Forecasting oak decline caused by *Phytophthora cinnamomi* in Andalusia:

Identification of priority areas for intervention

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Highlights

• Mediterranean oaks are endangered by infection with an invasive alien oomycete.

• Forecasts based on SDM showed an expansion of the plant pathogen within Andalusia.

• Our SDMs verified the known environmental suitability and provided new insights.

• Phytosanitary management zones may be set from the current and future distribution.

Abstract

Since the mid-20th century, trees in the Andalusian oak dehesa and forests have exhibited stress that often ends in the death of the tree. These events have been associated with *Phytophthora cinnamomi,* a soil-borne root pathogen, which causes root rot, bark cankers, decay and mortality - known as oak decline. *Phytophthora cinnamomi* is most virulent under high ambient temperatures combined with moist soils, i.e., in Mediterranean areas. We used presence/absence point locations of the Andalusian Network for Damage Monitoring in Forest Ecosystems (RED SEDA) pathogen survey and four categories of environmental variables - meteorological, edaphic, topographic and tree cover - to accurately predict *Phytophthora cinnamomi* current and future potential distribution within Andalusia, for a range of climate change scenarios, using ensemble species distribution models (SDMs). We assessed which categories of environmental variables explained the distribution of the pathogen, obtained accurate predictions for the current potential distribution of *Phytophthora cinnamomi* (AUC>0.95, TSS>0.70, Kappa>0.65) and forecasted its future potential distribution. Subsequently, we classified the sites of the pathogen survey within the RED SEDA network in three zones according to the already-recorded presence of the pathogen and the current and future predicted probability of occurrence. Finally, we suggested phytosanitary management strategies for each zone.

Key words: biomod2, Ensemble Species Distribution Modelling, Mediterranean oak woodlands, Oak Decline, *Phytophthora cinnamomi*

1. Introduction

Phytophthora cinnamomi Rands (Pc) is a soil-borne root pathogen, which causes root rot, bark cankers and mortality of many plant species including trees (e.g. oak, olive); shrubs and herbs (Serrano *et al.*, 2011; Shearer *et al.*, 2012; Jung *et al.*, 2017). This pathogen spreads by chlamydospores and water-borne zoospores. Its mycelium grows in the cortical cells, phloem and xylem of roots weakening the host. Pc is most virulent in high (>30ºC) ambient temperatures combined with moist soils (Shearer *et al.*, 2007; Burgess *et al.*, 2017; Jung *et al.*, 2017). The oomycete has been reported in eastern South Africa (Zentmyer, 1988), southern California (Kovacs *et al.*, 2011; Cunniffe *et al.*, 2016), western Australia (Shearer *et al.*, 2004; 2007; 2012) and southern Europe (Brasier, 1996; Duque-Lazo *et al.*, 2016); all areas with a Mediterranean climate; that is cool, wet, snow-free during winters alternating with hot, dry summers (de Sampaio e Paiva Camilo-Alves *et al.*, 2013; Scanu *et al.*, 2013; Burgess *et al.*, 2017). Since the mid-20th century, *Quercus* species in Andalusia have exhibited stress that usually ends in the death of the tree and have been associated with Pc (Brasier, 1996; Sánchez *et al.*, 2002).

In Andalusia, the evergreen Holm and Cork oak (*Quercus ilex* L. and *Q. suber* Lam.) are common trees. Locally, semi-deciduous Portuguese oak (*Quercus faginea* L.) and the Pyrenean oak (*Quercus pyrenaica* Willd.) occur. These oaks are widespread in the dehesa, an agro-silvo-pastoral ecosystem (Campos *et al.*, 2013; Duque-Lazo and Navarro-Cerrillo, 2017) with 10 –80 trees per hectare of semi-natural pasture, locally rotated with fodder crops (Esselink and van Gils, 1994; Campos *et al.*, 2013). Dehesa is usually monospecific and the oaks are uniformly spaced and lopped to maintain an open tree canopy for pasture and crop. Until the 1960s African swine fever epidemic, the dehesa was primarily an acorn-Iberian hog-charcoal farming system and since then mainly transformed into beef cattle and/or sheep ranching with a recreational hunting component (e.g. Paniza Cabrera, 2015). The crop (grains; vetch; clover) serves the livestock component. Dehesa is found in undulating and hilly terrain (Esselink and van Gils, 1994) while at steeper slopes oak forest occurs.

Worldwide, drier climates are forecasted for the 21st century in the Mediterranean Basin. In particular, a rise in mean annual temperatures of 0.3 to 0.5 °C and a decrease of about 15% in the average annual precipitation until 2050 (Acacio *et al.*, 2016) is expected. Recent studies show productivity decline (Iglesias *et al.*, 2016; Pulido *et al.*, 2017), reduced environmental tolerance (San Miguel-Ayanz *et al.*, 2016) and increased mortality (Colangelo *et al.*, 2017) in oaks, mainly related to changes in climate and/or land use (Godinho *et al.*, 2016). The transformation of dehesa farming in the 1960s may have contributed to the spread of the oak decline caused by Pc (Beaufoy, 1998; Plieninger *et al.*, 2015). In addition, climate change might enhance the activity of oak related pathogens, as Pc (de Sampaio e Paiva Camilo-Alves *et al.*, 2013; Burgess *et al.*, 2017), xylophage insects (Duque-Lazo and Navarro-Cerrillo, 2017) and other pests and diseases (Lieutier and Paine, 2016). For example, Pérez-Sierra *et al.* (2013) claimed that higher minimum winter temperatures might have a positive effect on Pc virulence.

Oak decline caused by Pc is a phytosanitary issue in Spain (Pérez-Sierra *et al.*, 2013), Portugal (Moreira and Martins, 2005; de Sampaio e Paiva Camilo-Alves *et al.*, 2013) and elsewhere in the Mediterranean Basin (Balcì and Halmschlager, 2003; Scanu *et al.*, 2013). The strategy is to prevent invasion of new areas by Pc by reduction of zoospores dispersal. Where the oomycete has been identified, access of humans, animals and nurseries stock is restricted. Other practices are application fungicide (e.g. potassium phosphonate), liming (Serrano *et al.*, 2012) and planting resistant oak (de Sampaio e Paiva Camilo-Alves *et al.*, 2013).

The potential geographic distribution of Pc under current climatic conditions has been modelled globally (Burgess *et al.*, 2017), for Europe (Brasier and Scott, 1994), France (Desprez-Loustau *et al.*, 2007), Italy (Scanu *et al.*, 2015), southwestern Spain and southwestern Australia (Duque-Lazo *et al.*, 2016) and southwestern USA (Cunniffe *et al.*, 2016) at coarse resolutions

(>1 km^2) based, among others on meteorological data. To the best of our knowledge, the distribution of Pc has not been forecasted based on climate change scenarios, at fine resolution and at subnational level.

The aim of this study is to forecast the distribution of Pc and therefore the future extent of the oak decline caused by Pc and determine which drivers influence its spatial distribution. Firstly; we assessed the importance of non-collinear variables from the Andalusia Environmental Information Network (REDIAM) dataset consisting of four categories of environmental variables: meteorological, edaphic, topographic, tree cover and their combinations. Secondly; the different categories of environmental variables were used individually and combined to predict the current distribution of Pc. Thirdly; model predictions were projected into the future to assess the distribution of the pathogen under climate change scenarios. Finally, the current and future probability of occurrence was intersected with the Andalusian Network for Damage Monitoring in Forest Ecosystems (RED SEDA) point locations to suggest an appropriate management strategy for control of Oak decline caused by Pc.

2. Material and Methods

2.1. Study area

We selected the area within Andalusia region (36.06º - 40.11º N and -8.09º - -1.47º W; 87,268 km^2) covered by semi-natural oak vegetation, of which about a third is covered by the dehesa (Figure 1). Andalusia is the southernmost region of Spain and is situated in the Mediterranean climatic domain, except for small areas above 2,000 m a.s.l. (Figure 1).

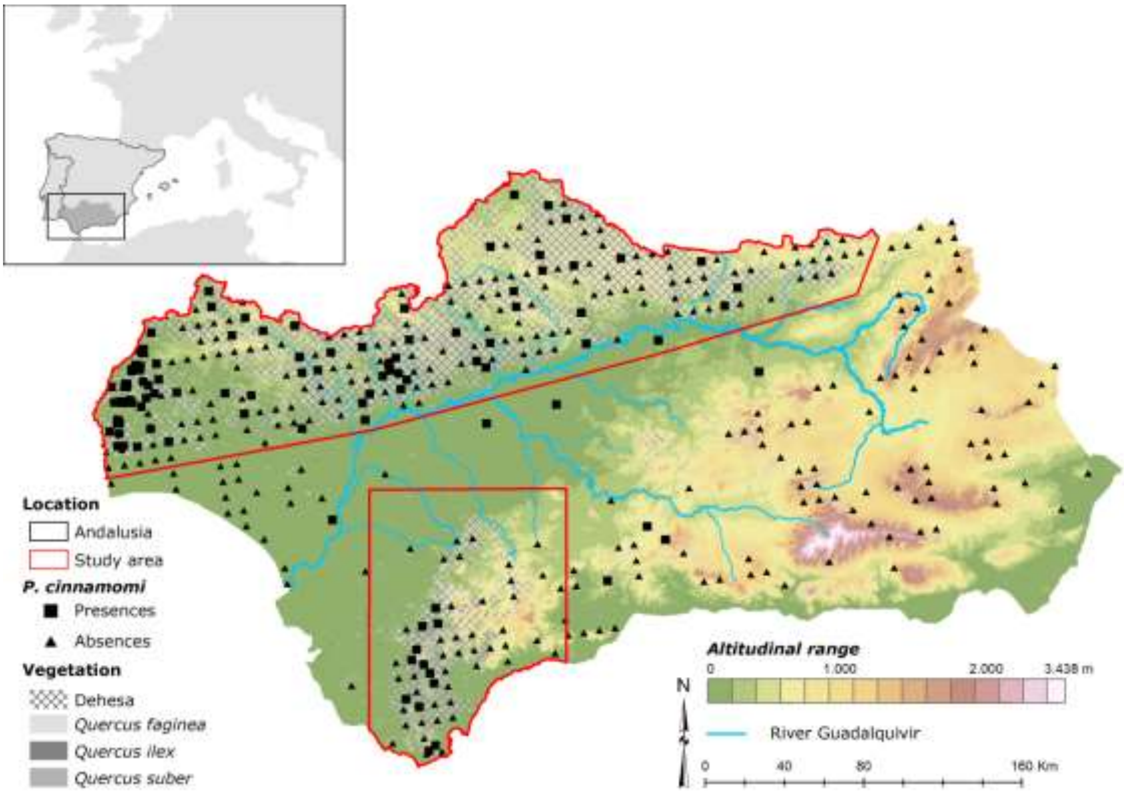

Figure 1. Location of the study area and the presence/absence of *Phytophthora cinnamomi* against the background of the *Quercus spp*. distribution, elevation, Guadalquivir River and the dehesa.

