations were used to assess relationships with environmental factors (topographic conditions, abiotic stress conditions and human influence) using maximum entropy models (hereafter, MaxEnt) and variance-partitioning. **OD** distribution seems to be principally influenced by land-use (mainly *dehesas*), followed by dryer areas and areas with low slope gradients facing south or southeast. The resulting model has been used to produce a detailed **OD** risk map in central-western Spain. Our modelling approach may contribute to inform conservation planning and to establish the adequate management policy for Iberian oak *dehesas*, by helping to identify regions where the risk of **OD** is high.

1. Introduction

Since the beginning of the twentieth century, **OD** has been a serious and frequently occurring disease in oaks world-wide (Brasier, 1992; Thomas et al., 2002; Haavik et al., 2015; Rodríguez-Calcerrada et al., 2017a, 2017b). Being a phenomenon of local and/or regional importance in the past, **OD** in its current phase has been devastating the oaks (major die-offs of trees at the genus or species level) since the beginning of the 1980s in the southwest of the Iberian Peninsula (Brasier et al., 1993; Sánchez et al., 2002; Moreira and Martins, 2005; Corcobado et al., 2013). **OD** symptoms are very unspecific and consist of wilting and leaf chlorosis, loss of foliage, branch lesions, epicormic shoots, tarry exudations, root rot and the sudden death of the trees (Brasier, 1992; Gallego et al., 1999; Jung et al., 2000; Thomas, 2008). In oak trees in the Mediterranean basin, **OD** is considered of paramount importance because this phenomenon involves oak species of the *Quercus* genus (e.g., *Q. ilex*, *Q. faginea*, *Q. suber*, *Q. pyrenaica*) which dominate the traditional agrosilvopastoral systems called "*dehesa*" in Spain and "*montado*" in Portugal (de Sampaio e Paiva Camilo-Alves et al., 2013). Oak trees are a major element in these systems and maintain ecosystem functions and services such as soil protection, enhancing diversity, provision of resources (e.g., forage, acorn, wood, cork, charcoal) and cultural services (Gea-Izquierdo et al., 2006; Olea and San Miguel-Ayanz, 2006; Kim et al., 2017). In this sense, their high socioeconomic and environmental values in the regions of the Mediterranean basin highlights the need to understand the main drives of their decline. The causes underlying this phenomenon are complex and uncertain, but it is believed that they are frequently associated with one or more global change drivers.

OD occurrence in Mediterranean ecosystems is considered a complex multifactorial phenomenon involving the combination of primary or predisposing factors (warmer climates, water stress, air pollutants, soil features, land use disturbance, leaf defoliators and bark beetles) and secondary or opportunistic factors (invasive pests and pathogens)

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(Thomas, 2008; Rodríguez-Calcerrada et al., 2017a, 2017b), operating at tree, stand, and landscape scales. In most cases, none of these factors act alone. The simultaneous interaction of at least two stress agents—where one of them comprises an extreme climatic event (e.g., drought)— has triggered important outbreaks of decline (Rodríguez-Calcerrada et al., 2017a, 2017b). Although Mediterranean oak species exhibit morphological and physiological adaptations that enable them to increase water deficit tolerance, changes in rainfall patterns- which may include a severe or prolonged drought- can initiate decline events by compromising the physiological capacity of mature oaks (Allen et al., 2010; Haavik et al., 2015; Rodríguez-Calcerrada et al., 2017a, 2017b). Also, physical landscape attributes such as topography (e.g., slope aspect, curvature) and land-use disturbances (silvicultural mismanagement) can induce highly variable moisture conditions with different impacts on the trees, thereby leading to the sudden death of affected trees or gradual decline until their death (Thomas, 2008). Secondary biotic agents, often termed contributing factors, include root pathogens of the genus *Phytophthora* (Haavik et al., 2015). Although several *Phytophthora* species have been isolated in soils from declining oak trees (Jung et al., 2015), *P. cinnamomi* is by far the most aggressive and has been recognized as a main biotic factor of oak mortality in the Iberian oaks (Hernández-Lambraño et al., 2018). This pathogen is not commonly capable of killing healthy oaks, but it can kill oaks weakened by some other primary factor such as drought (Thomas et al., 2002; Haavik et al., 2015). It is challenging to identify a cause that overcomes others, either because it may be related to other factors or because the proximate cause of death may mask the primary one (de Sampaio e Paiva Camilo-Alves et al., 2013). Despite the perception of an increasingly visible damage on Iberian oaks, the main causes and functional basis influencing the spatial distribution patterns of **OD** at landscape level remain unclear. To our knowledge few studies have investigated spatial patterns of **OD** in Iberian oaks (Costa et al., 2010; Serrano et al., 2016; Duque-Lazo et al 2016; Duque-Lazo et al 2018). This lack of evidence is primarily due to the inherent difficulties of surveying **OD** foci, monitoring and estimating the primary factors causing the decline in great extensions of oaks. Therefore, the description of the spatial patterns of **OD** could provide a better understanding of the possible primary causes that trigger this phenomenon as well as to evaluate its ecological and socio-economic impacts in the Mediterranean basin ecosystems, where reducing the rate of biodiversity loss has become a key target.

Successful strategies to prevent this phenomenon include adequate forestry practices such as forest harvesting to improve the vigour of adult oak trees in open field and sanitation measures to minimize pathogen spread (de Sampaio e Paiva Camilo-Alves et al., 2013; Rodríguez-Calcerrada et al., 2017a, 2017b). However, the resources available for the adequate implementation of actions against **OD** are frequently limited. In this sense, there is an urgent need for the efficient allocation of such scarce resources to maximize the efficiency of these actions (Keane et al., 2008). The identification of the primary or predisposing factors behind the **OD**, as well as identifying areas with most risk, would greatly facilitate the basis for where, when, how often, and what management alternatives should be used. In fact, the use of risk maps and model visualization has been widely used as a powerful tool in effective management of natural resources (Margules and Pressey, 2000; Yemshanov et al., 2013).

Nowadays, the use of systematic processes to optimize conservation plans based on scientific criteria has increased (Franklin, 2010; Yemshanov et al., 2013). Highlighted among these processes is the development of predictive models, specifically the Species Distribution Models (SDMs); an innovative GIS-based method used to produce predictive maps of where species are likely or not to occur across a landscape (Soberón and Nakamura, 2009). This approach is currently expanding its scope and is being applied not only to predict species occurrence probabilities, but as a set of processes that are closely tied to conservation biology (Mateo-Tomás et al., 2012; Santos et al., 2013; Silva et al., 2014; Yañez-Arenas et al., 2014; Garrote et al., 2018). In this way, SDMs offer a possible solution for the identification of the predisposing factors behind the **OD** and even the identification of areas of highest risk, by combining **OD** foci data with environmental factors considered to influence its occurrence.

This study aims to make a relevant contribution in conservation biology by employing a new approach using SDMs. To do this, we took advantage of an intensive monitoring programme about **OD** in central-western Spain conducted from 2015 until 2017, (i) to try to elucidate the influence of environmental factors on spatial patterns of OD in Iberian oaks and (ii) to produce a spatially explicit model of OD risk, to assist conservation managers dealing with this phenomenon. Given the changes in land-use patterns and frequent changes in highly variable rainfall patterns in the Mediterranean basin, we hypothesize land-use and drought to be important predictors for explaining the OD distribution patterns in central-western Spain.

