Environmental factors associated with the spatial distribution of invasive plant pathogens in the Iberian Peninsula: The case of *Phytophthora cinnamomi* Rands

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ABSTRACT

Although spatial variability in the distribution of soil organisms is often regarded as random, recent attempts have found significant spatial structure at several scales. Understanding the drivers of this variability at large scale could help to evaluate the ecological and socio-economic impacts of soil organisms in the ecosystems. In the present study we aim to (i) understand the relative role of environmental factors and human influence on the distribution of one of the World's most destructive and invasive plant pathogens, *Phytophthora cinnamomi* Rands, and (ii) to estimate its potential geographic distribution in the Iberian Peninsula as a proxy of its potential impact. For this purpose, we used a total of 277 records of *P. cinnamomi* (presence: *n* = 157; absences: *n* = 120) in the Iberian Peninsula and three sets of explanatory variables reflecting abiotic conditions (climate and soil), biotic conditions (main susceptible host tress distribution and vegetation cover based on NDVI) and human influence. The current distribution of *P. cinnamomi* in the Iberian Peninsula seems to be influenced principally by fine texture soil and climate, following the land use and lastly the presence of its main host forest species. Its potential distribution across the Iberian Peninsula suggests potential for further expansion along the northeast and southeast of Spain and central Portugal. Given the significant impact of this pathogen on forest ecosystems, the modelling of its distribution in the Iberian Peninsula offers an important decision tool for the monitoring and restoration of declining Mediterranean oak forests.

1. Introduction

Nowadays, soil pathogens are well recognized for their significant ecological and socio-economic impacts on the ecosystems (Ettema and Wardle, 2002; Gómez-Aparicio et al., 2012). Among the most important soil pathogens, the oomycete *Phytophthora cinnamomi* Rands, causes extensive economic losses in agriculture, horticulture and forestry and is a major threat to natural ecosystems and biodiversity around the world (Brasier, 1996; Brasier et al., 1993; Hardham, 2005; Weste and Marks, 1987). In Europe, its occurrence has been recorded since early 19th century (Brasier, 1996; Brasier et al., 1993; de Sampaio e Paiva Camilo-Alves et al., 2013; Jung et al., 2015; Zentmyer, 1988) but it only experienced a rapid spread during the last decades, leading to devastation of important agricultural crops and reduction of large woodland areas (de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005; Jung et al., 2015). Understanding where and when soil pathogens like *Phytophthora* spp. are more likely to cause great epidemics has long

been an important point of study in agricultural research (Otten et al., 2004). However, we have little knowledge about the complexity of their distribution patterns at large scales, particularly for natural and semi-natural habitats (Ettema and Wardle, 2002; Reinhart and Clay, 2009).

The abundance and diversity of phytopathogenic fungi in soil are not usually randomly distributed (Ettema and Wardle, 2002). These exhibit spatially predictable patterns influenced by a variety of environmental factors (Agrios, 2005; Ettema and Wardle, 2002). For instance, abiotic factors such as high temperature, high soil water content and its dynamics are key in the establishment, spread and longevity of *Phytophthora* spp. (Corcobado et al., 2013a, 2013b; Hardham, 2005; Weste and Marks, 1987). Soil textures ranging from loamy to silty or clayey have been associated with the occurrence of *Phytophthora* spp., as these soil factors favour moist conditions and sporulation (Corcobado et al., 2013b; Jönsson et al., 2005; Jung et al., 2000). Furthermore, *Phytophthora* spp. require nutrient rich soils with $pH_{(H_2O)}$ values

between 4.0 and 4.8 to stimulate sporangia production (Jönsson et al., 2005; Jung et al., 2000). On the other hand, biotic factors such as vegetation is a major determinant of the spatial distribution of soil pathogens (Ettema and Wardle, 2002). Host plant species can affect pathogen abundance in the forest soil directly by providing living host tissue, or indirectly by generating environmental conditions that affect their reproductive activity (Augspurger, 1990; Saetre, 1999). Other factors that could be associated with the spreading of introduced plant pathogens are related to human influence such as, cropland and grazing, built up areas or transportation infrastructures (Corcobado et al., 2013b). These human-altered areas are a common reservoir of soil pathogens and may increase the risk of dispersal into natural or semi-natural areas.

P. cinnamomi is well adapted to the climate of the Iberian Peninsula and it is recognized as the main biotic factor of oak decline in the Mediterranean forests in Spain and Portugal (Corcobado et al., 2013a, 2013b; Moreira and Martins, 2005; Sánchez et al., 2002). These ecosystems, dominated by evergreen cork oaks (*Quercus suber* L.) and holm oaks (*Q. ilex* L.), are among the most representative Iberian Mediterranean landscapes and have considerable conservational and socioeconomical value. In this study, we try to elucidate the influence of environmental factors and human influence on the distribution of *P. cinnamomi* in the Iberian Peninsula. Specifically, we considered the following questions: (i) which is the relative importance of environmental factors (biotic and abiotic) and the degree of human influence for explaining the distribution of *P. cinnamomi*? and (ii) considering the most important drivers of *P. cinnamomi* occurrence, which is its current potential distribution in the Iberian Peninsula? We discuss the findings in relation to the dynamics and restoration of the declining Mediterranean oak forests.