2.2. Phytophthora cinnamomi data

Location records (2001-2013) of the presence (n=125) and absence (n=203) of Pc were extracted from the Andalusian Network for Damage Monitoring in Forest Ecosystems (RED SEDA; Junta de Andalucía, 2016) and from Duque-Lazo *et al.* (2016). The RED SEDA surveys the plots centered at the nodes of an 8 x 8 km grid established by a random systematic sample design within the dehesa and oak forest areas (Figure 1). Within each plot, twenty-four living trees (diameter at breast height >7cm), located around each grid node, are annually inspected visually for the following decline symptoms: chlorosis, cankers or defoliation without an apparent causal agent (Duque-Lazo and Navarro-Cerrillo, 2017). In addition, the surveyors take two soil samples per tree with decline symptoms, one close to the trunk and the other at a distance of 1.5 m. Subsequently, the laboratory at Cordoba University tests for the presence of *P. cinnamomi* by soil analysis (Ruiz-Gomez *et al.*, 2012).

2.3. Environmental variables

The environmental data layers were downloaded from the Andalusia Environmental Information Network (REDIAM; http://www.juntadeandalucia.es/medioambiente/site/rediam/portada/). The dataset (72) contains four categories of variables: meteorological (e.g. temperature, precipitation, evapotranspiration; 18), topographic (e.g. elevation, slope steepness, slope aspect; 24), edaphic (e.g. texture, soil pH, sand content; 17) and tree cover (e.g. tree density, coniferous, broadleaf, woodland, 13). The meteorological data cover the period from 1960 to 2000 and the topographic variable were obtained and re-sampled from a digital elevation model with 5 meter spatial resolution (Junta de Andalucía, 2016). All variables were re-sampled to a final spatial resolution of 200x200 m (Table 1, Appendix A).

The number of initial variables (72) was reduced by stepwise analysis of collinearity (Kukunda *et al.*, 2018) and a selection procedure based on the optimisation of the Area Under the Curve (AUC) of the receiver Operating characteristic (ROC) value generated by the random forest (RF) model using the AUCRF R package (Calle *et al.*, 2011). Variables with a Variance Inflation Factor (VIF)>10 were removed from the posterior analysis (Table 1). The collinearity analysis was performed in R (R Core Development Team, 2017) using the R package usdm (Naimi, 2013).

We generated ensemble species distribution models (SDMs) with all combinations of the four categories of variables (Table A1, Appendix A) and forecasted for the periods 2011-2040, 2041-2070 and 2071-2099. For each period, we considered four Global Circulation Models (BCM2, CNCM3, ECHAM5, EGMAM) and three special reports on emission scenarios (SRA1B, SRA2, SRB1; IPCC, 2014). In addition, we averaged the layers of the climate forecasts of the four considered Global Circulation Models (GCMs) into a merged model (MEAN), which was used as another layer set to predict the future distribution of Pc; i.e., we ended up with five GCMs (BCM2, CNCM3, ECHAM5, EGMAM, MEAN) and three scenarios (SRA1B, SRA2, SRB1),

Table 1. Accuracy of all combinations of categories of predictor variables. AUCcv: AUC value after cross-validation. No cat: number of categories; No var: Number of selected variables; Model selection (bold font) by AUC.

Categories of environmental variables	**Max AUC**	**AUC cv**	**No cat**	**No var.**	**Model (*codes for variables in Table A.1, Appendix A*)**
Tree cover + Climate + Topographic	**0.806**	**0.777**	**3**	**8**	**TP_ELEV+FR_OAK+NDC+ETO+TP_PEND+NDF+COD_HID+DS_WATER**
Tree cover + Topographic + Edaphic	**0.796**	**0.775**	**3**	**6**	**FR_OAK+TP_ELEV+CA+PH+TP_RSD_V+CRAD**
Tree cover + Topographic	**0.795**	**0.778**	**2**	**6**	**TP_ELEV+FR_OAK +TP_PEND+ COD_HID+DS_WATER+TP_RSD_O**
Tree cover + Climate + Topographic + Edaphic	**0.790**	**0.776**	**4**	**6**	**TP_ELEV+FR_OAK+TP_PEND+CRAD +DS_WATER**
Tree cover + Climate + Edaphic	0.780	0.763	3	9	CA+FR_OAK+ETO+T_MIN+NDF+TMC+CRAD+MO_SUP+PS
Tree cover + Climate	0.776	0.764	2	8	FR_OAK+T_MAX+ETO+T_MIN+TMC+FR_OLIVE+BROADLEAVES+CONIFEROUS
Climate + Topographic	0.772	0.736	2	7	TP_ELEV+TP_PEND+ETO+TMC+COD_HID+DS_WATER+BH
Tree cover + Edaphic	0.769	0.756	2	9	FR_OAK+CA+OH+MO_SUP+MO+ARC+FR_WATER+FR_OLIVE+BROADLEAVES
Climate + Topographic + Edaphic	0.767	0.734	3	6	TP_ELEV+PH+LIM+MO_SUP+DS_WATER+TMC
Edaphic	0.745	0.730	1	4	CA+PH+MO_SUP+CIC
Climate + Edaphic	0.744	0.721	2	8	CA+ETO+MO_SUP+TMC+T_MIN+NDF+CRAD+DF
Climate	0.739	0.720	1	2	T_MIN+ETO
Topographic + Edaphic	0.721	0.700	2	6	CA+TP_PEND+MO_SUP+COD_HID+TP_RSH_O+PS
Topographic	0.720	0.693	1	4	TP_ELEV+TP-PEND+COD_HID+TP_RSH_O
Tree cover	0.689	0.636	1	2	FR_OAK+FCC_TREE

generating 15 possible future predictions of Pc distributions per combination of explanatory variables (Duque-Lazo *et al.*, 2018).

2.4. Species Distribution Models

We used all 10 SDM techniques available in the biomod2 R package (See footprint Figure 3). Ensemble models were built to reduce the biases and limitations inherent to the use of individual SDM techniques; the assembly platform of biomod2 version 3.3.1 was used(Thuiller *et al.*, 2017).

2.5. Model Evaluation

The evaluation model focused on quantifying the reliability of the results of the models. In the absence of an independent dataset, we split the data into 70% training and 30% evaluation subsets (Duque-Lazo *et al.*, 2016). Because SDMs predict probabilities of occurrence ranging between zero and one, but observations are binary absence/presence values (represented by zero and one, respectively), a transformation was required to validate model output. This can be done by setting a threshold, and recoding probabilities into presence or absence. However, the selection of a threshold for recoding may be subjective and therefore we applied a threshold-independent statistic, the area under the curve (AUC) of receiver operator plots, to evaluate the discriminatory capacity of the model output. In addition, maximum Cohen's Kappa and the maximum True Skills Statistics (TSS, Allouche *et al.*, 2006) were used. These defined the threshold as the value where this statistic reaches its maximum value. AUC values above 0.9 represent high discriminatory capacity for a distribution model, while values between 0.7 and 0.9 indicate models with good discriminatory capacity (Thuiller *et al.*, 2003). Cohen's Kappa (K) corrects the overall accuracy of model predictions for the accuracy expected to occur by chance, values close to one represents perfect agreement. The TSS compares the number of correct forecasts, minus those attributable to random guessing, to that of a