2. Material and methods

2.1. Study area

The study was conducted in central-western Spain within the Mediterranean ecological region in the province of Salamanca, between 40°50′ N and 6°00′ O, with a total area of 12 349 km^2 (Fig. 1). The study area consists of wide flat or gently undulating plains in the north-east part with an average elevation of 800 m a.s.l. The main geographical features are the southern mountain ranges (Sierras de Gata, Béjar and Francia), which reach almost 2000 m a.s.l. and the deep river valleys of the north-west part (Arribes) with heights of 150 m a.s.l. The climate is mostly Mediterranean continental with an average annual temperature of 12 °C, mean annual rainfall of 400 mm, and an acute summer drought during two-three months, between June and September, when there is no risk of frost (Peris et al., 1992). The most widespread soils, classified by the WRB-FAO, are Dystric or Eutric Cambisols and Regosols on slates and granites, and Haplic Luvisols and Eutric Cambisols on sediments (Martín-Sanz et al., 2015). The zone is representative of oak trees in Spain, populated mainly by holm-oaks (*Q. ilex*) and other *Quercus* species (*Q. faginea*, *Q. suber*, *Q. pyrenaica*), with a total area of 4844 km^2 and managed as a traditional agro-sylvo-pastoral system mainly for livestock (*dehesa*), with grazing areas intercropped with pasture areas of grasslands and legumes (Regato-Pajares et al., 2005). Other semi-natural forests (pinewoods and chestnut groves) are present in the south of the province.

2.2. Data acquisition

GPS locations of **OD** foci ($n = 68$, see Fig. 1) within the study area were obtained for the period of 2015–2017 by the program "Methodology for the inventory and monitoring of oak masses affected by oak decline in the province of Salamanca" from the Hispano-Luso Institute of Agrarian Research of the Salamanca University (**CIALE** Spanish acronym). This program has surveyed trees within the *dehesa* and oak forest areas across the study area. Living oak trees (diameter at breast height > 7 cm) were inspected visually for the following decline symptoms: death, chlorosis, cankers or defoliation without an apparent causal agent. Other semi-natural forests (pinewoods and chestnut groves) are only present in the south of the province and were not the object of this study.

To characterize the most important predisposition factors to **OD** in the study area, we used 13 variables as predictors, related to (1) topographic conditions, (2) abiotic stress conditions and (3) land-use (Table 1). These variables were chosen based on our knowledge of the **OD** phenomenon (Rodríguez-Calcerrada et al., 2017a, 2017b), and were assumed to be at least correlated with more proximal causal factors.

Variations in topographic features can cause differences in edaphic

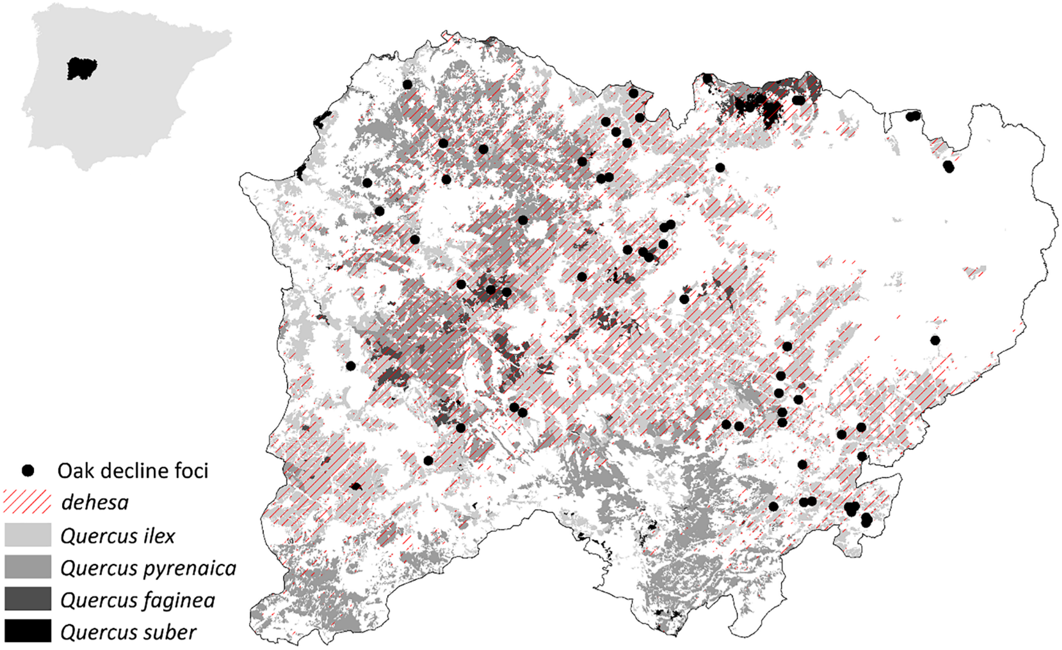

Fig. 1. Location of the study area and the occurrence of Oak Decline foci against the background of the *Quercus* spp. distribution and the *dehesa*.

factors, such as moisture and availability of nutrients with different impacts on the trees, thereby leading to the sudden death of affected trees or gradual decline until their death (Esselink and van Gils 1994; Thomas, 2008; de Sampaio e Paiva Camilo-Alves et al., 2013). Herein, the topographic features of the study area were derived from a Digital Elevation Model (**DEM**) by National Center for Geographic Information of Spain at 5 m spatial resolution (**CNIG** Spanish acronym; http://centrodedescargas.cnig.es). We calculated slope and aspect using the Spatial Analyst Tool in ArcGIS v.10.3.1 (ESRI, 2015), to account for gravitational processes and effects of potential solar radiation. Terrain surface curvature (**curvature**), was calculated using Spatial Analyst Tool in ArcGIS to account for soil erosion patterns as well as the distribution of water on study area (Zevenbergen and Thorne, 1987). The curvature can be positive (indicating peaks), negative (indicating valleys) or zero (indicating flat surface). The topographic position index (**TPI**), was calculated using the Slope Position tool in Geomorphometry and Gradient Metrics toolbox v.2 (Evans et al., 2014) for ArcGIS. **TPI** compares the elevation of each cell in a **DEM** to the mean elevation of a specified neighbourhood (3 × 3 pixels) around that cell (De Reu et al., 2013). Positive **TPI** values indicate that the central point is located higher than its average surroundings, while negative values indicate a position lower than the average. **TPI** can be used as a proxy of available soil moisture in the study area (Das et al., 2015). Finally, we estimated a Heat load index (**HLI**) using the HLI tool in Geomorphometry and Gradient Metrics toolbox for ArcGIS. **HLI** shows that a south facing slope should have warmer temperatures than a north facing slope, even though the amount of solar radiation they receive is equivalent (McCune and Keon, 2002). Values range from 0 to 1, where higher

Table 1
Main variables considered for modelling the oak decline occurrence in the study area. Those variables finally used to run the models after reducing multicollinearity (i.e. high correlation between variables, $r_s > |0.7|$) are shown in bold.