2. Material and methods

2.1. Study area

Our study area is the entire Iberian Peninsula (Portugal and Spain; Fig. 1). This extends over a surface of 582,925 km^2 from latitude 43° 47′ N to 36° 01′ N and longitude 9° 30′ W to 3° 19′ E, encompassing several mountain ranges (the Pyrenees, the Cantabrian Mountains, the Northwest ranges, the Central Range, the Iberian Range and the Betic Range) (Oliva et al., 2016). The climate of the area is divided by two major climate zones: (i) the Atlantic climate characterized by mild summers and cold, rainy winters and (ii) the Mediterranean climate with mild winters and hot, dry summers (Dasari et al., 2014). The main vegetation types vary from semi-desertic flora, Mediterranean oak forests, steppeland areas and evergreen pine forests, to deciduous vegetation and subalpine and alpine vegetation (Pascual et al., 2011). Due to these characteristics, the Iberian Peninsula currently stands out as hosting almost 50% of European plants and terrestrial vertebrate species and with > 30% of endemic species (Araujo et al., 2007).

2.2. The modelled species

P. cinnamomi, a soil-borne fungus, is one of the world's most destructive and invasive plant pathogen (Brasier, 1996; de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005). *P. cinnamomi* is thought to be native to Southeast Asia, but it is now present in most temperate and tropical regions and is responsible for severe crop losses and strong disturbances in natural ecosystems (Brasier, 1996; Zentmyer, 1988). It was first recorded in Europe in the 19th century, most likely linked to contaminated nursery stock and other plant material (Hardham, 2005). In susceptible hosts, *P. cinnamomi* colonizes the roots causing necrosis, loss of fine roots, root rot and ultimately death (Corcobado et al., 2013a; Hardham, 2005; Ruiz Gómez et al., 2015; Sánchez et al., 2002). *P. cinnamomi* may persist in soil or infected plants as chlamydospores, and when conditions favouring mycelium growth

predominate, the pathogen enters the asexual sporulation cycle (de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005). This asexual cycle of reproduction may be repeated many times, and thus rapidly amplifying the inoculum potential in infected areas (Hardham, 2005).

2.3. Key susceptible hosts in the Iberian Peninsula

A large part of forests in the Iberian Peninsula are currently dominated by evergreen oak species susceptible to *P. cinnamomi* such as cork (*Q. suber* L.) and holm oak (*Q. ilex* L.). These woodlands are of high conservation and socioeconomic value within their areas of geographic distribution around the Mediterranean basin (de Sampaio e Paiva Camilo-Alves et al., 2013). In Western Iberia, holm and cork oaks occupy large extensions forming traditional agrosilvopastoral systems called "dehesa" in Spain and "montado" in Portugal (de Sampaio e Paiva Camilo-Alves et al., 2013; Gea-Izquierdo et al., 2006). This multifunctional system is characterized by offering a diversity of products such as forage, acorn, wood, and cork, and its long-term ecological sustainability derives from the sub optimization of the resources and continued management (de Sampaio e Paiva Camilo-Alves et al., 2013).

2.4. Phytophthora cinnamomi dataset

To analyse the patterns of distribution of *P. cinnamomi* in the study area, we gathered a total of 295 presence/absence records (presence: $n = 175$; absences: $n = 120$; Fig. 1) in the Iberian Peninsula from four different datasets: Corcobado et al. (2013b), Moreira and Martins (2005), Red SEDA (2015) and Romelaro-Tapia (2008). In all of these cases, data was obtained from soil sampled in forest surveys (details in: Appendix A – Table A2). We used a grid resolution of 1 × 1 km to remove duplicate records (i.e. only one occurrence record per grid square of 1 × 1 km). This filtering decreased the number of presence/absence records for *P. cinnamomi* in the Iberian Peninsula to 277 grids of 1 × 1 km (presence: $n = 157$; absences: $n = 120$).

This compiled database is the result of an extensive search of the occurrence of *P. cinnamomi* in the study area. The spatial independence of these datasets is an important underlying assumption of this study as it allows an accurate representation of the observed occurrence of the species in the study area. However, we acknowledge that this database may not represent the full range of environmental conditions in which the species can be found outside of the study area (e.g. other introduced areas). Thus, our estimates will always be a conservative representation of the full potential distribution of the species.

2.5. Explanatory variables

Modelling success depends on using appropriate variables linked to relevant ecological processes. Herein, to characterize the most important habitat heterogeneity and environmental conditions for the establishment and spread of *P. cinnamomi* in the study area, we used 15 broad-scale variables as predictors, related to abiotic conditions (climate and soil), biotic conditions (susceptible host plants and vegetation cover) and human influence (Table 1). These variables were chosen based on our knowledge of the species' ecology (Corcobado et al., 2013b; de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005; Moreira and Martins, 2005; Weste and Marks, 1987), and were assumed to be at least correlated with more proximal causal factors.