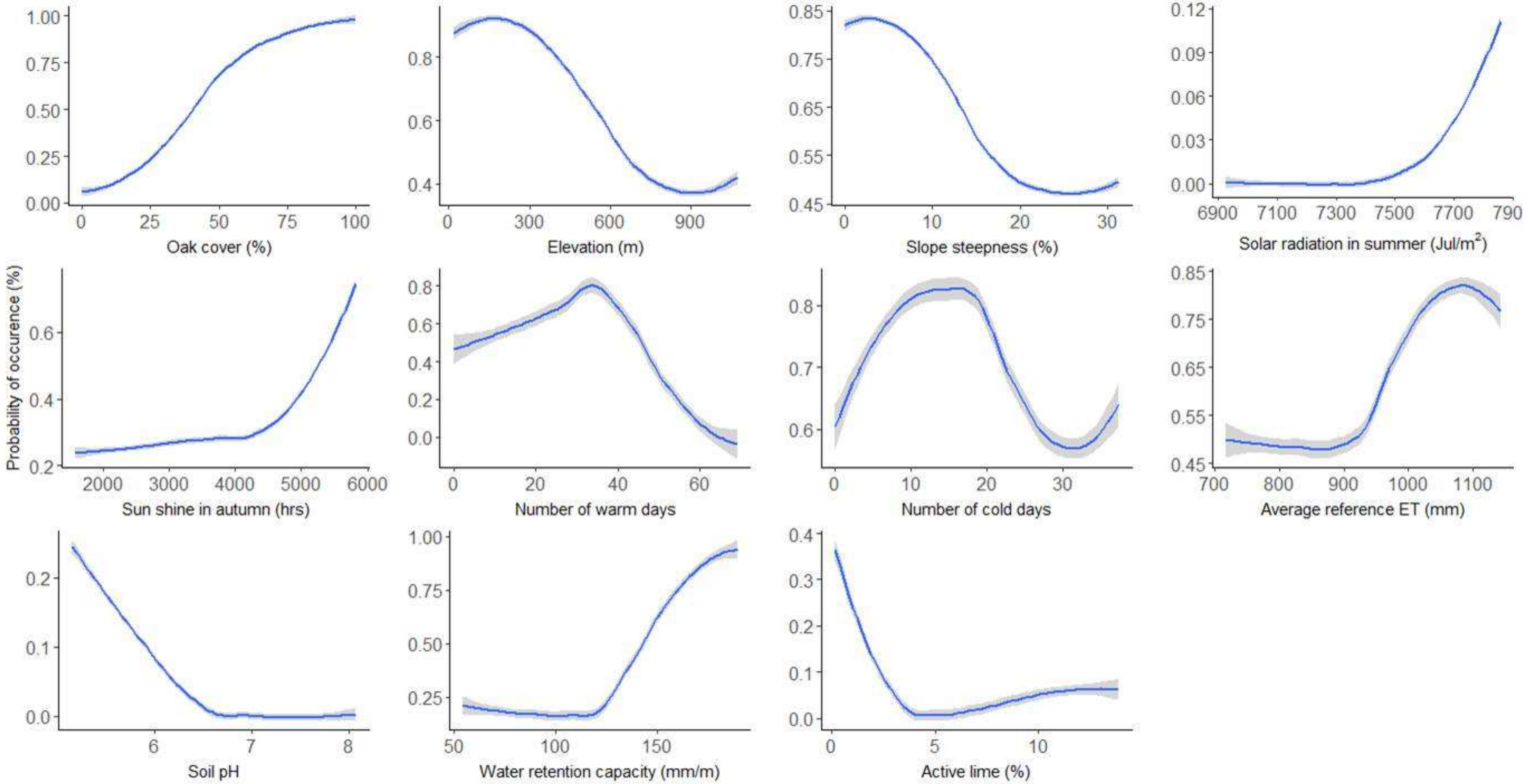

Figure 2. Average response curve of *Phytophthora cinnamomi* for the selected models (see Table 2). Grey band indicates the standard deviation between the response curves of different model predictions selected in Table 2.

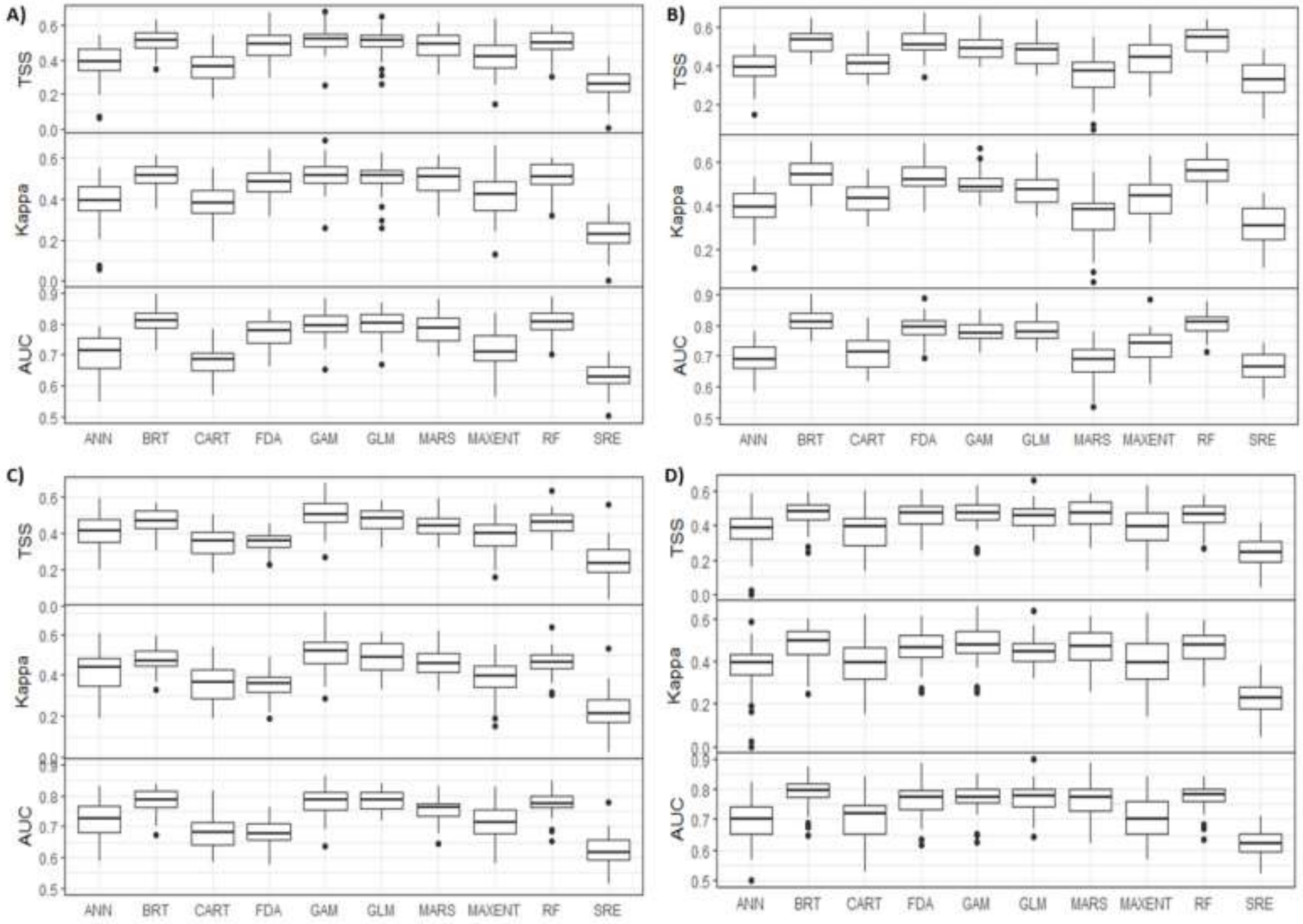

Figure 3. Boxplots of adjusted accuracy values (AUC, Kappa, TSS) obtained with the following ten different distribution model algorithms: Artificial Neural Networks (ANN), Boosted Regression Trees (BRT), Classification and Regression Tress (CART), Flexible Discriminate Analysis (FDA), Generalize Additive Models (GAM), Generalize Lineal Models (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MAXENT), Random Forest (RF) and Surface Range Envelop (SRE). A) Tree cover, climatic and topographic variables; B) Tree cover, topographic and edaphic variables; C) Tree cover and topographic variables; and D) Tree cover, climatic, topographic and edaphic variables.

hypothetical set of perfect forecasts, where +1 indicates perfect agreement and zero or negative values indicate a performance no better than random (Allouche *et al.*, 2006)..

2.6. Ensemble modelling

Ensemble models combine several distribution models to obtain a single model minimizing the biases and inaccuracies of single models(Duque-Lazo and Navarro-Cerrillo, 2017; Duque-Lazo *et al.*, 2018; Kukunda *et al.*, 2018). In this study, we report on the mean, median, coefficient of variation, upper and lower confidence interval (CISUP and CIINF respectively), committee averaging (CA) and probability mean weight decay (MWD) ensemble modelling techniques. The CISUP & CIINF are calculated as the confidence interval around the mean probability (Thuiller *et al.*, 2016). The CA was achieved by a binary (presence/absence) transformation using the threshold of single model predictions. The threshold is the maximum score of the evaluation metric (TSS) for the evaluated dataset. Subsequently, the probability value of each pixel was calculated by the mean of single pixel predictions. The MWD ensemble modelling scaled the individual model predictions according to their accuracy statistic value (AUC) and the sum of all individual models(Duque-Lazo and Navarro-Cerrillo, 2017; Duque-Lazo *et al.*, 2018; Kukunda *et al.*, 2018). We made ensemble predictions based on all single models with an AUC>0.80

2.7. Forecasts

To assess the future distribution of Pc we used the model with the best AUC values. We kept the current values of the tree cover, edaphic and topographic variables constant over the forecasted period. The climatic variables were obtained by projecting the identified important climatic variables into the future for each of the selected climate change scenarios.

2.8. Distribution maps and management strategy

To assess the priority areas for phytosanitary interventions, we developed distribution categories from the predicted current and future potential distribution of Pc and the associated distribution map of oaks. We proposed the following phytosanitary zones. Zone A for areas with identified Pc presence; Zone B for areas where Pc is currently absent but its presence is predicted with high probability under current environmental conditions or is forecasted with high probability under future climatic conditions; Zone C applies to areas where Pc is currently absent and its presence is predicted and forecasted with low probability. We classified probability categories for the distribution map as <25% (low) versus >25% (high) probability of occurrence. The 25% threshold was selected in order to favour oak conservation versus its threatened status due to the presence of Pc (Liu *et al.*, 2005). The recommended phytosanitary policy for zone A is prevention of outward dispersal of the oomycete. Zone B areas are to be protected against introduction of the oomycete. For Zone C continued monitoring of the symptoms of oak decline caused by Pc is foreseen.