Name	Description	Range
(1) Topographic features		
Slope	Slope of the terrain (degrees)	0–41.4
Aspect	The terrain slope direction. Eight aspect classes were considered: east (E), southeast (SE), south (S), southwest (SW), west (W), northwest (NW), north (N) and northeast (NE)	NA
HLI	Heat load index	0.67–0.88
Curvature	Terrain surface curvature	−1.64 to 3.01
TPI	Topographic position index (m)	−4.05 to 8.31
LST_*w*	Land surface temperature in winter (°C)	4.82–15.5
LST_*s*	Land surface temperature in summer (°C)	19.2–38.2
LST_*sd*	Variability of the land surface temperature between 2015 and 2017 (°C)	1.64–6.43
(2) Abiotic stress conditions		
NDII_*w*	Soil water availability in winter	0–0.51
NDII_*s*	Soil water availability in summer	0–0.42
NDII_*sd*	Variability of the soil water availability between 2015 and 2017	0–0.26
NDVI_*w*	Winter average of the Normalized Difference Vegetation Index	0–061
NDVI_*s*	Summer average of the Normalized Difference Vegetation Index	0–0.57
NDVI_*sd*	Variability of the Normalized Difference Vegetation Index between 2015 and 2017	0–0.19
(3) Human influence		
Land-use	Land-use composition classes. Five land-use classes were considered: (1) artificial surfaces, (2) agricultural areas, (3) agro-forestry areas, (4) *dehesas* and (5) forestry areas	NA
Pond	Minimum distance to ponds (km)	0.08–23.7

NA = categoric variable.

values indicate slopes with warmer temperatures.

In European Mediterranean regions, successive droughts have been a recent climatic feature of most areas with **OD** presence, and thus have frequently been proposed as the primary factor in these declines. Herein, we estimated Normalized Difference Infrared Index (**NDII**) as a proxy for variability of the water availability in the study area (Sriwongsitanon et al., 2016), using Landsat 8 OLI/TIRS satellite data (for more details see https://lta.cr.usgs.gov/L8). **NDII** has be effectively used to detect canopy stress (Emmerik et al., 2015), according to the property of shortwave infrared reflectance, which is negatively related to leaf water content due to the large absorption by the leaf (Sriwongsitanon et al., 2016). Landsat 8 OLI/TIRS satellite images were acquired from the United States Geological Service's Earth Explorer (USGS; https://earthexplorer.usgs.gov/) for the summer and winter periods from 2015 to 2017. The **NDII** was calculated for each of the satellite images using near infrared reflectance (NIR; band 5) and short-wave infrared reflectance (SWIR; band 6) of the Landsat images as shown in the following equation: $(\rho NIR - \rho SWIR)/(\rho NIR + \rho SWIR)$. The **NDII** was averaged for each of the periods (winter and summer). Also, as a measure of seasonal variation of water availability in the study area, we calculated standard deviation (**SD**) of **NDII** for the period between 2015 and 2017. In addition to **NDII**, we calculated the Normalized Difference Vegetation Index (**NDVI**) (Tucker, 1979), as a proxy of the shifts in plants' performance in response to environmental changes. The **NDVI** has been effectively used to monitor and investigate the health of Mediterranean forests (Jucker Riva et al., 2017; Recanatesi et al., 2018). The **NDVI** was calculated using near infrared reflectance (NIR; band 5) and red reflectance (RED; band 4) as shown in the following equation: $(\rho NIR - \rho RED)/(\rho NIR + \rho RED)$. The **NDVI** was averaged for each of the periods (winter and summer) and the **SD** for the period between 2015 and 2017 was calculated. Finally, we calculated land surface temperature (**LST**) as a proxy of the temporal and spatial variations of water balance in the study area. The **LST** is widely used in a variety of fields including evapotranspiration, climate change, hydrological cycle and vegetation monitoring, among others (Ottlé et al., 2004). The **LST** in degrees Celsius was calculated from thermal band 10 (Cristóbal et al., 2018), using the Semi-Automatic Classification Plugin tool (**SCP**) (Congedo, 2016), for QGIS open-source software version 2.18 (http://www.qgis.org). The **LST** was averaged for each of the periods (winter and summer) and the **SD** for the period between 2015 and 2017 was calculated. Prior to analyses, atmospheric correction of the Landsat 8 OLI/TIRS images was carried out using the Dark Object Subtraction (**DOS**) approach (Nazeer et al., 2014), implemented in **SCP** for QGIS.

Change in land-use patterns in the Mediterranean basin, such as overgrazing and the neglect of traditionally maintained oak pasture systems have been a recent land feature of most areas with **OD** presence. In the 1960s, due to the emergence of swine fever, there was a marked reduction in the use of pasture for this type of livestock activity. At the same time, as a consequence of the common agricultural policies in the European Union, an intensification of the agricultural use in the pasture was favoured. All this led to a depreciation of the value of the acorn and consequently, less interest in maintaining the forest cover that traditionally forms part of this habitat (Esselink and van Gils 1994). However, from the 1990s to present day, the revaluation of meat products from the pasture has led to a significant livestock overload on many farms. This radical change in use has frequently been proposed as an important factor in these declines (Brasier, 1996; Rodríguez-Calcerrada et al., 2017a, 2017b). To characterize human influence in the study area, a land-use variable was constructed with a 30 m spatial resolution, based on a 1:50 000 land-use map from Third National Forest Inventory (**IFN3** Spanish acronym) of Spain (MAGRAMA, 2007). Five land-use classes were considered in this study: artificial surfaces (i.e. urban areas, roads and construction), agricultural areas (i.e. permanent crops and annual crops), agro-forestry areas (i.e. land principally occupied by tree cultures, mainly olive groves and fruit trees), *dehesas* (i.e. agro-sylvo-pastoral systems for livestock, populated mainly by *Q. ilex* and other *Quercus* species such as *Q. suber*, *Q. faginea* and *Q. pyrenaica*) and forestry areas (i.e., coniferous and broadleaf forests). Recently, Manzano et al. (2016) related decline and mortality of cork and holm oaks in central-western Spain to the presence of hydraulic infrastructures (e.g., ponds) resulting from agricultural activities. These water bodies- built taking advantage of the terrain relief- is usually for the use of water by livestock and irrigation of forage crops. Therefore, this could induce important modifications in the water table in those area with **OD** presence. Herein, we calculated proximity to ponds as a proxy of the modifications in the water table in the study area. To do this, each pond was accurately checked for location using high resolution orthophotos (0.5 m) from the photogrammetric campaign of the National Plan for Aerial Orthophotography in 2014 (**PNOA** Spanish acronym: http://centrodedescargas.cnig.es). Then, we calculated the distance (in meters) to ponds using the Euclidean distance tool by ArcGIS.

All environmental data were standardized to Universal Transverse Mercator coordinate (Datum ETRS-89) at a spatial resolution of 30 × 30 m. Finally, to reduce multicollinearity between variables, we calculated the Spearman's correlation coefficients (r_s). Variables with values of $r_s > |0.7|$ were excluded (Hernández-Lambraño et al., 2017).

2.3. Model development

OD in the study area was modelled using MaxEnt version 3.4.1, a machine-learning process that uses presence-only data (Phillips et al., 2006). MaxEnt gives insight about what predictors are important and estimates the relative suitability of one place vs. another, as well as the probability of occurrence (Elith et al., 2011). This approach has been demonstrated to perform well in a diverse set of modelling scenarios and is widely used in a great number of studies in ecology, biogeography and conservation (Elith and Leathwick, 2009; Franklin, 2010; Duque-Lazo et al., 2016; Duque-Lazo et al., 2018).