Climatic variables were available from WorldClim climate database at 1 km resolution (Hijmans et al., 2005). We selected relevant aspects of temperature and rainfall such as annual ranges and mean temperature of wettest quarter in the Iberian Peninsula (Table 1). Soil texture (content of clay and sand) and soil pH at 1 km resolutions were downloaded from ISRIC-World Soil Information SoilGrids database (Hengl et al., 2014). Soil water content was downloaded from CGIAR-
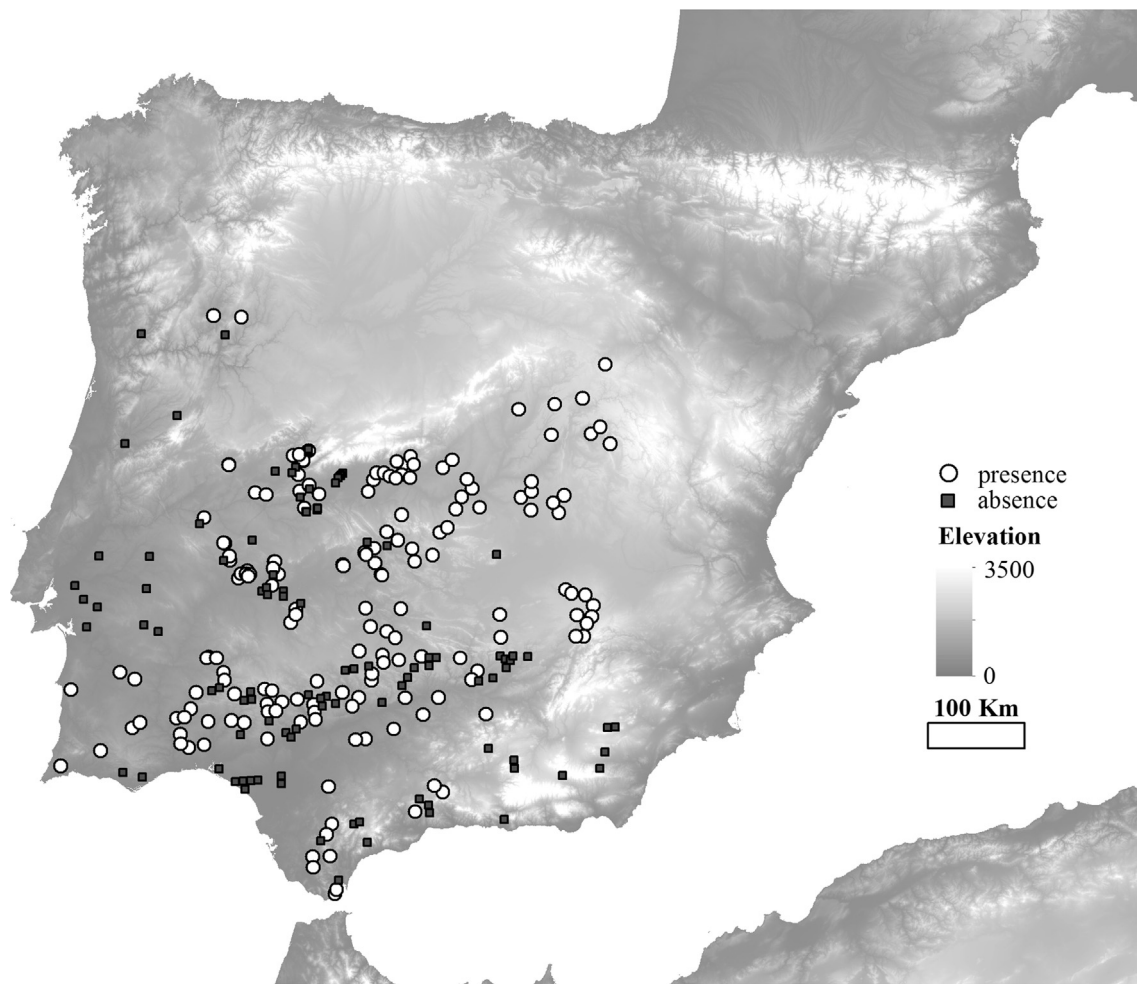
Fig. 1. Observed distribution of *Phytophthora cinnamomi* Rands in the Iberian Peninsula (presence: *n* = 157; absences: *n* = 120).

Table 1
Variables used as predictors of the *P. cinnamomi* presence in the Iberian Peninsula.

Variable	Descriptions	Source	VIF
Abiotic factors			
TEMP	Mean annual temperature (°C)	WorldClim	11.26
TEMP_R	Temperature annual range (°C)		**3.332**
TEMP_W	Mean temperature of wettest quarter (°C)		**2.250**
RAIN	Annual precipitation (mm)		68.71
RAIN_S	Precipitation Seasonality		18.76
RAIN_W	Precipitation of wettest quarter (mm)		83.93
pH	Soil pH in water suspension (10^{-1})	ISRIC	**3.517**
Clay	Clay content in soil (%)		**1.193**
Sand	Sand content in soil (%)		**1.169**
Silt	Silt content in soil (%)		15.90
SWater	Water content in soil (mm)	CGIAR-CSI	**3.649**
Biotic factors			
QIlex	Suitable habitats for the occurrence of *Quercus ilex*	Model (App. 1)	**2.162**
QSuber	Suitable habitats for the occurrence of *Quercus suber*		**7.559**
NDVI	Vegetation cover: annual average Normalized Difference Vegetation Index	NASA-MODIS	**1.464**
Human influence			
Artificial	Percentage of artificial surfaces (continuous and discontinuous urban fabric, industrial and commercial units, mines, dumps, and construction)	Modified from CORINE	**1.350**
Agricultural	Percentage of agricultural areas (arable land, permanent crops, annual crops, land principally occupied by agriculture with significant areas of natural vegetation and agro-forestry areas)		**1.160**
Pasture	Percentage of pasture areas (land used to support grazing animals)		**1.312**
Road	Minimum distance to roads (km)	OpenStreetMap	**1.214**

Variables in bold were included in the final analysis to avoid collinearity.