3. Results

3.1. Model selection

The combination of non-collinear variables (Table A2) of tree cover, climatic and topographic variables yielded the highest AUC (0.81) and cross-validation AUC_{cv} (0.777) value (Table 1). The combination tree cover, topographic and edaphic variables ranked second and showed a nearly-identical AUC value (0.80) and a marginally-lower AUC_{cv} value (0.775; Table 1). The combination of tree cover and topographic variables ranked third, with equally high values for AUC (0.80) and AUC_{cv} (0.778; Table 1). The combination of all four categories of variables was the fourth-most accurate, performing nearly the same as the other three models, with an AUC value of 0.79 and an AUC_{cv} value of 0.775 (Table 1). These results suggested that the distribution of Pc within the study area might be independent of the type of variables used. Furthermore, it seems that climate is less influenced category of variable.

3.2. Variable importance and response curves

Oak cover (FR_OAK) together with elevation (TP_ELEV), were the most-important environmental predictors across all four models (A-D) (Table 2). The oak cover was correlated positively and almost-linearly with the probability of Pc occurrence. The relationship between elevation and probability of Pc occurrence presented a negative relationship the higher the elevation the lower the probability of Pc occurrence. The average number of hot days (NDC) and the average number of cold days showed a decreasing probability of Pc. The lower the average reference evapotranspiration, the lower was the probability of Pc occurrence. The topographic variables showed that the oomycete avoid steep slopes and prefer zones with higher incoming solar radiation in summer and sunny autumns. The soil pH and active lime (AC) were the most-important pair of edaphic variables, but at low probability levels, followed by water retention capacity. It seems that Pc avoid alkaline soils (lower pH and high content of active lime) while it prefers soils with high water retention capacity (Figure 2).

3.3. Model selection and validation

The single-algorithm model predictions were compared by their accuracy given by TSS, Kappa and AUC and showed, overall, high model accuracy (Figure 3 A-D). The highest values were achieved by the single-algorithm models developed with the tree cover, climatic and edaphic variables, followed by the model developed with the tree cover, edaphic and topographic variables and the model built with tree cover and topographic variables; the models developed with the complete set of variables presented the lowest accuracies. AUC values >0.85 were reached by GAM, GLM, MAXENT, RF and BRT, though MAXENT generally showed a higher standard deviation. Overall, the BRT and GAM delivered the best accuracies, considering the

Table 2. Variable importance ranking for models built with combinations of the four categories of variables A-D). In bold selected variables to run the forecast. Selected variables in bold.

Nº Selected Variables	**A) Tree cover, Climatic & Topographic**			**B) Tree cover, Topographic & Edaphic**			**C) Tree cover & Topographic**			**D) All categories**		
	Variable	*Importance*	*Probability*	*Variable*	*Importance*	*Probability*	*Variable*	*Importance*	*Probability*	*Variable*	*Importance*	*Probability*
1	**Elevation**	**18,96**	**1,00**	**Elevation**	**22,81**	**1,00**	**Elevation**	**31,97**	**1,00**	**Elevation**	**26,84**	**1,00**
2	**Oak cover**	**16,83**	**1,00**	**Oak cover**	**21,90**	**1,00**	**Oak cover**	**28,18**	**1,00**	**Oak cover**	**22,27**	**1,00**
3	**Warm days**	**14,61**	**0,95**	**Active lime**	**17,23**	**0,99**	**Slope**	**23,46**	**1,00**	**Slope**	**16,36**	**0,97**
4	**Evapotranspiration**	**13,71**	**0,95**	**pH**	**16,38**	**0,97**	**Hydraulic conditions**	**21,05**	**0,84**	**Water retention**	**16,09**	**0,90**
5	**Slope**	**12,02**	**0,85**	**Radiation summer**	**13,61**	**0,81**	**Distance to water**	**20,63**	**0,97**	**Distance to water**	**15,36**	**0,95**
6	**Cold days**	**11,75**	**0,69**	**Water retention**	**13,20**	**0,84**	**Radiation autumn**	**17,62**	**0,51**			
7	Hydraulic cond.	11,19	0,66									
8	Distance to water	10,18	0,59									

Table 3. Adjustment values obtained with the ensemble models of *Phytophthora cinnamomi*. A-D from Table 2.

	Ensemble model	Kappa	TSS	AUC	Sensitivity	Specificity
A)	**Ensemble model**	**Kappa**	**TSS**	**AUC**	**Sensitivity**	**Specificity**
	Mean	0.69	0.70	0.93	0.90	0.80
	Lower Confident interval (CIINF)	0.69	0.70	0.93	0.83	0.86
	Upper Confident interval (CISUP)	0.69	0.70	0.93	0.90	0.81
	Median	0.68	0.68	0.92	0.86	0.83
	Committee averaging (CA)	0.70	0.72	0.95	0.94	0.78
	Probability mean weight decay (MWD)	0.69	0.70	0.93	0.90	0.80
B)	**Ensemble model**	**Kappa**	**TSS**	**AUC**	**Sensitivity**	**Specificity**
	Mean	0.65	0.65	0.90	0.78	0.87
	Lower Confident interval (CIINF)	0.64	0.64	0.89	0.79	0.85
	Upper Confident interval (CISUP)	0.67	0.66	0.90	0.78	0.89
	Median	0.64	0.65	0.88	0.82	0.83
	Committee averaging (CA)	0.65	0.66	0.92	0.86	0.79
	Probability mean weight decay (MWD)	0.65	0.65	0.90	0.78	0.87
C)	**Ensemble model**	**Kappa**	**TSS**	**AUC**	**Sensitivity**	**Specificity**
	Mean	0.63	0.63	0.91	0.89	0.74
	Lower Confident interval (CIINF)	0.63	0.63	0.90	0.89	0.74
	Upper Confident interval (CISUP)	0.62	0.63	0.91	0.90	0.74
	Median	0.62	0.62	0.89	0.90	0.72
	Committee averaging (CA)	0.68	0.65	0.93	0.71	0.94
	Probability mean weight decay (MWD)	0.63	0.63	0.91	0.89	0.74
D)	**Ensemble model**	**Kappa**	**TSS**	**AUC**	**Sensitivity**	**Specificity**
	Mean	0.63	0.63	0.91	0.89	0.74
	Lower Confident interval (CIINF)	0.63	0.63	0.90	0.89	0.74
	Upper Confident interval (CISUP)	0.62	0.63	0.91	0.90	0.74
	Median	0.62	0.62	0.89	0.90	0.72
	Committee averaging (CA)	0.68	0.66	0.93	0.71	0.94
	Probability mean weight decay (MWD)	0.63	0.63	0.91	0.89	0.74

three statistics (Kappa, TSS and AUC). The maximum values obtained for TSS were acceptable (>0.65) for RF, BRT, MAXENT and GAM; as well as the Kappa values (K>0.65) for GAM and BRT. The predictive performance of the rest of the single-algorithm models was poorer (Figure 3). The ensemble models outclassed the accuracy of the single-algorithm model predictions with an overall AUC>0.90 (good), TSS>0.63 (acceptable) and K>0.60 (acceptable). The committee averaging (CA) ensemble approach built with the combination of tree cover, climatic and topographic variables generated the highest individual AUC (0.95), Kappa (0.70) and TSS (0.72) values. Moreover, this ensemble model presented a true positive rate (sensitivity) of 0.94 and a true negative rate (specificity) of 0.78 (Table 3). With the same set of response variables, the mean and MWD ensemble models also returned accurate predictions (Table 3).

3.4. Distribution maps: Predicted and forecasted distribution

A high probability of occurrence was predicted in western and central north Andalusia (Figure 4). The second area with a high probability of occurrence was Los Alcornocales Natural Park in the southwest (Figure 4), while the eastern part of the study area showed lower probabilities of occurrence. Consequently, even without climate change nearly all oak formations seem to be threatened. The Pc distribution area was forecasted to shrink in the coming decades (Figure 5). Later on, the Pc distribution may increase (GCM, CNCM3 and ECHAM5, Figure 6). Only minor differences in the forecasted distribution areas were obtained with the various climate scenarios and ensemble models. The forecasted direction of the expansion is the same across scenarios and ensemble models (Figure 5).