To investigate the most important factors associated with **OD**, we carried out MaxEnt models including a different subset of non-collinear variables: only topographic conditions, only abiotic stress conditions and only human influence. For each MaxEnt model, we calculated the relative contribution values ($\boldsymbol{R_c}$) to rank the variables in order of importance in relation to **OD**. The $\boldsymbol{R_c}$ value is calculated based on how much the variable contributed to the model depending on the path selected by Maxent for a particular model run (Phillips et al., 2006). We selected the best variables (largest $\boldsymbol{R_c}$) for each block of non-collinear predictors and performed a final model; combining the best variables of each block (full model). We performed 10 replications using a bootstrap procedure in which we divided our dataset using 80% of data for model calibration and retaining 20% of the data to evaluate models. For the test values, we reported the mean and standard deviation of the area under the curve of the receiver operating characteristic (**AUC**) for the 10 runs. **AUC** measures the ability of a model to discriminate between sites with **OD** occurrence, versus those where it is absent. The AUC ranges from 0 to 1 (0.5 = random, 1 = perfect). Runs used herein were conducted using the MaxEnt default parameters (Phillips et al., 2006). Background points were randomly chosen within the area enclosed by a minimum convex polygon comprising all **OD** foci (Elith et al., 2011). Response curves were calculated to interrogate the relationship between the response (i.e., **OD** risk) and each explanatory variable. These show how a given explanatory variable influences the response variable while keeping all other predictors at their average (Phillips et al., 2006).

2.4. Deviance partitioning

Assuming that the deviance is a good measure of the variability explained by a model (Borcard et al., 1992), we performed a hierarchical partitioning procedure to determine the amount of independent and shared information contained in the topographic, abiotic stress and human influence variables. We fitted generalized linear models (**GLMs**) with presence and background data as the response variables and using a different subset of the best predictors selected in the above section: only the topographic variables (topography), only the abiotic stress variables (abiotic stress), only human influence (land-use). The deviance explained by each model was then used to identify the single and shared effects on the occurrence of **OD** by simple equation systems. We used R v.3.4.2 (R Core Team, 2017), in all analyses and the *varpart* function of the R package "vegan" v.2.4-6 (Oksanen et al., 2018), for variance partitioning procedures. For the **GLM**, we selected 10 000 random background points from throughout the sampling region, as suggested by Barbet-Massin et al., (2012)

2.5. Oak decline risk map and identification of priority areas for management interventions

We used all available occurrences of **OD** to calibrate the model combining the best variables of each block (i.e., topographic, abiotic stress and human influence) and we projected its final potential distribution to all the 30 × 30 m grids in the study area. We classified probability categories for the **OD** risk map using the threshold that represents the value that maximizes the sum of sensitivity and specificity (Liu et al., 2005). This was selected to favour oak conservation versus its threatened status due to the **OD** occurrence. The **OD** risk map and the associated distribution maps of oaks in the study area were used to assess the priority areas for management interventions (Duque-Lazo et al., 2018). Oak maps were obtained from **IFN3**. We proposed the following areas: prevention, for areas with identified **OD** occurrence; protection, for areas where **OD** is currently absent, but its occurrence is predicted with high probability; and conservation, for areas where **OD** is currently absent, and its occurrence is predicted with low probability. The recommended management strategies for the proposed areas are summarized in the Table 3.

3. Results

3.1. Oak decline risk models

The MaxEnt models including a different subset of non-collinear variables (i.e., topography, abiotic stress and human influence) exhibited a good discrimination capacity, with average **AUC** values ranging between 0.64 and 0.82. Despite the initial good performance of the models, the combination of the best variables in a final model (i.e., full model) resulted in higher mean **AUC** values (0.93 ± 0.03, $F_{3,39} = 108.2$, $P < 0.0001$; see Fig. 2).

3.2. Factors influencing the distribution of oak decline in central-western Spain

The variables that contributed most highly to the **OD** models are presented in Table 2.

The model developed with best variables showed that the likelihood of **OD** risk in the study area was higher in *dehesas* than in other land-uses (see Fig. 3). Moreover, areas with ponds located at less than 2.5 km from **OD** foci were associated with an increase **OD** risk. The probability of **OD** occurrence was negatively associated with abiotic stress conditions (i.e., **NDII** and **NDVI**). The lower these indices the higher the probability of **OD** occurrence. Additionally, areas with lower variation values (**SD**) presented by these indices were associated with the high probability of **OD** occurrence. These low values suggest repeated and protracted drought periods in the affected areas. Concerning topographic features, higher **OD** risk was predicted for flat slopes (< 5%) and for south and south-easterly facing slopes. Moreover, the probability of **OD** risk was associated positively with land surface temperature (i.e., **LST**). The higher land surface temperature the higher the risk of **OD** occurrence.

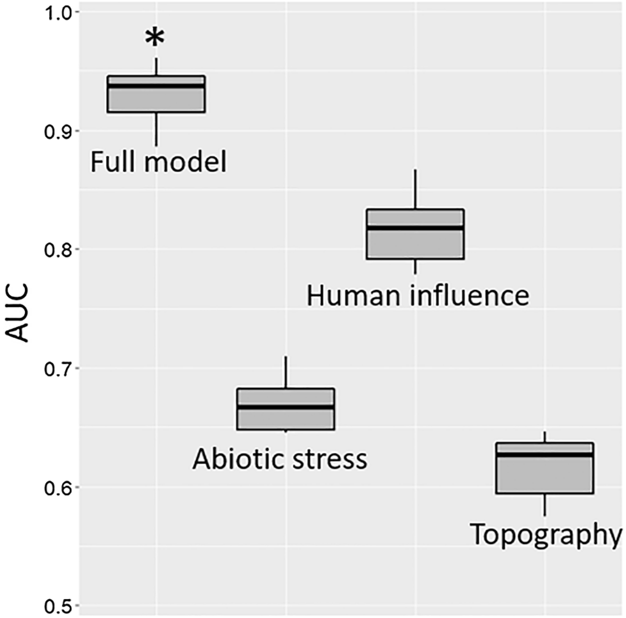

Fig. 2. The boxplots of AUC values obtained by 10-replications (bootstrap procedure) for each of the models using a different subset of non-collinear variables: just the topographic variables (topography), just the abiotic stress variables (abiotic stress), just human influence variables (human influence), and the combination of the best predictors (largest ***Rc***) of each subset of variables (full model). Asterisk (*) on top of box indicates significant difference when compared to full model, Bonferroni's Multiple Comparison Test $P < 0.05$.

Table 2
Mean values of the relative contributions (%) of the predictor variables for the MaxEnt models. Mean values were calculated from the 10-replications of the models. The R_c1 column indicates contribution values of the predictor variables for the models developed with each block of non-collinear predictors (i.e., topography, biotic stress and human influence) and the R_c2 column indicates contribution values of the predictor variables for the final model (full model) developed with best variables (largest R_c1) of each block. See Table 1 for variable descriptions.