CSI at 1 km resolution (Trabucco and Zomer, 2010). To characterize human influence at landscape scale, we extracted the percentage area of the following land cover at 100 m grid from the CORINE Land-cover Map 2006 (European Environment Agency; http://www.eea.europa. eu/); artificial surfaces (i.e. continuous and discontinuous urban fabric, industrial and commercial units, mines, dumps, and construction), agricultural areas (i.e. arable land, permanent crops, annual crops, land principally occupied by agriculture with significant areas of natural vegetation and agro-forestry areas) and pasture areas (i.e. land used to support grazing animals). Finally, we calculated the minimum distance to roads from the centre of each 1 km grid based on the road network of the global community-owned OpenStreetMap project (Neis et al., 2012), using the Euclidean distance (in km) by ArcGis program version 10.3.1. (ESRI, 2015).

In order to capture the geographical variation in the presence of two key host forest species susceptible to *P. cinnamomi* in the Iberian Peninsula, we built species distribution models for *Q. ilex* and *Q. suber* using Generalized Linear Models (GLMs) (see in Appendix A – A1). We used all available occurrence records for each susceptible host from the Third National Forest Inventory (MAGRAMA, 2007) and GBIF (www. gbif.org) and a set of environmental variables describing climate, topographic and soil texture of the study area based on the species' ecology (Barbero et al., 1992; Magri et al., 2007; Serra-Diaz et al., 2013). The final results are raster grids at 1 km resolution in which values range from 0 to 1 (Fig. 2), where higher values indicate more suitable habitats for the occurrence of the species. Several studies have shown that the values of these grids also correlate with species abundance, where localities with higher values have greater abundance values for the species being studied (Oliver et al., 2012; Tôrres et al., 2012). We used the R package "dismo" to build the models (Hijmans et al., 2013).

Finally, to represent the status of vegetation in the study area, we used an annual average from the Normalized Difference Vegetation Index (NDVI; January-December 2014) from the NASA-MODIS/Terra dataset at 250 m resolution (Justice et al., 1998). This vegetation index has been used successfully to calibrate species distribution models in other studies (Benito et al., 2013). All data were re-sampled to 1 km spatial resolution using an interpolation bilinear re-sampling technique (ESRI, 2015). Prior to analyses all variables were checked for collinearity using the Variance Inflation Factor (VIF). All variables with VIF > 10 were discarded for further analyses (Barea-Azcón et al., 2014; Zuur et al., 2010).

2.6. Statistical analyses

2.6.1. Multimodel inference

Multimodel inference is a model selection method frequently employed to identify the model that is best supported by the data (i.e. best model) from among the candidate sets and it also allows the measurement of the importance (i.e. weight of evidence) of each independent variable to explain the response variable (Burnham and Anderson, 2002; González-Moreno et al., 2013; Thuiller et al., 2007). Herein, we performed multimodel inference based on the all-subsets selection of Generalized Linear Models (GLMs) using Akaike's information criterion corrected for a large number of predictors (AICc). GLMs using a binomial distribution and a logistic link function were fitted using presence/absence of *P. cinnamomi* as the response variable and the sets of variables as predictors. The response variable considered was first related separately to either a linear or quadratic function of each variable in order to take possible curvilinear relationships into account (Lobo et al., 2006). The best function for each variable (i.e. lowest AICc) was then used in the rest of the modelling procedure. Then, for each candidate model in the final selection, we calculated the weight of evidence (Wi) to rank the predictors in order of importance explaining the presence of *P. cinnamomi*. We summed the model AICs weights for all models within four AICc units from the best model in which each predictor appeared (González-Moreno et al., 2013). However, the Wi values are relative and not absolute because they will be > 0, even if the predictor has no explanatory importance (Brook et al., 2006; Burnham and Anderson, 2002; Thuiller et al., 2007). To avoid this problem, we used a stratified permutation test to calculate the absolute weight of evidence (ΔWi) (Brook et al., 2006; Thuiller et al., 2007). We randomized the data for each predictor separately within the data set, then re-calculated Wi and repeated this procedure 100 times for each predictor. The ΔWi was then calculated by subtracting the median value of the 100 randomized Wi from the original Wi. Only predictors with ΔWi > 0 have true explanatory power on the occurrence of *P. cinnamomi* in the Iberian Peninsula.

We also used multimodel inference to calculate regression coefficients and their confident intervals (with the adjusted standard error) within the best models subset ($\Delta AICc$ < 4). We calculated the coefficient for a given predictor as the sum across all possible models where the predictor was present, of the predictor's coefficient multiplied by the Wi as in Burnham and Anderson (2002).