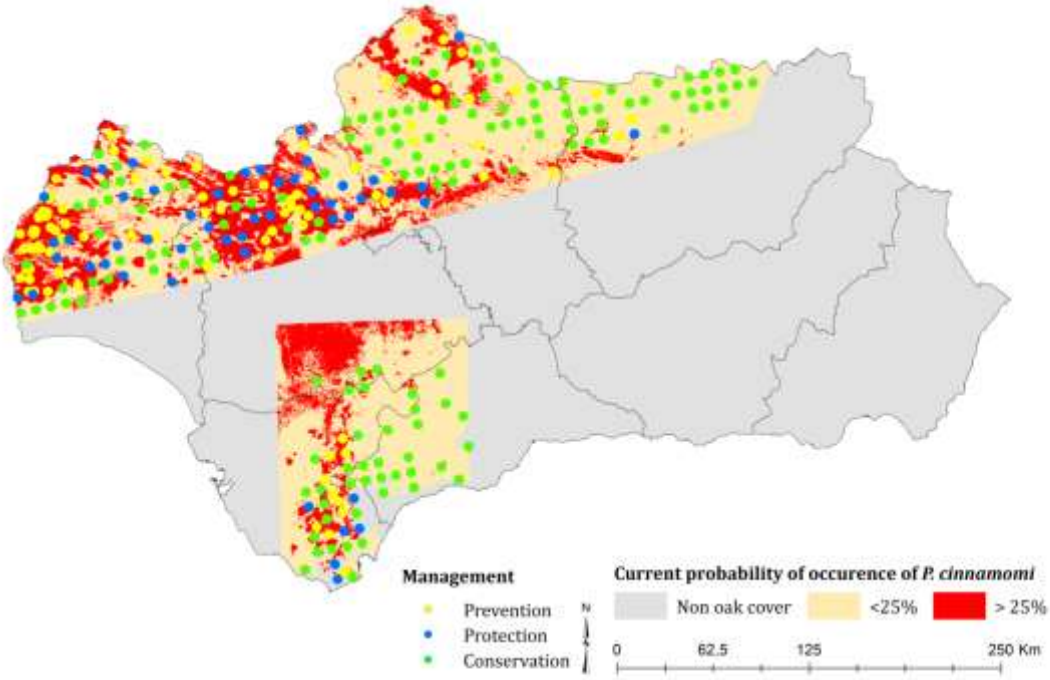

Figure 4. Current probability of oak decline caused by *Phytophthora cinnamomi* occurrence as predicted by the committee averaging ensemble models in Table 3A built with tree cover, climatic and topographic type of environmental variables;

The distribution area of Pc within Andalusia might expand in response to climate change scenarios (Figure 6). All forecasted based on the GCMs and scenarios showed larger suitability areas for Pc in 2099 compared with the prediction for the current climate condition. The forecasts showed a downward trend in the next two decades up to 2040 and from them an upward trend ultimately exceeding the predicted current distribution. The most-pessimistic scenarios were provided by CNCM3 and ECHAM5 in the SRA1B scenario. The average forecasted trend (MEAN) was a rapid decrease until 2040, a rapid gain until 2070 and a minor increase in the last period (Figure 6). The ensemble model estimated by MWD over-predicted the distribution of Pc in comparison with the prediction assessed by the CA ensemble model (Figure 6).

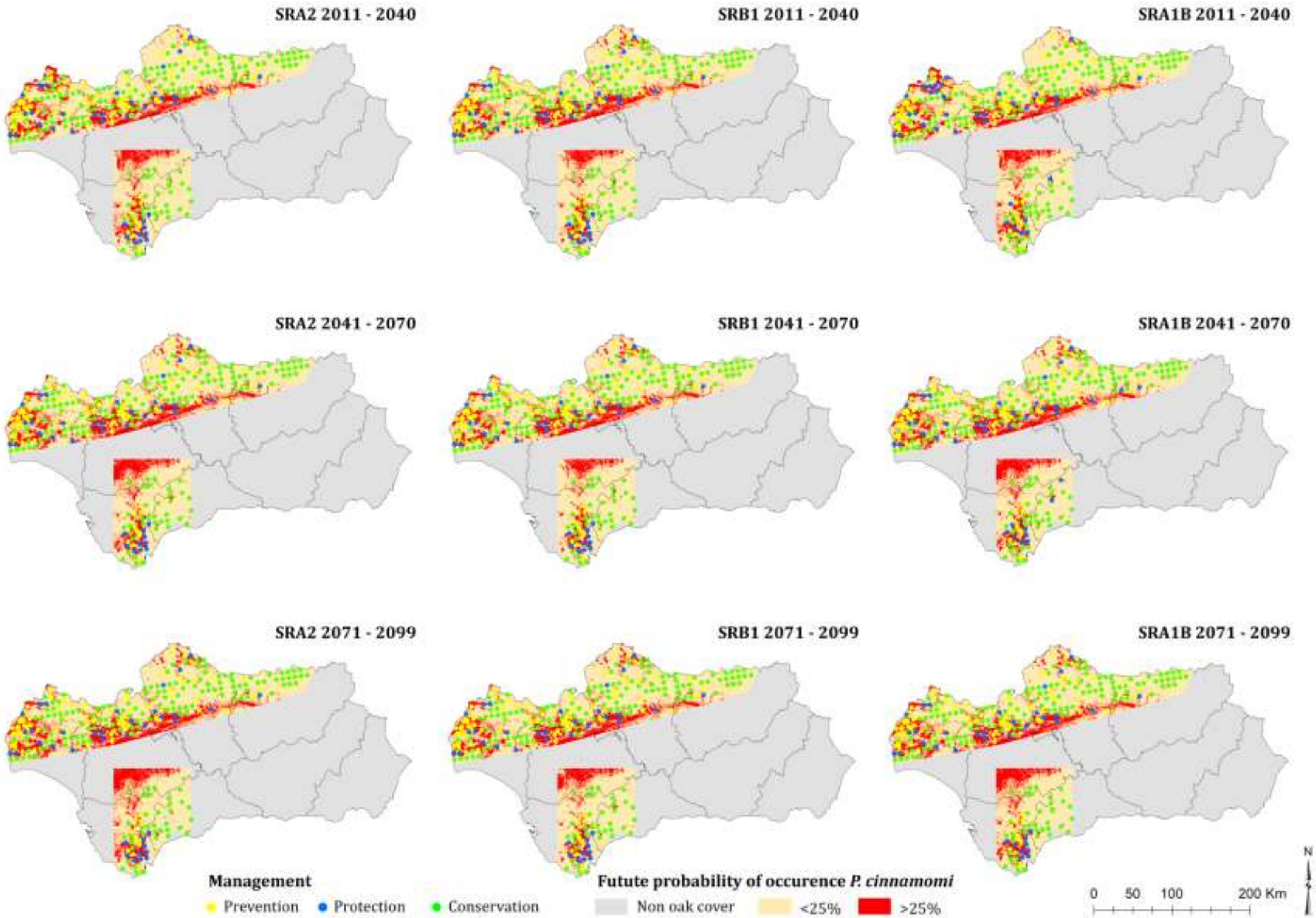

Figure 5. Future potential distribution *of Phytophthora cinnamomi* across future climate change scenarios estimates by the MEAN GCM and predicted by committee averaging ensemble model built with tree cover, climatic and edaphic variables. Colour range indicated the probability of occurrence of *Phytophthora cinnamomi* and colour dots refers to the assigned management zones to the RED SEDA point locations.

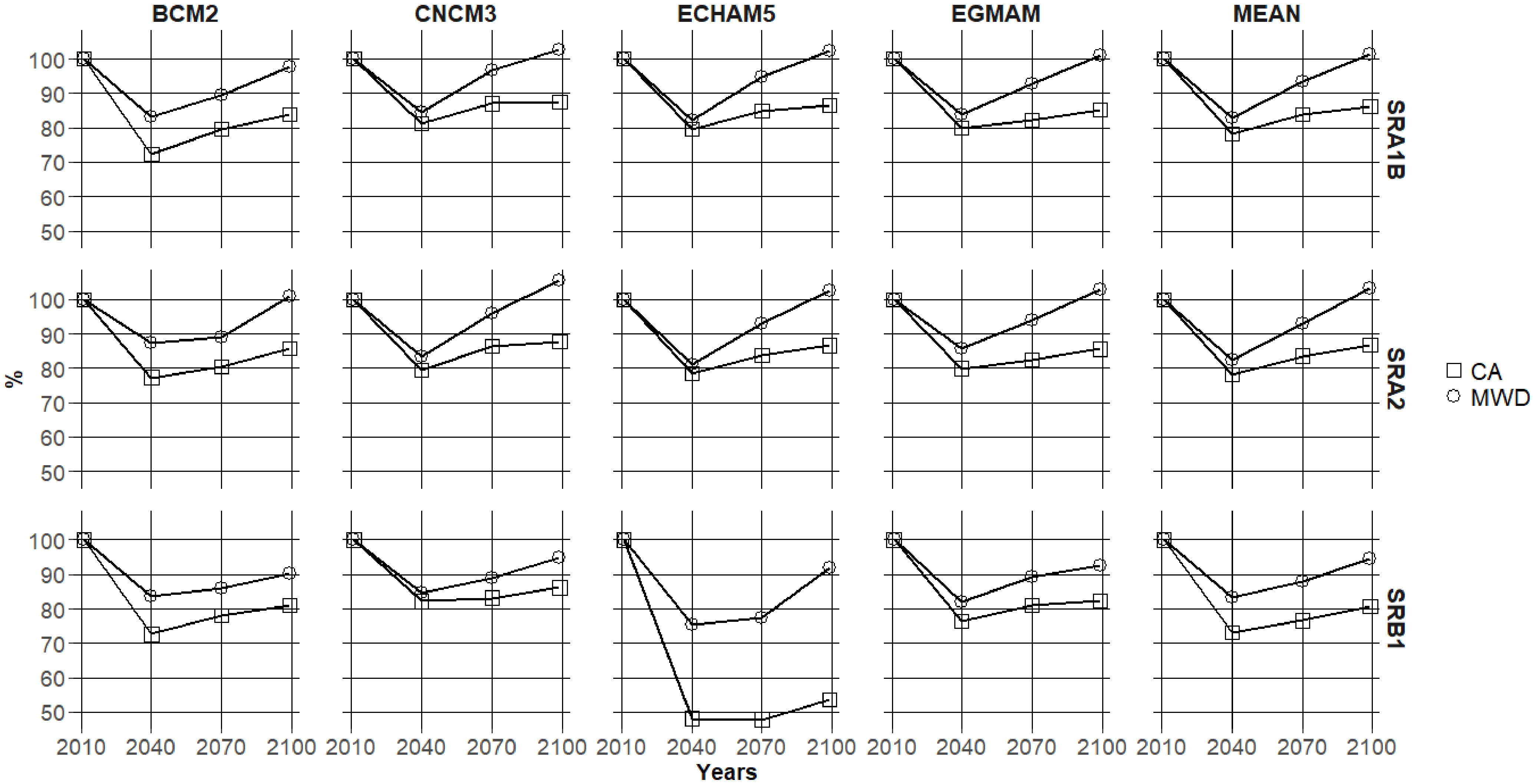

Figure 6: Percentage of loss area of habitat suitability of *Phytophthora cinnamomi* under future projections (2040. 2070 and 2099); different scenarios (SRA2. SRA1B and SRB1), five Global Circulation Models (GCM): BCM2, CNCM3, ECHAM5, EGMAM and MEAN; Percentage of habitat suitability increased/decreased over the total present (100%) area of *Phytophthora cinnamomi* predicted by the Probability Mean Weight Decay (MWD) and Committee averaging (CA) ensemble model.