Variables	R_c1	R_c2
Human influence		
Land-use	59.2	46.8
Pond	40.8	32.6
Abiotic stress conditions		
NDII_*s*	30.5	4.10
NDVI_*sd*	24.0	3.90
NDVI_*s*	23.7	0.30
NDII_*sd*	15.0	2.00
NDVI_*w*	6.20	–
NDII_*w*	0.60	–
Topographic features		
Aspect	28.6	8.20
LST_*s*	26.9	1.80
Slope	21.1	0.30
LST_*w*	14.8	–
LST_*sd*	8.60	–

The results of the variation partitioning are shown in Fig. 4. Human influences explain most of the variation, followed by influence of abiotic stress variables, whereas topography accounts for a smaller proportion of the variation. The magnitude of the shared effect represents the proportion of the model variation that is attributable to the combined effect of the three sets of variables. In our case, the shared component had a large proportion of the variation, indicating strong

Table 3
Summary of recommended forestry practices according to the identification of presence and predicted probability of occurrence of oak decline.

Area	Occurrence		Policy	Forestry practices	Reference
	Identified	Prediction			
Prevention	yes	high	Control, mitigation	Selective thinnings of suppressed stems, girdling selected stems in multi-stems trees, inoculation of endophytes or chemical cocktails, prevention of the spread of xylophage insects and fungal pathogens, good planning of the grazing activities	(Rodríguez-Calcerrada et al., 2011; de Sampaio e Paiva Camilo-Alves et al., 2013; Oberhuber et al., 2017; Rodríguez-Calcerrada et al., 2017a, 2017b)
Protection	No	high	Monitoring	Selective cut of smaller trees from the midstory and thinning of forest by removing some of the mature trees	(Clatterbuck and Kauffman, 2006; Wang et al., 2013)
Conservation	No	low	Monitoring	Increase sexual regeneration through sowing/planting, preservation of marginal oak populations	(Clatterbuck and Kauffman, 2006; Rodríguez-Calcerrada et al., 2017a, 2017b)

dependent contributions of the three sets of predictors, explaining distribution patterns of **OD** in the study area.

3.3. Risk map of the potential distribution of oak decline in central-western Spain: analysis of current protection and conservation

Considering the value that maximizes the sum of sensitivity and specificity as a threshold (i.e., 0.35), the area predicted by the full model with high risk of OD (i.e., risk probability above the considered threshold) was 80% of the total area populated by oak trees in the study area, while the remaining 20% was predicted with low risk (Fig. 5). In agreement with our observations, the map showed an **OD** risk scattered throughout oak areas with higher probabilities in the northern and central part of the study area, while the northwest and southern part showed lower probabilities of occurrence. These areas coincide broadly with holm-oak pastures, although **OD** foci were also found in *Q. faginea dehesas.*

According to the identification of **OD** foci and its predicted risk probabilities in the study area, several sites were proposed as potential areas for management interventions (Fig. 6). All sites where **OD** was present were dominated by oaks (*Q. ilex*, *Q. faginea* or *Q. pyrenaica*). With the aim of mitigating the extent of decline at the sites with **OD** foci, the following strategies have been recommended: harvesting practices to improve the vigour of trees, application of biological treatments to stimulate the defence mechanisms of the fine roots of the oak stands suffering decline, sanitation measures to minimize pathogen spread and control over the population densities of the xylophage insects (Cerambyx complex) (see Table 3) (de Sampaio e Paiva Camilo-Alves et al., 2013; Rodríguez-Calcerrada et al., 2017a, 2017b).

4. Discussion

4.1. The important role of predisposing factors influencing the spatial distribution patterns of oak decline in central-western Spain

Our study reveals that it is possible to identify the most influential variables explaining the spatial distribution patterns of **OD** using maximum entropy modelling and variance-partition techniques. This approach was found to be capable of capturing the relationship between risk probability of **OD** and predisposing factors on oaks in central-western Spain. The variables with the largest $\boldsymbol{R_c}$ revealed that **OD** distribution seems highly dependent on land-use, followed by abiotic stress conditions and lastly topographic features.

Land-use was an important predictor, explaining the **OD** distribution patterns. In fact, in the study area, most of the **OD** foci were found in *dehesas* land-use with abundant understorey shrubs (encroached). This is in agreement with observations made in regions with similar topographic features, where the shrub encroachment dominated by shrub gum rockrose (*Cistus ladanifer*) as a consequence of land-use changes was considered to be a decisive factor in tree decline (Cubera and Moreno, 2007; Costa et al., 2010). This negative effect could be related to a significant increase in competition for soil water (Moreno and Pulido, 2009; Caldeira et al., 2015) and frequent changes in the soil nutrient content (Esselink and van Gils, 1994). The high density of shrubs in invaded stands with their dense shallow rooting system can promote the drying out of the surface soil layers and thus a decreased deep soil moisture recharge, contributing to the lower recovery and resilience of the oak trees in the invaded stands (Rolo and Moreno, 2011). However, in areas with no water limitations or with other shrub species (*Retama sphaerocarpa*), competition may be absent (Rolo and Moreno, 2011). Therefore, the effect of the understory in the ecophysiological status of trees in the Iberian oak *dehesas* could depend on the shrub species that are involved and on water availability, which, in turn, may depend on other characteristics like topography (Rolo and Moreno, 2011; de Sampaio e Paiva Camilo-Alves et al., 2013). On the other hand, the high density of evergreen shrubs in the invaded stands