Finally, spatial autocorrelation across the geographic space is an inherent property of most ecological data and it might break the assumption of independence of the data modelled (Legendre, 1993). For
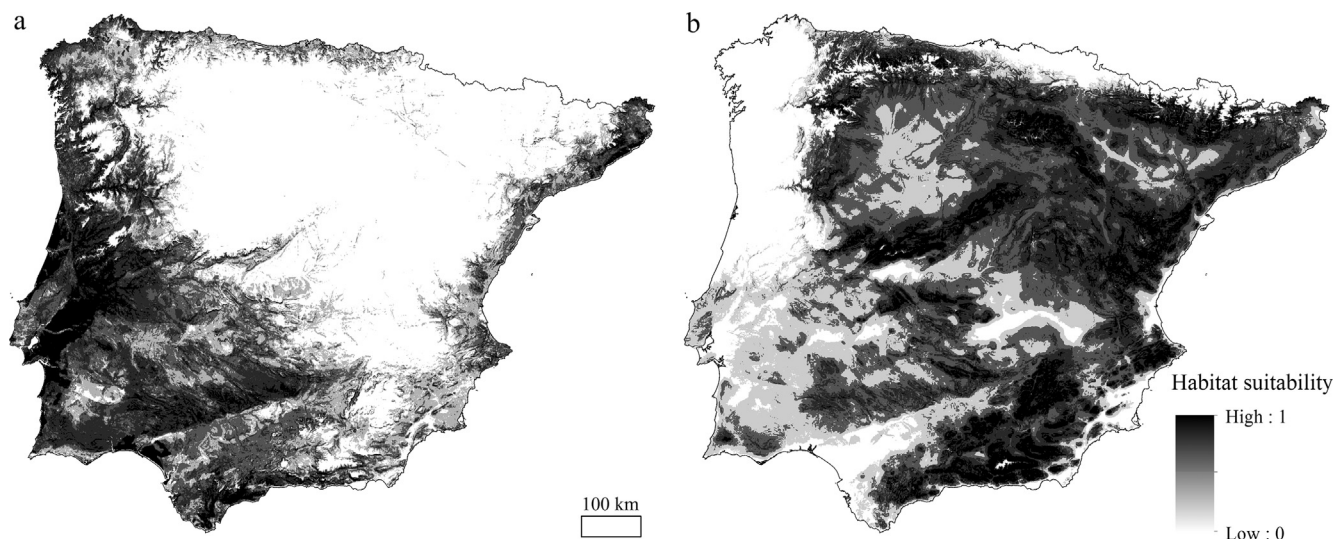

Fig. 2. Predicted potential distribution of two key hosts forest species susceptible to *P. cinnamomi* in the Iberian Peninsula. (a) *Q. suber* and (b) *Q. ilex.*

each GLM in the multimodel inference procedure we tested the spatial autocorrelation in the model's residuals by the Moran's index. We did not detect significant spatial autocorrelation in the residuals of the subset of models within four AICc units from the best model (see in Appendix A – Table A5).

2.6.2. Deviance partitioning

Assuming that the deviance is a good measure of the variability explained by a model (Borcard et al., 1992; Carrete et al., 2007), we performed a hierarchical partitioning procedure to specify how much of the variation of the GLMs were explained by the pure effect of each set of explanatory variables (i.e. abiotic, biotic and human influence factors) and which proportion was attributable to their shared effects (González-Moreno et al., 2013; Muñoz et al., 2005). We set up GLMs including a different subset of non-collinear variables: only abiotic, only biotic, only human influence and the combination of the three. The deviance explained by each model was then used to identify the single and shared effects on the occurrence of *P. cinnamomi* by simple equation systems.

2.6.3. Prediction of the potential distribution of P. cinnamomi in the Iberian Peninsula

Potential distribution is defined as the geographic area in which the environment of the modelled species is suitable at a given time (Rodríguez et al., 2015). To predict the potential distribution of *P. cinnamomi* across the entire Iberian Peninsula, we divided the presence/absence data randomly from the study area into training (80%) and testing (20%) datasets for calibrating and testing the accuracy of the best model (smallest AICc) obtained by multimodel inference. We performed a 10-fold cross-validation, calibrating the best model with the training dataset and projecting it into the testing dataset. We evaluated the predictive performance of the model using two statistics, the area under the Receiver Operating Characteristic curve (AUC) and correlation (COR) (Elith et al., 2006). AUC measures the ability of a model to discriminate between sites where a species is present, versus those where it is absent. The AUC ranges from 0 to 1 (0.5 = random, 1 = perfect). COR measures how far the prediction varies from the observation (Elith et al., 2006). AUC and COR values were computed by *k*-fold validation (ten groups). Finally, we used all available occurrences of *P. cinnamomi* to calibrate the best model and we projected its final potential distribution to all of the Iberian Peninsula's 1 × 1 km grids.

All analyses were performed with the R-CRAN software version 3.3.3. (R Core Team, 2015). We used the R package "MuMin" for the procedures of the multimodel inference method, the R package "VEGAN" as the base code for deviance-partition, the R package "ncf" and "spdep" for spatial autocorrelation analysis, the R package "dismo" to estimate the potential distribution and finally we used the function "evaluate" from the R package "dismo" to evaluate the predictive performance of the models (Hijmans et al., 2013).

3. Results

3.1. Factors influencing the distribution of P. cinnamomi in the Iberian Peninsula

The presence of *P. cinnamomi* in the study area was significantly associated with soil properties (Table 2). Soil clay content showed a positive effect, while the association with sand content and pH was negative. Temperature annual range and mean temperature of wettest quarter had a significant effect. On the other hand, the presence of *P. cinnamomi* was significantly associated with lands principally occupied by agriculture, as well as with the presence of one of its susceptible host species (Q. suber) and high NDVI.