3.5. *Analysis of current and future protection and conservation*

There were detected 120 sites (38%) with Pc (yellow dots) and 203 sites (62%) without it (blue and green dots; Figures 4 & 5; Table 4). All sites where Pc was present were dominated by oak (*Q. ilex, Q. suber, Q. faginea* or *Q. pyrenaica*). At the sites with Pc, prevention of the dispersal of the oomycete has been recommended (de Sampaio e Paiva Camilo-Alves *et al.*, 2013). We have assumed that the actual presence of Pc will remain constant over time and therefore the need for dispersal prevention as well (Table 4). In the current situation there are more sites in conservation zones than in protection zones. Under the forecasted conditions, conservation would have to be converted to protection zones. Conversion to conservation zoning status would be most often required for oak-dominated sites.

Table 4: Percentage of points classified according to the current and future management zones based on the forecasted probability of occurrence of *Phytophthora cinnamomi*. All refers to all tested sites and oak dominated stands to those sites where oaks were the main species. Values represent the percentage of sites presence in each category.

Scenarios	Year	***All***			***Oak dominated stands***		
		Prevention	**Protection**	**Conservation**	**Prevention**	**Protection**	**Conservation**
Present	2011	38,11	9,45	52,44	19,51	5,79	37,50
SRA1B	2040	38,11	10,98	50,91	19,51	7,32	35,98
	2070	38,11	11,28	50,61	19,51	7,32	35,98
	2099	38,11	10,98	50,91	19,51	6,71	36,59
SRA2	2040	38,11	10,98	50,91	19,51	7,32	35,98
	2070	38,11	11,28	50,61	19,51	7,62	35,67
	2099	38,11	11,28	50,61	19,51	6,71	36,59
SRB1	2040	38,11	10,98	50,91	19,51	7,62	35,67
	2070	38,11	10,98	50,91	19,51	6,71	36,59
	2099	38,11	12,20	49,70	19,51	7,62	35,67

4. Discussion

4.1. *Categories of environmental variables*

Our study reveals that it is possible to predict the current and future distribution of the oak decline caused by *Phytophthora cinnamomi* within the oak cover in Andalusia and, consequently determine which drivers influence in its spatial distribution. The current distribution could be assessed by various combinations of two to four categories of environmental variables (Table 1, first four rows). However, the nearly-identical model outcomes suggest that these categories might be spatially related notwithstanding prior removal of collinear variables (Table A2, Appendix A). Substitution of major categories of variables without effect on SDM accuracy was also reported elsewhere (van Gils *et al*., 2014). Combinations of tree cover, climatic and topographic variables were also used successfully to predict the distribution of *Phytophthora ramorum* associated with Sudden Oak Death in Oregon (Václavík *et al.*, 2010). In Addition, dispersal distance at the ten meters scale differentiated the actual from the potential distribution of the *Phytophthora sp*. Instead in our study, tree cover and flow direction were used as a proxy of Pc dispersal direction (Sena *et al.*, 2018). Earlier predictions of the potential distribution of *Phytophthora sp*. used a more limited set of variable categories (Wilson *et al.*, 2003; Meentemeyer *et al.*, 2004; Guo *et al.*, 2005; Moreira and Martins, 2005; Václavík *et al.*, 2010; Chadfield and Pautasso, 2012; Scanu *et al.*, 2013; Duque-Lazo *et al.*, 2016).

These studies mainly considered climatic and land cover predictors of potential host species. Soil variables have rarely been taken into account (but see Moreira and Martins, 2005), though the impact of edaphic variables on infection by Pc has been established (Corcobado *et al.*, 2013). Moreover, soil waterlogging, soil depth and soil compaction have also been identified as significant factors associated with Holm and Cork oak decline (de Sampaio e Paiva Camilo-Alves *et al.*, 2013) and has been pointed out that the distribution of Pc at landscape level depend on soil moisture and temperature (Sena *et al.*, 2018).

4.2. *Selected variables and response curves*

As expected, topographic variables (elevation, slope steepness, solar radiation, hours of sunshine and distance-to-water) contributed to the resulting models (Duque-Lazo *et al.*, 2016).

Elevation and Slope steepness could be proxies for oak presence/absence in the coarser resolution of the cited previous article. The importance of oak related variables together with topographic variables suggests that the topo-climate variables, elevation and Incoming Solar Radiation, were better spatial climatic predictors for the pathogen than the regional meteorological climate variables. Elevation might be a ‘paradoxical’ climate proxy in the context of probability of occurrence of oak decline caused by Pc. This may be explained by the nature of DEM-derived data (elevation and Incoming solar radiation) versus are interpolated point measurements of meteorological stations that are further apart than the grid size of the digital elevation model. Moreover, meteorological stations are unlikely to be randomly distributed in the research area and/or elevation and/or aspect (van Gils *et al.*, 2014). We found that the higher the elevation (the colder the climate), the lower the probability of the pathogen occurrence; the lower the reference evapotranspiration (the wetter the soil) the higher the probability of the pathogen (both as expected). The steeper the slope, the lower the probability of the pathogen; this might be related to the water availability. In steeper slopes can water run off downhill carrying the spores of Pc. We found that cover of the potential Pc host (*Quercus* sp.) was positively related with the probability of occurrence of Pc (cf. Guo *et al.,* 2005; Chadfield and Pautasso, 2012; Duque-Lazo *et al.*, 2016).

The response curves of the number of frost and hot days were Gaussian, which is at an intermediate number of days with extreme temperatures, high or low, the probability of the pathogen is high. This seems fitting for a species of tropical origin (Jung *et al.*, 2017) as in the tropics temperatures are neither so low nor such high as at montane Mediterranean elevations or continental Mediterranean latitudes (Sena *et al.*, 2018).

Furthermore, cold and hot stresses were also found to be relevant indicators of the probability of occurrence of Pc (Burgess *et al.*, 2017), as were minimum and maximum temperature (Meentemeyer *et al.*, 2004) or mean summer temperature (Duque-Lazo *et al.*, 2016). The importance of the number of days with minimum temperature <5ºC in our models corresponds with the finding that Pc occurs in areas free of severe frosts (Burgess *et al.*, 2017). The increased probability of occurrence with the number of days above 35ºC might be related to the ability of Pc to cope with drought better than the roots of the oaks (de Sampaio e Paiva Camilo-Alves *et al.*, 2013). Moreover, it has been found winter temperature controls the distribution of Pc at landscape level (Burgess *et al.*, 2017; Sena *et al.*, 2018).

We found that the more alkaline the soil, the higher content on active lime, the lower the probability of Pc occurrence. Pc shows low virulence and incidence in soils with medium-high calcium content in Andalusia (Serrano *et al.*, 2012) and Australia (Broadbent and Baker, 1974); therefore, the Australian liming remedy has been recommended for Andalusia (Serrano *et al.*, 2012). The higher the water retention capacity of the soil (the wetter the soil, i.e. the longer the soil might stay wet), the higher the probability of Pc. Water it is known as the natural dispersal medium of Pc. Pc requires humid soil, soils with high water retention capacity tend to maintain the humidity for longer periods, or free running water in the soil together with the presence of root of the host to be able to colonize new individuals (Sena *et al.*, 2018). Consequently, oak growing in acid soil with high water retention capacity might be more suitable to be infected.

4.3. *Model accuracy*

The most accurate individual models were BRT, GAM, RF, GLM and MAXENT. The robustness of MAXENT and GLM for Pc distribution in Andalusia has been reported previously (Duque-Lazo *et al.*, 2016). Elswhere, RF has been shown to be a solid alternative (Duque-Lazo *et al.*, 2018). Although the Kappa values were sometimes acceptable (>0.70, GAM), mostly they were only just better than random (>0.65). As expected, the ensemble model approach achieved still -higher accuracies (Duque-Lazo and Navarro-Cerrillo, 2017). Though, TSS values were mainly acceptable (>0.70), Kappa value rarely was over 0.70 (see committee averaging ensemble model, Table 3A). These results suggest that we developed models with high discriminatory capacity but we assessed acceptable accurate maps. This might be due to that we are estimating the spatial distribution of an invasive species which is not in equilibrium with the environment (Václavík and Meentemeyer, 2009).

4.4. Distribution maps

The areas highlighted as higher probability of occurrence of the oak decline caused by Pc corresponded with already positive identified presence of the pathogen. The probability of occurrence of Pc increased in areas closer to the Guadalquivir River (Duque-Lazo *et al.*, 2016), while the areas identified with high probability of occurrence decreased north-east. This trend might have a climate component determine by lower temperatures which is support by the future predictions increasing the probability of occurrence in areas closer to the Guadalquivir river (Duque-Lazo *et al.*, 2016; Sena *et al.*, 2018).

4.5. Forecast distribution

Our forecast of Pc distribution shows a reduction of the habitat suitability in the next two decades and expansion afterwards, assuming the unchanged presence/absence of the host oak over the forecasting period. However, climate change may also affect oak distribution. The distribution of Holm oak has been predicted to expand (Vayreda *et al.*, 2016), while those of Cork, Portuguese and Pyrenean oaks within Andalusia were predicted to diminish under the CNCM3 SRA1B climate change scenario (López-Tirado and Hidalgo, 2016). Moreover, the decreased might be given for an increasing aridity in the study area.