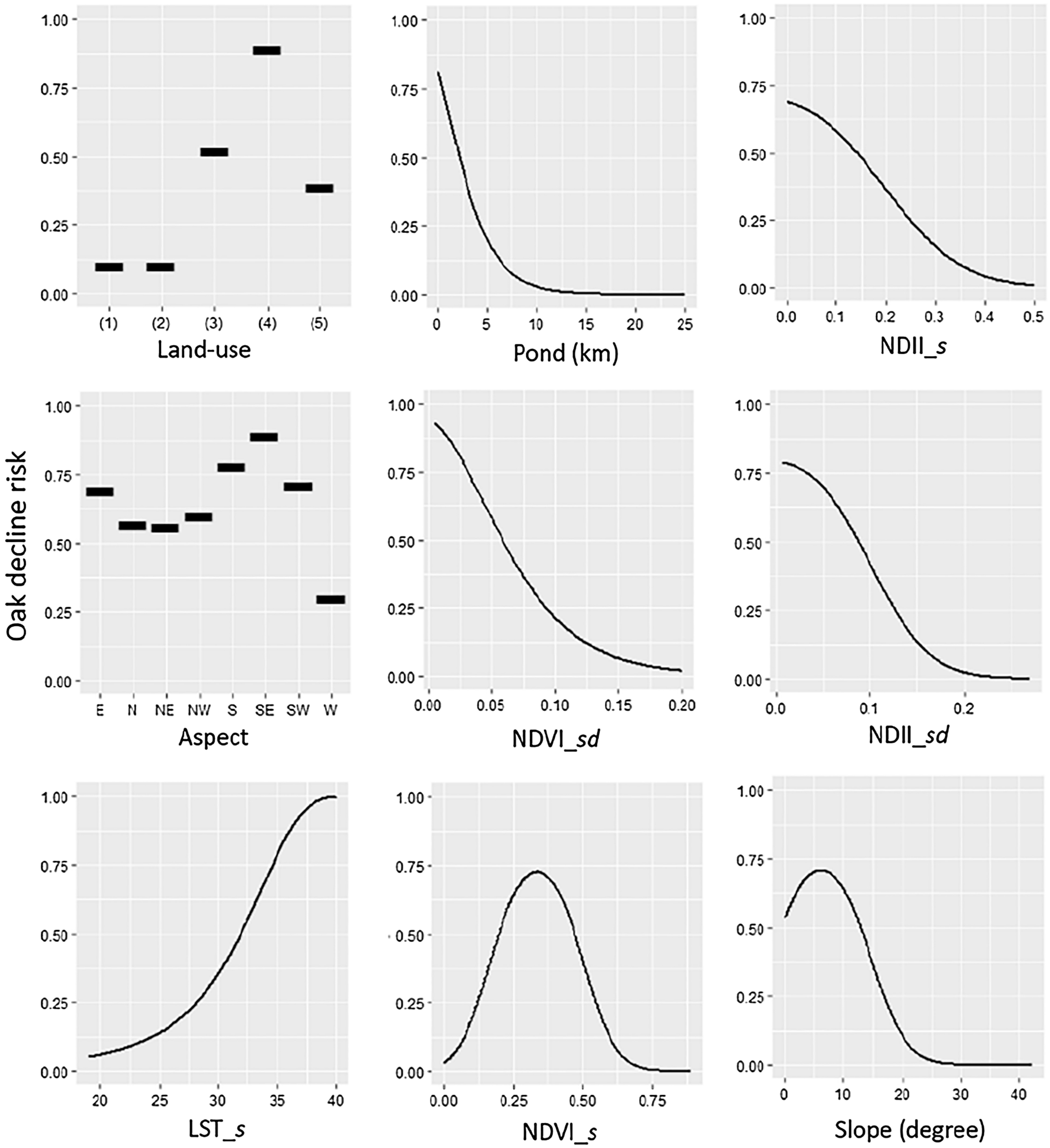

Fig. 3. Response curves of the variables most related to oak decline risk. Response curves were calculated for the full model calibrated with all oak decline foci in the study area. See Table 1 for variable descriptions.

can promote P deficiency in the soil, due to a competitive advantage of shrubs on these soils by their higher efficiency of nutrient use (Esselink and van Gils, 1994). This might therefore contribute to the lower recovery of the affected trees in the invaded stands.

Oak trees experiencing decline in Spain have been influenced by some extent by human activities. Oak trees forming *dehesas*, have been managed to obtain multiple products and benefits. The continued exploitation of these stands has been intensified in response to new socioeconomic circumstances, which lead, in most cases, to an inappropriate use of the forests, causing damages over the system and in particular over the natural regeneration of the tree layer (González-Alonso, 2008). For instance, *dehesas* where livestock are feeding directly on the acorns from the trees, usually lose stability and suffer damages when the carrying capacity is exceeded. The creation of closed areas with fences in order to keep the animals from gaining weight in a particular portion of the *dehesa*, often cause problems such as compression of the soil, contamination of soils by an excessive accumulation of excrements, dust accumulation over the leaves and numerous mechanical damages on trees (e.g., debarking of the base of trunks) (González-Alonso, 2008). These problems can result in a loss of tree vigour and in a decrease of natural regeneration due to lack of viable seeds on the site.

The existence of water bodies (i.e., ponds) near the areas affected by decline were associated with an increase in OD risk probabilities. This

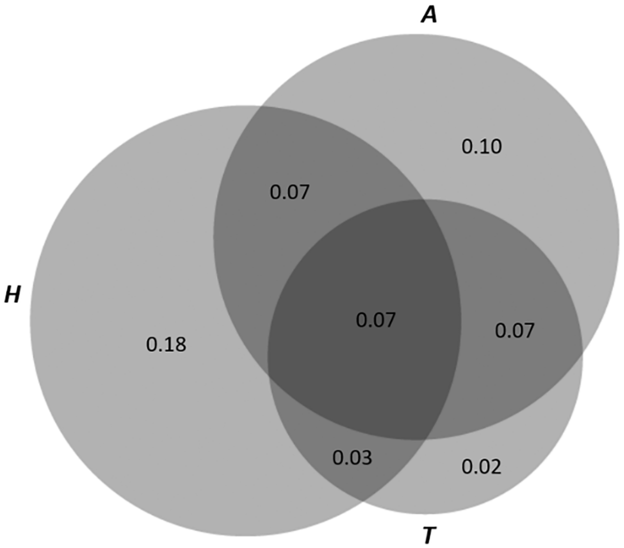

Fig. 4. Variation partitioning of the occurrence of oak decline in study area. Each circle corresponds to a group of variables. (*H*) human influence, (*A*) abiotic stress and (*T*) topographic conditions. The numbers within the circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared (overlapped part of circles). R^2 unexplained = 0.46.

finding is considered interesting from the point of view of the soil waterlogging in the study area. These water bodies are usually built for the use of water by livestock and irrigation of forage crops. Thus, repeated and/or protracted rain periods could increase the waterlogging around affected trees. In European oak forests, waterlogging can affect the health of trees due to a deficient soil aeration (Gaertig et al., 2002). Moreover, high water content favours root infection by pathogenic fungi (Hernández-Lambraño et al., 2018). In fact, Duque-Lazo et al., (2016) and Duque-Lazo et al., (2018) report distance to water bodies (i.e., rivers) and water retention capacity of the soil as powerful predictors of OD caused by *P. cinnamomi*. Water is known as the natural dispersal medium of *P. cinnamomi*. In this sense, ponds in affected stands by *P. cinnamomi*, are likely to be able to maintain the humidity for longer periods and/or free running water in the soil, this, together with the presence of root of the host, can allow for colonization of new trees (Duque-Lazo et al., 2018).

Unsurprisingly, soil water availability significantly influenced the presence of **OD**, with dryer areas (i.e., low **NDII** index) associated with affected sites. Similarly, dryer areas were associated with low **NDVI** indices. These findings can be used to inform management both in terms of species choice when planting new areas, but also the choice of site preparation and silvicultural systems employed. In European Mediterranean regions, successive droughts have been a recent climatic feature of most areas with **OD** presence, and thus has frequently been proposed as the primary factor in these declines (Allen et al., 2015). Repeated and protracted drought periods in unmanaged stands can affect the health of oak trees via two distinct pathways: (i) carbon starvation, which is a gradual process that occurs when stomata close, restricting transpiration and limiting photosynthesis; and (ii) xylem embolisms, this hydraulic failure can result in a substantial impairment of xylem transport (Bréda et al., 2006; Rodríguez-Calcerrada et al., 2017a, 2017b). In this manner, the trees can be predisposed for the impact of additional stressors; or can suffer severe damages due to an inefficiency in regeneration processes if they are already weakened by the action of other stress factors (Thomas, 2008). Indeed, General Circulation Models forecast an increase in drought frequency, duration, and intensity, which might decrease the distribution areas suitable for oak trees (Acácio et al., 2017) and enhance the performance of oak-related pests (Duque-Lazo et al., 2018). Oak trees will probably undergo substantially stronger water limitations by the end of the 21st century (Ruffault et al., 2014), phenomenon recently observed in the south of France during the four last decades and which raises the question of oak forests' vulnerability in the future (Ruffault et al., 2013). On the other