The deviance partition analysis revealed that 42% of the variability in *P. cinnamomi* was explained by the best model (Fig. 3 and Appendix A – Table A4). The decomposition of the variation showed that purely

abiotic factors were able to explain most of the variation while human activity and biotic factors showed little single effect. A large proportion of the variation was explained simultaneously by abiotic and biotic variables independently of human activity.

3.2. Potential distribution of P. cinnamomi in the Iberian Peninsula

The average of AUC and COR values for a set of 10-replicate of the best model ranged between 0.82 and 0.88 (mean AUC = 0.85 ± 0.01) and 0.53–0.66 (mean COR = 0.61 ± 0.01) respectively. These values indicated overall good ability to predict the potential geographical distribution of *P. cinnamomi* in the Iberian Peninsula.

The current suitable habitats for *P. cinnamomi* were predicted in the South West of the Iberian Peninsula with patches in the North-Northeast. Furthermore, the model suggests the existence of areas with suitable environments where records of *P. cinnamomi* were not found. These predicted areas were located in the North East of Cataluña, the South East of Spain and central Portugal (Fig. 4).

4. Discussion

4.1. The important role of abiotic and biotic factors and human influence in the distribution of P. cinnamomi

We identified the most influential variables explaining the distribution of *P. cinnamomi* using multimodel inference of GLMs and variance-partition techniques. The variables retained by regression models as statistically significant revealed that *P. cinnamomi* distribution is highly dependent on abiotic factors such as soil properties and temperature, followed by human influence variables and lastly biotic factors such as the presence of one of its main susceptible host. According to Soberon and Peterson (2005), biotic, historical and human factors contribute together to control the distribution and abundance of species. Mapped representations of these factors are often used as explanatory variables to predict species distribution (Guisan and Thuiller, 2005). However, biotic interactions and human influence are usually disregarded in large-scale analyses as effective variables determining the distributions of the modelled species, because they are assumed to characterize only local effects (Dirnböck et al., 2003; Soberón and Nakamura, 2009). In contrast to these criticisms, our findings demonstrate the important additional information that biotic variables (susceptible host and NDVI index) and human influence (agricultural lands) contribute to explain the distribution of *P. cinnamomi* in the Iberian Peninsula. These results are consistent with those found by other studies, which indicate a significant effect of these variables in the explanatory power of species distribution models at macroscales and particularly for invasive species (Gallardo et al., 2015; Heikkinen et al., 2007; Jetz et al., 2007).

Fine textured soil seems to favour the occurrence of pathogen more than coarse textured soils, presumably as a result of the direct influence on water availability. In coarse textured soils, water depletes quickly, which is detrimental for the production of sporangia and release of zoospores, while in fine textured soils, water retention strongly benefits the activity of the pathogen and provides conditions for inoculum increase (Corcobado et al., 2013b; Gómez-Aparicio et al., 2012; Hardham, 2005; Jönsson et al., 2005; Jung et al., 2000). These results support previous findings by Gómez-Aparicio et al. (2012) and Corcobado et al. (2013b), who suggest that the presence of *P. cinnamomi* is significantly constrained to soils with high clay content and low sand content. In addition, in this study, soil pH was associated negatively with the presence of the pathogen. Based on lab studies *Phytophthora* spp. show reduced activity at pH values below 4.0 (Jung et al., 2000). Increases in soil pH have been shown to inhibit mycelial growth, as well as sporangial formation and germination (Jönsson, 2006).

Climatic variables were also important to explain the distribution of

Table 2
Multimodel inference results: non-corrected and unbiased weight of evidence, averaged and standardized coefficient estimates (β) and confidence intervals (95% CI) of abiotic, biotic and human influence predictors for *P. cinnamomi* presence in the Iberian Peninsula.

Variable	Type	Weight	Unbiased weight	β Averaged	Adjusted SE	Lower CI	Upper CI
Intercept				**−11.34**	3.404	−18.36	−3.479
TEMP_R	Abiotic	1.000	0.815	**0.405**	0.066	0.265	0.525
Clay	Abiotic	1.000	0.800	**0.084**	0.029	0.026	0.141
Sand	Abiotic	1.000	0.798	**−0.053**	0.019	−0.092	−0.015
TEMP_W	Abiotic	1.000	0.788	**13.42**	4.929	3.362	22.73
TEMP_W^2	Abiotic			**−13.27**	4.989	−23.01	−3.410
Agricultural	Human influence	1.000	0.779	**0.052**	0.017	0.018	0.086
NDVI	Biotic	0.984	0.771	**3.671**	1.517	0.609	6.710
QSuber	Biotic	0.946	0.732	**2.952**	1.143	0.530	5.417
pH	Abiotic	0.925	0.719	**−0.564**	0.261	−1.175	−0.068
SWater	Abiotic	0.407	0.176	−0.713	1.282	−4.167	0.930
QIlex	Biotic	0.358	0.141	2.185	1.841	−1.380	6.199
Pasture	Human influence	0.340	0.093	−1.747	1.337	−5.362	1.599
Road	Human influence	0.197	−0.026	−2.893	6.043	−14.981	9.127
Artificial	Human influence	0.175	−0.057	−0.004	0.011	−0.028	0.018