4.6. Identification of priority areas for intervention

Sixty percent of the surveyed sites were classified as protection or conservation zones, mostly within oak-dominated stands. Consequently, strategies are required to prevent the spread of the oomycete. However, the implementation of a general management strategy, which satisfies the requirements of each site, is a complex task. Each site might need a specific study to assess the combinations of factors related to the oak decline caused by Pc and, consequently, a customised management strategy (Sena *et al.*, 2018).

We propose the following measures for zone A (Table 5): restricted entry of humans and animals, avoidance of earth moving or activities with the potential to move soil and the wash-down of cars, boots and tools(Dell *et al.*, 2005; Shearer *et al.*, 2007; Sena *et al.*, 2018). In addition, the following are also recommended: disinfection with potassium phosphonate (Corcobado *et al.*, 2013; de Sampaio e Paiva Camilo-Alves *et al.*, 2013), use of calcium containing fertilisers or lime (Serrano *et al.*, 2012), trunk injections of potassium phosphonate (Moreno and Obrador, 2007) and afforestation with resistant tree species or resistant varieties of *Quercus* sp. (Weste and Marks, 1987; Sena *et al.*, 2018). Liming or calcium containing fertilisers might be only applied where Cork oak is not present (de Sampaio e Paiva Camilo-Alves *et al.*, 2013). In zone B (Table 5), we recommend wash-down of cars and boots upon entry, prohibition of the introduction of plant material from nurseries that are not certified free of *Phytophtora* sp. and afforestation with resistant oak varieties (Weste and Marks, 1987; de Sampaio e Paiva Camilo-Alves *et al.*, 2013). Finally, in zone C (Table 5), the entry of plant material from nurseries that are not certified free of *Phytophtora* sp. should be prohibited and hygienic and disinfection measures when people, animals or machinery enter from zones A and B should be implemented. More information about the direction for conservation and management could be found in Sena *et al.* (2018)

5. Conclusions

Andalusian dehesa are endangered by oak decline caused by Pc. Ensemble SDMs accurately predicted the current and future distributions of Pc within the oak cover of Andalusia. Topographic and tree cover variables showed to be the most important categories of variables. Climatically, the numbers of hot and cold days stood out as relevant predictors, while pH and active line were the most significant edaphic variables. The current and future potential distributions suggest that intervention measures should be implemented to prevent the dispersal of the oomycete. However, we have also identified areas within the oak distribution where Pc is not present yet and has a low probability of occurrence. The Andalusian government should propose and encourage action against oak decline caused by Pc, focusing on prevention of outward dispersal of the oomycete from the current presence zone (A), protection of suitable zones (B) and conservation of unsuitable zones (C). Guidelines should be put in place carefully and each site must be studied and treated individually due to the multi-causality of oak decline caused by Pc. These results might help to prevent the infection of oak by Pc.

Acknowledgments

We thank the "*Consejeria de Medioambiente y Ordenación del Território*" (Junta de Andalucía) and the "RED SEDA" (Junta de Andalucía) for providing the *Phytophthora cinnamomi* data. We also thank M. Jiménez Pizarro for her help with an early draft of this manuscript; and F.J. Ruíz Gómez, R. Sánchez de la Cuesta, the ERSAF group and, particularly, the staff of the Dendrochronology, Silviculture and Climate Change Laboratory at Cordoba University, for their assistance during this research.

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Appendix A

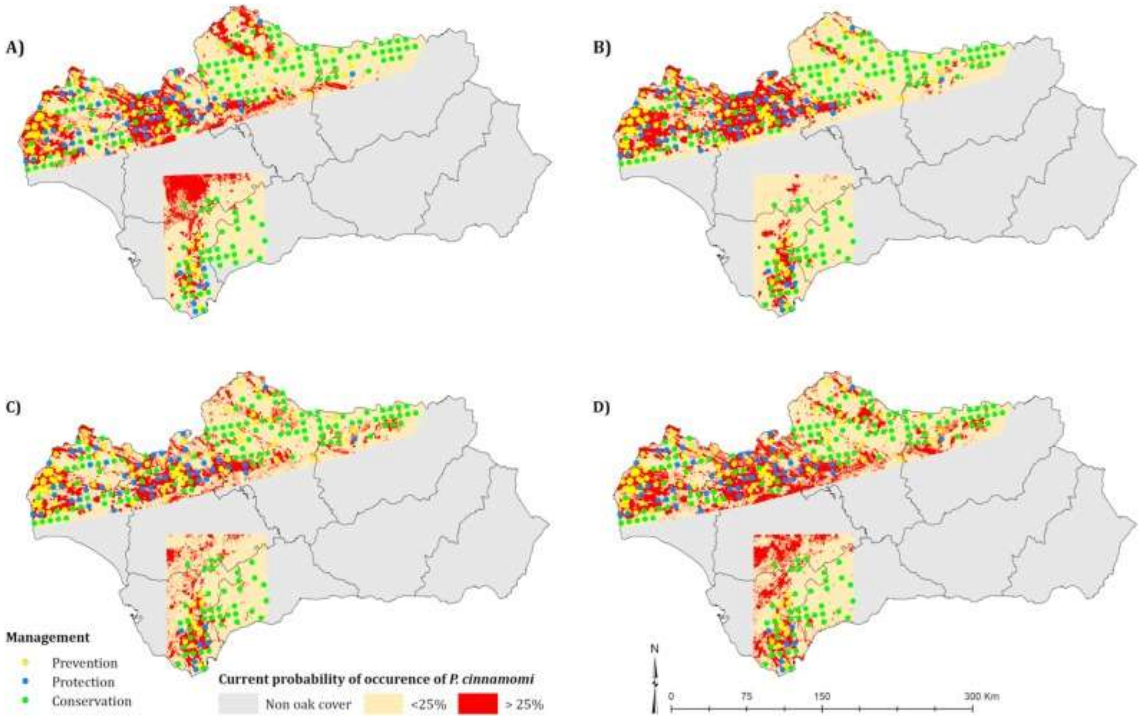

Fig. A1. Current probability of oak decline caused by *Phytophthora cinnamomi* occurrence in four classes as predicted by the ensemble models highlighted in Table 2. A) Tree cover, climatic and topographic variables; B) Tree cover, topographic and edaphic variables; C) Tree cover and topographic variables; and D) Tree cover, climatic, topographic and edaphic variables.

Table A1. Environmental data used to predict the potential distribution of *Phytophthora cinnamomi* (Source: REDIAM).

Variable	CODE	UNITS
Climatic		
Sum of water balances at the end of each month	BH	mm
Average Net Primary Production	DF	Hours
Average reference ET	ETO	mm
Aridity index	IAR	
Number of hot days (T-max ≥35 °C)	NDC	Days
Number of cold days (T-min ≤0 °C)	NDF	Days
Annual precipitation	PRC	mm
Annual radiation	RN	Julian/m^2
Annual sum negative differences of precipitation and ET	SDEF	mm
Average snow precipitation	SNOW	mm
Annual sum positive differences of precipitation and ET	SSUP	mm
Average T-max	T_MAX	°C
Average T-mean	T_MED	°C
Average T-min	T_MIN	°C
Average T-max of warmest months	TMAXC	°C
Mean temperature warmest month	TMC	°C
Mean temperature coldest month	TMF	°C
Average T-min of coldest months	TMINF	°C
Edaphic		
Average clay content	ARC	%
Average sand content	ARE	%
Active limestone	CA	%

Variable	CODE	UNITS
Cation exchange capacity	CIC	meq/100 g
Water retention capacity	CRAD	mm/m
Edaphic soil types	EDAPH	Categorical
Average silt content	LIM	%
Lithology	LITHO	Categorical
Average organic matter in the profile	MO	%
Average organic matter surface horizon	MO_SUP	%
Nitrogen content	N_SUP	%
Percent base saturation	PBS	%
Soil pH	PH	–
Soil depth	PS	cm
Substrate	SUBST	Categorical
Texture	TEXTURE	USDA-class
Average content of fine particles (Ø < 2 mm)	TF	%
Topographic		
Hydraulic conditions	COD_HID	–
Distance to pastures	DS_PAST	m
Distance to river	DS_RIVER	m
Distance to water	DS_WATER	m
Flow accumulation	FLOWACUM	L
Flow direction	FLOWDIR	m
Flow direction down	FLOWDIRD	m
Flow direction up	FLOWDIRUP	m
Composite topographic index	ICT	–

Variable	CODE	UNITS
Topographic moisture index	ITH	–
DEM	TP_ELEV	m
East – west orientation	TP_ES_OE	Degree
Slope aspect	TP_EXPO	Degree
Slope steepness	TP_PEND	Degree
Radiation in winter	TP_RSD_I	Julian/m^2
Radiation in autumn	TP_RSD_O	Julian/m^2
Radiation in spring	TP_RSD_P	Julian/m^2
Radiation in summer	TP_RSD_V	Julian/m^2
Sunshine	TP_RSH	Hours
Sun shine in winter	TP_RSH_I	Hours
Sun shine in autumn	TP_RSH_O	Hours
Sun shine in spring	TP_RSH_P	Hours
Sun shine in summer	TP_RSH_V	Hours
North to south orientation	TP_SU_NO	Degree
Tree cover		
Agroforestry	AGROF	Categorical
Broadleaf	BROADL	Categorical
Canopy FCC (Trees and shrubs)	FCC	%
Canopy FCC by trees	FCC_TREE	%
Coniferous	CONIF	Categorical
Density of trees	FR_TREE	%
Distance to tree	DS_TREE	m
Mixed forest cover	MIXF	Categorical

Variable	CODE	UNITS
Normalize difference vegetation index	NDVI	Value * 100
Oak cover	FR_OAK	%
Olive tree cover	FR_OLIVE	%
Olives grove	OLIVES	Categorical
Woodland cover	WOODLANDS	Categorical

Table A2. Collinearity analysis for each combination of response variables analysed. A) Tree cover, climatic and topographic variables; B) Tree cover, topographic and edaphic variables; C) Tree cover and topographic variables; and D) Tree cover, climatic, topographic and edaphic variables.