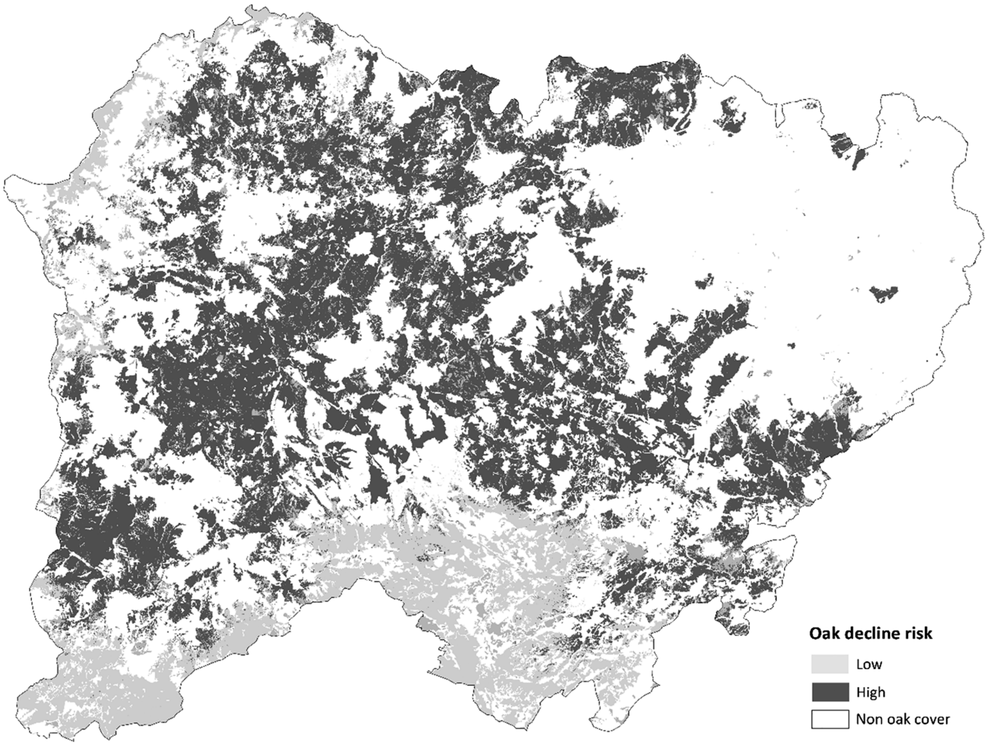

Fig. 5. Current probability of oak decline using MaxEnt modelling. Colour range indicates the probability of OD occurrence in central-western Spain oaks. We classified probability categories for the OD risk map according to occurrence probability as < 0.35 (low) and ≥0.35 (high).

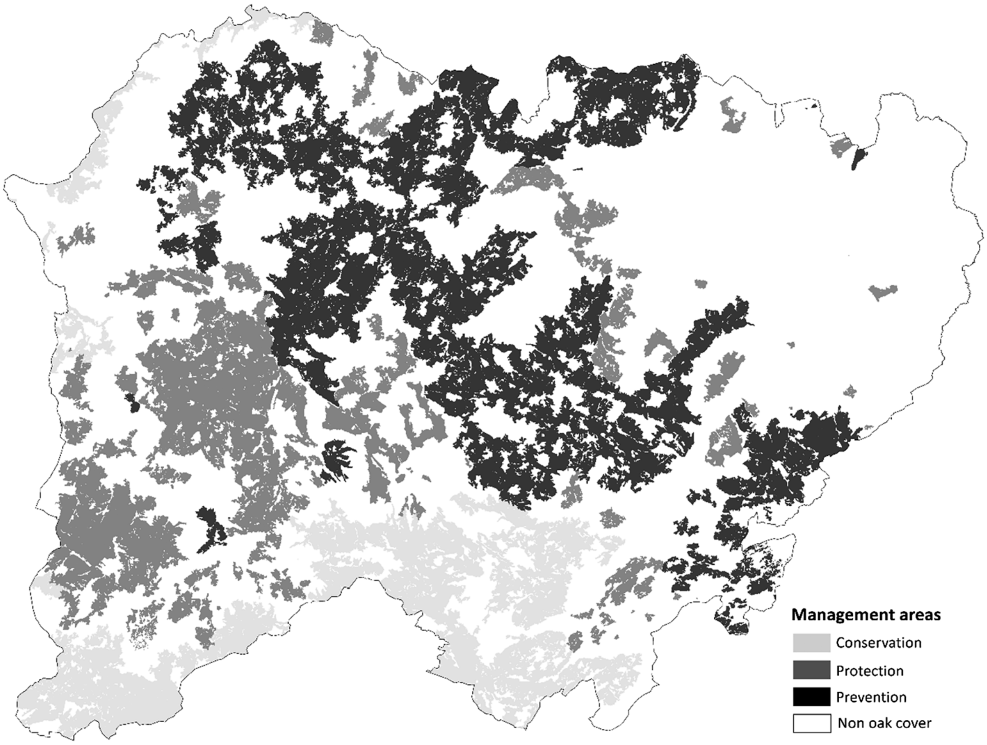

Fig. 6. Proposed areas for management interventions focused to reduce the negative impact of Oak Decline in central-western Spain oaks. Prevention (black), for areas with identified **OD** occurrence; protection (dark grey), for areas where **OD** is currently absent, but its occurrence is predicted with high probability; and conservation (light grey), for areas where **OD** is currently absent, and its occurrence is predicted with low probability.

hand, future predictions of OD caused by *P. cinnamomi* in southern Spain suggest an expansion of the pathogen distribution in response to climate change scenarios (Duque-Lazo et al., 2018). This therefore, could increase the incidence of periods favouring the growth of this pathogen and, thus increase its negative impact on the oaks in central-western Spain.

Concerning topographic features, low slope gradients with south or southeast facing orientation were associated with higher **OD** risk. In such geomorphic conditions the enhanced water stress may be caused by a more intense solar radiation. Similar trends were also registered by Costa et al. (2010) for cork oaks in south-western Portugal. In North America, Kabrick et al. (2008) also reported that decline in deciduous oak was more severe in southernly or south-westerly slopes. Moreover, the probability of **OD** risk was associated positively with soil temperature (i.e., **LST**): the higher soil temperature, the higher the risk of **OD** occurrence. In fact, as has been shown in Haldimann et al. (2008) an increase in temperature could affect tree performance by limiting photosynthesis. This negative effect could be exacerbated by a long-lasting combination of drought and high solar irradiance in Iberian Mediterranean regions, leading to the sudden death of affected trees or gradual decline until their death (Leininger, 1998; Haldimann et al., 2008).

In this study, variance-partitioning demonstrated that the different categories of variables exerted a clear influence on **OD** risk. In our case, it is important to note that the shared component had a significant proportion of the variation, indicating strong dependent contributions of the three sets of predictors explaining distribution patterns of **OD** in central-western Spain. In fact, **OD** occurrence in Iberian oaks is considered a complex multifactorial phenomenon, involving the combination of predisposing factors operating at tree, stand, and landscape scales (Rodríguez-Calcerrada et al., 2017a, 2017b). In most cases, none of these factors have acted alone (de Sampaio e Paiva Camilo-Alves et al., 2013). The simultaneous interaction of at least two stress agents–where one of them comprises an extreme climatic event (e.g., drought)–has triggered important outbreaks of decline (Rodríguez-Calcerrada et al., 2017a, 2017b).