Predictors are sorted by importance according to the unbiased weight of evidence. Significant averaged coefficients are shown in bold. See Table 1 for a complete description of variables.
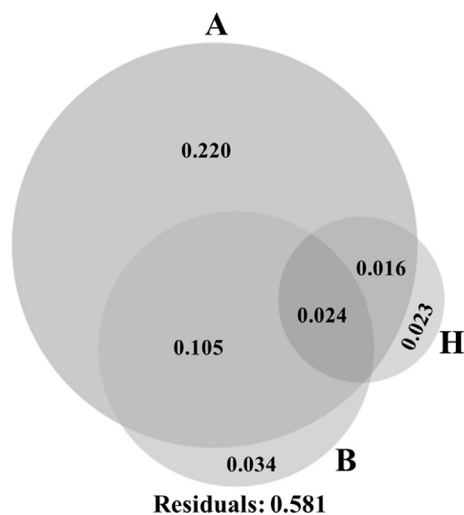

Fig. 3. Variation partitioning of the presence of *P. cinnamomi* in the Iberian Peninsula. Each circle corresponds to a group of variables. (A) abiotic, (B) biotic and (H) human influence. The numbers within the circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared (overlapped part of circles). Residuals indicate the non-explained deviance by the models.

this pathogen and its potential impact en Mediterranean oak forests. The probability of *P. cinnamomi* occurrence was positively associated with very seasonal climates while the relation with temperature in the wettest quarter showed a hump shape with optimum at 18 °C in the study area. This result is consistent with our knowledge of the species, as warmer soils, particularly combined with moist conditions, are optimum for its development and virulence (Brasier, 1992; Brasier et al., 1993; Shearer, 2014). The important effect of climate conditions on the development and virulence of *P. cinnamomi* has also been investigated with respect to possible effects of global warming on its distribution and impact. Martín-García et al., (2015) establish a clear effect of temperature on the survival of germinating holm oak acorns. High temperatures in infested soils with *P. cinnamomi* caused rot on embryos and necrosis on emerging acorn radicles (Martín-García et al., 2015). From a conservation point of view, seed germination and radicle elongation represents a crucial step in the processes of natural forest regeneration. Any limitations of the radicle during germination may have a significant impact on the plant's ability to tolerate extreme climatic events

(e.g. drought) (Cubera et al., 2012). On the other hand, analysis of scenarios with increasing temperature predicts that global warming could result in a increase in the incidence of periods favouring the growth of this pathogen and thus, increase its range towards areas in the northeast of the European continent (Bergot et al., 2004; Brasier, 1996). However, these predictions are based solely on the effects of temperature on the habitat suitability for the pathogen. Predicting the impacts of climate change on the distribution *P. cinnamomi* must also consider the host-pathogen interactions, human influence and changes in rainfall patterns, particularly in Mediterranean regions (Yáñez-López et al., 2012).

One important finding of this study is the positive association between the presence of *P. cinnamomi* and the distribution of one of susceptible host species (*Q. suber*). The presence of *P. cinnamomi* and their virulence may represent an important threat to the stability of Mediterranean forests in the Iberian Peninsula which are dominated by evergreen holm and cork oaks. These forest ecosystems are particularly vulnerable to oak decline processes mainly because of the combined effect of extreme weather conditions such as warmer climates, water stress, soil disturbances and widespread distribution of exotic pathogens (Brasier et al., 1993). In fact, an extensive mortality and decline of oaks, principally *Q. suber*, has occurred in parts of southern Spain and Portugal in recent decades and *P. cinnamomi* has been cited as the main biotic factor of oak decline being responsible for multiple fine-root infections followed by substantial root girdling and death (de Sampaio e Paiva Camilo-Alves et al., 2013; Gómez-Aparicio et al., 2012; Moreira and Martins, 2005). Another important aspect to consider is the positive association between the presence of *P. cinnamomi* and high NDVI. Higher vegetation index represents areas of higher tree density, where we expect higher competition for resources among neighbouring plants. These negative interactions will be exacerbated by extreme climatic events (e.g. drought) increasing the susceptibility of the less competitive plants to infections by *P. cinnamomi* (Corcobado et al., 2014). In the current scenario for the Iberian Peninsula of low-intensity forest management and increasing biomass, this competition process might exacerbate the spread the pathogen to large areas of oak forests across its suitable abiotic area.