Models	A)	B)	C)	D)
Non-collinear variables				
Climatic				
1 BH	5.16	–	–	5.89
2 DF	5.69	–	–	6.66
3 ETO	7.86	–	–	8.41
4 NDC	6.74	–	–	7.95
5 NDF	3.13	–	–	4.17
6 RN	8.23	–	–	8.77
7 TMC	3.43	–	–	4.54
		Edaphic		
8 ARC	–	5.61	–	5.84
9 CA	–	1.86	–	2.42
10 CIC	–	2.10	–	2.41
11 CRAD	–	4.20	–	4.44
12 EDAPH	–	1.21	–	1.25
13 LIM	–	6.08	–	5.99

Models	A)	B)	C)	D)
Non-collinear variables				
14 LITHO	–	1.61	–	1.62
15 MO	–	6.14	–	6.75
16 MO_SUP	–	5.21	–	5.85
17 N_SUP	–	1.81	–	1.93
18 PH	–	3.86	–	4.34
19 PS	–	2.68	–	2.92
20 PSB	–	1.49	–	1.59
21 SUBSTR	–	2.15	–	2.34
22 TEXTURE	–	3.76	–	3.75
23 TF	–	2.30	–	2.36
Topographic				
24 COD_HID	1.36	6.38	1.22	6.34
25 DS_WATER	1.59	1.60	1.45	1.64
26 DS_PAST	1.53	1.65	1.51	1.61
27 DS_RIVER	1.24	1.23	1.22	1.24
28 FLOWACUM	3.18	5.17	4.32	3.72
29 FLOWDIR	1.42	1.50	1.42	1.45
30 FLOWDIRDOWN	1.30	1.37	1.25	1.33
31 FLOWDIRUP	3.83	6.08	5.10	4.37
32 ICT	1.80	1.84	1.82	1.81
34 ITH	3.06	2.71	2.71	2.71
35 TP_ELEV	4.00	2.85	1.86	4.89
36 TP_ES_OE	1.65	1.68	1.62	1.68

Models	A)	B)	C)	D)
Non-collinear variables				
37 TP_EXPO	1.66	1.68	1.62	1.71
38 TP_PEND	8.96	–	–	–
39 TP_RSD_I	3.93	3.53	3.46	3.95
40 TP_RSD_O	3.12	3.12	3.00	3.14
41 TP_RSD_V	7.04	3.85	3.64	4.00
42 TP_RSH_O	3.13	3.06	3.01	3.20
43 TP_RSH_P	4.82	4.96	5.14	4.88
44 TP_RSH_V	5.84	5.75	5.70	5.80
45 TP_SU_NO	2.94	3.08	2.90	2.97
Tree cover				
46 AGROF	1.82	1.84	1.85	1.99
47 BROADL	1.55	1.60	1.51	1.65
48 CONIF	1.29	1.32	1.28	1.31
49 DS_TREE	1.59	1.63	1.61	1.67
50 FCC_TREE	2.64	2.73	2.11	2.95
51 FCC_TOT	2.44	2.34	2.16	2.54
52 FR_TREE	1.59	1.62	1.55	1.66
53 FR_OLIVO	2.94	2.72	2.57	3.06
54 FR_OAK	2.29	2.45	2.17	2.53
55 MIXF	1.04	1.04	1.04	1.06
56 NDVI	1.65	1.74	1.68	1.71
57 OLIVES	2.65	2.39	2.36	2.57
58 WOODLANDS	1.27	1.36	1.24	1.36

Table A3. Parametric characterization of *Phytophthora cinnamomi* defined by the Upper Confident interval ensemble model approach developed by the tree cover, climate and topographic categories of variables (A).

Variable	Min	1st Q	Median	3rd Q	Max
Climatic					
Sum of water balances at the end of each month	24.7	631.9	974.2	1550.0	8570.0
Average Net Primary Production	560.0	1858.2	2384.0	2791.1	3935.0
Average reference ET	709.2	995.4	1029.7	1060.4	1242.4
Aridity index	56.9	143.6	170.3	197.0	321.9
Number of warm days (T-max ≥35 °C)	0.0	0.1	0.1	0.1	0.3
Number of cold days (T-min ≤0 °C)	0.0	390.3	438.8	482.6	756.0
Annual precipitation	0.0	58.0	118.7	204.7	372.3
Annual radiation	312.4	537.7	607.1	704.1	1539.5
Annual sum negative differences of rain and ET	49.2	104.0	107.0	108.6	116.6
Average snow precipitation	333.3	583.5	628.6	672.0	804.6
Annual sum positive differences of rain and ET	7.3	151.6	204.9	279.9	1110.0
Average T-max	199.6	227.0	235.4	241.7	256.4
Average T-mean	138.0	163.0	172.0	177.0	189.0
Average T-min	65.5	99.0	107.0	115.0	143.0
Average T-max of warmest months	279.0	341.0	346.0	351.7	378.0
Mean temperature warmest month	223.0	256.7	263.0	267.0	290.0
Mean temperature coldest month	24.7	85.0	96.0	103.0	123.0
Average T-min of coldest months	15.3	33.0	45.0	54.3	92.0
Edaphic					
Average clay content	7.9	23.3	27.1	32.1	57.4
Average sand content	8.8	42.3	48.7	55.5	79.5

Variable	Min	1st Q	Median	3rd Q	Max
Active limestone	0.1	1.3	1.8	6.3	25.3
Cation exchange capacity	0.2	10.9	13.8	17.2	41.3
Water retention capacity	63.1	127.2	135.9	145.4	199.2
Edaphic soil type	1.0	14.0	17.0	42.0	57.0
Average silt content	2.2	18.7	22.9	27.0	54.7
Lithology	1.0	12.0	25.0	37.0	41.0
Average organic matter in the profile	0.4	1.0	1.2	1.4	3.4
Average organic matter surface horizon	0.3	1.4	1.6	1.9	3.8
Nitrogen content	4.7	5.8	6.3	7.5	8.2
Percent base saturation	25.0	100.0	148.1	150.0	250.0
Soil pH	7.6	92.4	97.2	99.9	100.0
Soil depth	1.0	1.0	1.0	1.0	1.0
Substrate	1.0	2.0	7.0	7.0	11.0
Texture	5.0	44.2	57.7	74.7	100.0
Average content of fine particles (Ø < 2 mm)	7.9	23.3	27.1	32.1	57.4
Topographic					
Hydraulic conditions	11.8	22.1	31.2	46.9	259.0
Distance to pastures	0.0	209.6	486.7	904.4	7730.9
Distance to river	0.0	44.7	214.1	686.2	7175.4
Distance to water	0.0	0.4	2.1	10.3	14669.5
Flow accumulation	1.0	4.0	13.4	42.1	255.0
Flow direction	0.0	1590.0	3578.6	8278.3	82765.2
Flow direction down	0.0	67.5	321.2	911.6	45127.7
Flow direction up	2.6	4.4	5.4	6.7	19.1

Variable	Min	1st Q	Median	3rd Q	Max
Composite topographic index	4.3	7.0	8.0	9.0	17.0
Topographic moisture index	1.0	1.0	1.0	1.0	1.0
DEM	9.0	138.7	225.2	384.5	833.7
East – west orientation	1.0	38.3	50.0	65.4	100.0
Slope aspect	0.0	2.5	6.7	14.8	137.6
Slope steepness	0.6	2075.7	2180.4	2307.7	4040.3
Radiation in winter	1244.2	3954.6	4871.0	5183.0	5907.8
Radiation in autumn	2508.4	5209.2	5295.0	5400.3	6455.7
Radiation in spring	5226.0	7636.8	7671.9	7704.8	7849.0
Radiation in summer	2.9	9.4	10.0	11.0	12.0
Sunshine	6.7	11.3	12.0	12.0	12.0
Sun shine in winter	9.0	13.7	14.0	14.3	15.0
Sun shine in autumn	0.0	28.2	49.7	62.9	100.0
Sun shine in spring	11.8	22.1	31.2	46.9	259.0
Sun shine in summer	0.0	209.6	486.7	904.4	7730.9
North -south orientation	0.0	44.7	214.1	686.2	7175.4
Tree cover					
Agroforestry	1.0	1.0	1.0	1.0	1.0
Broadleaf	1.0	1.0	1.0	1.0	1.0
Coniferous	1.0	1.0	1.0	1.0	1.0
Canopy FCC	0.0	197.0	624.4	1375.5	6844.3
Canopy FCC by trees	4.0	23.4	30.1	36.5	81.8
Olive trees cover	4.1	62.8	78.2	86.7	98.8
Oaks cover	0.0	1.0	2.7	4.7	97.9

Variable	Min	1st Q	Median	3rd Q	Max
Density of trees	0.0	2.0	8.3	23.4	98.3
Distance to tree	0.0	215.7	505.7	902.0	4303.8
Mixed forest cover	0.0	48.6	71.5	89.3	100.0
Normalize difference vegetation index	1.0	1.0	1.0	1.0	1.0
Olives grove	0.0	7.3	14.8	25.5	91.5
Woodland cover	1.0	1.0	1.0	1.0	1.0