4.2. Potential distribution of oak decline and insights for prioritising target areas and measures for intervention

We developed a spatially explicit model to represent the potential distribution of **OD** in central-western Spain. The strength of our model relies on the availability of high-quality records of **OD** foci for the study area, a robust dataset of explanatory variables (Land-use and Remote-sensing derivate variables) and a biologically relevant selection of the most important variables explaining the **OD** risk. Remote-sensing techniques (space-borne and air-borne remote-sensing instruments) have transformed ecological research by providing both spatial and temporal perspectives on ecological phenomena that would otherwise be difficult to study (He et al., 2015; Vogeler and Cohen, 2016). A key advantage of these techniques is the capability to perform synoptic, spatially continuous and frequent observations of ecological indicators without interpolation or geographical biases at varying spatial and temporal resolutions (He et al., 2015), advantages that have huge potential when it comes to improving the ability to predict one of the most important phenomenon that threat the biodiversity of the forest ecosystems in the Iberian Peninsula.

Despite the MaxEnt models each being calibrated with distinct non-colinear variables (i.e., topography, abiotic stress and human influence) they exhibited a good discrimination capacity, the combination of the best variables in the final model resulted in the increase in mean AUC. This increase is likely to be caused by a reduction of commission errors, suggesting that the combination of the best variables narrows model predictions to areas that have high risks of OD. This supports earlier findings that OD is considered a complex multifactorial phenomenon, involving the combination of predisposing factors operating at tree, stand, and landscape scale (Rodríguez-Calcerrada et al., 2017a, 2017b; Duque-Lazo et al., 2018). Given the observed occurrence of **OD**, predictions of its potential distribution across the study area suggest that a further expansion of this phenomenon is possible along the northern and central part of the study area, where the *dehesa* is the main component of the landscape and the local economy. Moreover, special attention in monitory efforts should focus on the northwest and southern part of the Salamanca province. These zones dominated by oak forests have been included in the European lists of priority habitats for conservation, (Annex I of Council Directive 92/43/EEC) which provide a wide variety of environmental benefits: structural and biological diversity, environmental stability (erosion, climate, nutrient and water cycles, fire), tourism, cultural heritage, among others.

According to the identification of **OD** foci and predicted risk probability, management strategies are required to prevent a possible expansion into target areas with high socioeconomical and environmental values. However, the implementation of a general management strategy that satisfies the requirements of the proposed areas for management interventions (see Fig. 5), is a complex task (Duque-Lazo et al., 2018). Each site might need a specific study to assess the combinations of factors related to the **OD** and, consequently, a customised management strategy (Sena et al., 2018). Forestry practices have been widely recognized as the main management strategy to alleviate oak decline (Rodríguez-Calcerrada et al., 2017a, 2017b). For areas with identified **OD** occurrence (i.e., prevention area), we propose the following measures (Table 3): Selective thinnings of suppressed stems to increase irradiance and the availability of soil water and nutrients for residual trees (Rodríguez-Calcerrada et al., 2011). This increase in resources availability is reflected in a better physiological status of residual trees (Rodríguez-Calcerrada et al., 2017a, 2017b; Cabon et al., 2018). In addition, other studies developed in the Iberian Peninsula found a relationship between oak cover and the presence of *P.cinnamomi* (Duque-Lazo et al., 2018). Girdling selected stems in multi-stems trees. This practice could favour the accumulation of nonstructural carbohydrates above the girdled zone and produce more acorns (Oberhuber et al., 2017; Rodríguez-Calcerrada et al., 2017a, 2017b). The inoculation of endophytes or chemical cocktails could be a promising practice to recover the vigour of weakened trees, particularly those with a significant cultural value. However, its use on a forest-wide basis is likely to be unadvised (Clatterbuck and Kauffman, 2006; Rodríguez-Calcerrada et al., 2017a, 2017b). **OD** has mainly been related to biotic factor such as *Phytophthora* sp. and xylophage insects (Cerambyx complex). Thus, the prevention of the spread of *Phytophthora* sp. together with control over the population densities of the beetles should be implemented to limit the expansion of **OD** into areas with high socioeconomical and environmental values (for more details about these management strategies see Duque-Lazo and Navarro-Cerrillo, 2017; Duque-Lazo et al., 2018). Regarding *dehesas* where livestock graze, a good planning of the grazing activities is crucial. Recommendations lead to avoid grazing at the end of summer and beginning of autumn, mainly for decreasing damages caused by the animals on the natural regeneration of the oak trees (González-Alonso, 2008). Postponed grazing plans are more appropriate to be sustainable when oak decline is already taking place.

For the protection areas (Table 3), we recommend improving the existing trees by selectively cutting smaller trees from the midstory and thinning the trees by removing some of the larger trees to develop oak seedlings and saplings (Clatterbuck and Kauffman, 2006). These practices also reduce the number of less desirable competitors. (Rodríguez-Calcerrada et al., 2017a, 2017b) In conservation areas (Table 3), the sowing of acorns and planting of young seedlings are viable strategies to assist sexual regeneration (Rodríguez-Calcerrada et al., 2017a, 2017b). For initial seedling growth and survival, the selection of microsites of sowing/planting is important. In general, sowing/planting should be conducted in forest understories and gaps where canopy cover is enough to moderate solar radiation and improve soil physicochemical properties (Rey Benayas et al., 2005). Likewise, these sites should not provide excessive shade or competition for availability of soil water and nutrients (Rey Benayas et al., 2005; Dickie et al., 2007). The optimal light availability ranges from 20 to 50% of full sunlight among species and populations (Gardiner et al., 2001). One factor that is being given increasing consideration in sowing/planting practices is the use of plant material from species with higher genetic tolerance to drought (Aitken and Bemmels, 2016). Finally, the preservation of marginal oak populations could therefore be crucial to species' conservation (Rodríguez-Calcerrada et al., 2017a, 2017b).

The application of these forestry practices could reduce the expansion and strength of the OD disease. However, an important factor to guarantee the success of these recommendations is for different collectives to address the issue. Therefore, support from the government is crucial in these cases. Specifically, in Spain, if a Quercus' *dehesa* becomes unproductive, the owners will be unlikely to apply treatments for the recovery of the trees unless they can be sure that these practices will actually work in the short term and that they will be able to obtain benefits again. In this sense, it is of upmost importance that the government economically supports these recommendations for mitigating the negative impact of the decline process.

5. Conclusions

This study provides new insights into the complex spatial distribution of **OD** and reveals the degree to which predisposing factors can explain its distribution in central-western Spain. **OD** distribution seems to be principally influenced by land-use, followed by dryer areas and areas with low slope gradients facing south or southeast. Given the higher likelihood of occurrence of OD in oak areas embedded in a *dehesa* matrix, the government of Salamanca should propose and encourage management actions against OD, focusing on prevention of expansion of this phenomenon from current presence zones, protection of suitable zones and conservation of unsuitable zones. Guidelines should be put in place carefully and each site must be studied and treated individually due to the complex etiology of the OD. Finally, our modelling approach provides an important decision tool for the control, monitoring and restoration of declining Iberian oaks.

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Conflict of interest statement

We declare that we have no conflict of interest.

Author contributions

All authors contributed to the formulation of ideas and the writing of the manuscript.

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