Our results suggest a significant association of the presence of *P. cinnamomi* with an increasing area occupied by agriculture. Recently, Manzano et al., (2016) relate decline and *P. cinnamomi*-induced mortality of corn and holm oaks to the presence of hydraulic infrastructures (e.g. ponds) resulting from agricultural activities. Fine texture soils, moist conditions and the abundance of suitable hosts in crops could not only increase the inoculum potential (see above) but also derive in
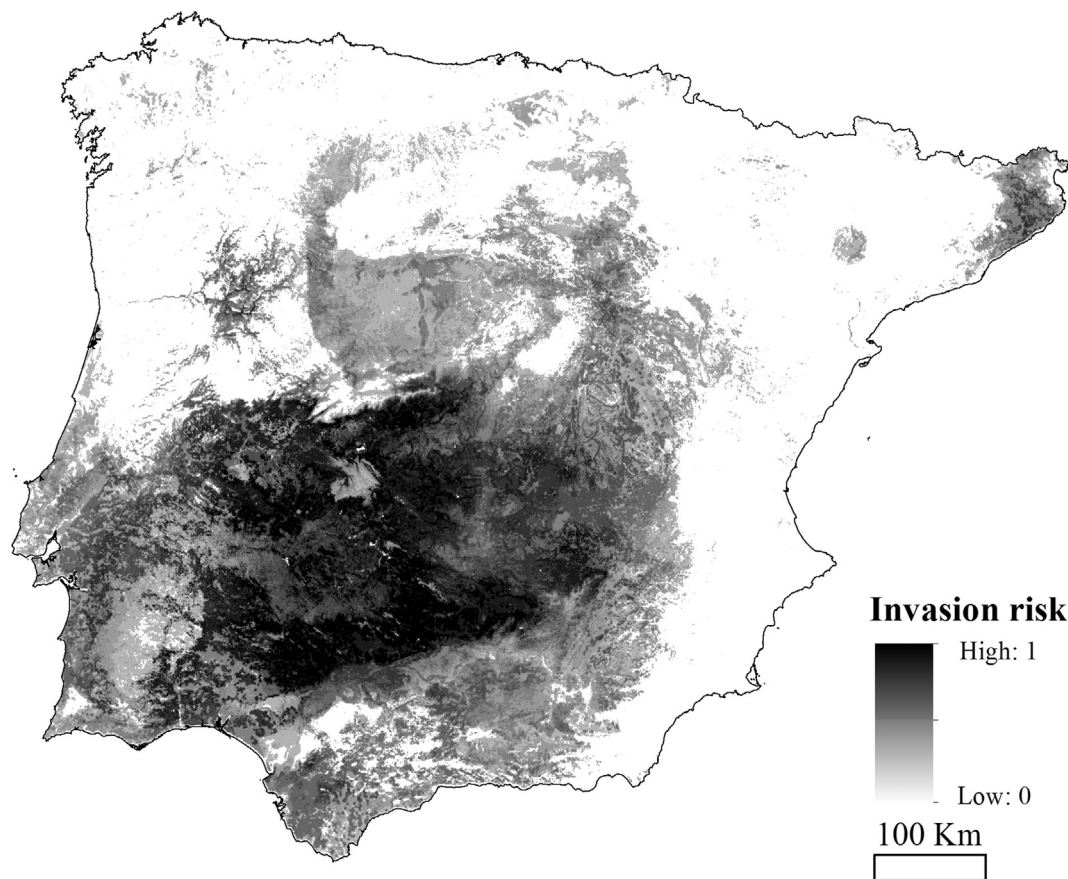
Fig. 4. Potential distribution of *P. cinnamomi* invasion risk (0–1 scale) in the Iberian Peninsula using the best GLM model obtained by multimodel inference.

important implications for hygiene management, as clayey soils would more easily adhere to passing humans and vehicles, and thus increase risk of pathogen dispersal. Human activities, by promoting parasite transport, have been and will be major factors potentially favouring the spread of soil-borne pathogens (Anderson et al., 2004). This finding reinforces the important effect of human influence variables on invasive species distribution, and the importance of performing sensitivity analyses to quantify its true relevance (Gallardo et al., 2015).

4.2. Predicting the potential distribution of P. cinnamomi

We developed a conservative predictive model to represent the potential distribution of one of the most widely distributed and destructive forest pathogens in the Iberian Peninsula. The strength of our model relies on the availability of high quality records of *P. cinnamomi* (presence/absence) for the study area and a robust and biologically relevant selection of explanatory variables. The high values of performance (AUC and COR) of our model in predicting the potential distribution of *P. cinnamomi* in the Iberian Peninsula indicates a high dependence of the occurrences data and the set of variables included in the analysis (Roura-Pascual et al., 2009). Given the observed occurrence of *P. cinnamomi*, predictions of its potential distribution across the Iberian Peninsula suggest that a further expansion of this soil pathogen is possible along the northeast of Spain (Cataluña), the southeast of Spain and central part of Portugal. Special attention in scrutiny efforts should focus on the southern part of the central plateau of Spain, where the "dehesa" is the main component of the landscape and the local economy. Furthermore, given the dependence of *P. cinnamomi* activity on soil properties, control efforts should focus along South-eastern Spain (Andalusia) where the high clay contents represent suitable conditions to its establishment and spread.

5. Conclusion

This study provides new insights into the highly complex spatial distribution of soil-borne pathogens and reveals the degree to which abiotic and biotic factors and human influence can explain pathogen distributions at large scales. *P. cinnamomi* distribution seems to be influenced principally by fine texture soil, seasonal and warm climates, followed by abundance of agriculture area and by the presence of its susceptible host forest species in the Iberian Peninsula. The higher likelihood of occurrence of *P. cinnamomi* in forest areas embedded in an agricultural matrix suggests that adequate management farming practices involving manipulations of the soil, equipment transport and drainage should be implemented to limit the expansion of this soil pathogen into forest areas. Finally, given the significant impact of this pathogen on forest ecosystems, the modelling of its potential distribution in the Iberian Peninsula provides an important decision tool for the monitoring and restoration of declining Mediterranean oak forests, highlighting areas of potential further expansion, especially along Southeast Spain and central Portugal.

Acknowledgments

Conflict of interest

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.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.026.

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