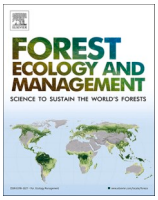
Forest Ecology and Management 582 (2025) 122566

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Climate-driven increase in mistletoe infestation in Iberian pine forests

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ARTICLE INFO

Keywords:
Forest health
Monitoring
Geostatistical techniques
Global change
Damage
Decline

ABSTRACT

Mistletoe is a common hemiparasitic plant in forest in Spain. However, more studies on mistletoe infestations are needed to determine the spatial and temporal patterns and to develop control and monitoring programmes for forest health. For this purpose, we used harmonised data from three existing forest damage networks in Spain, including ICP-Forest, from which only national data was taken, including climatic variables to model the distribution and to predict the degree of mistletoe infection using geostatistical techniques. Having selected the variables, the spatial models were evaluated using the area under the curve statistic to predict the distribution area (AUC=0.99) and one-out cross-validation to predict the degree of infection in areas with mistletoe presence. Overall, 87 % of the pine forest area is free of mistletoe. Within the affected distribution area, the Alpine region (23 %) has the highest percentage of area affected, followed by the Mediterranean region (14 %), with no records available in the Atlantic region. Regarding mistletoe abundance, the variation throughout the study period according to damage-degree class reveals a decrease of 18.2 % in "slight" class, a decrease of 2 % in "moderate" class, an increase of 15 % in "moderate-high" class and an increase of 5.2 % in "severe" class. Our results indicate that the incidence and severity of mistletoe infection are highly spatially concentrated and strongly related to climatic conditions, especially temperature and precipitation in previous years. Prediction maps showing the spatial patterns of mistletoe distribution can be useful for damage prevention and risk control.

1. Introduction

The importance of forest ecosystems in mitigating climate change and contributing to the development of a more sustainable bio-economy is receiving increasing technical, media, and political attention. In this regard, the health and vitality of forests are essential for their sustainability (Rohner et al., 2021). Abiotic and biotic disturbances can, however, cause significant social, economic, and environmental losses in forest ecosystems (Kautz et al., 2017). These disturbances include, but are not limited to, fire, pests and diseases, invasive species, air pollution, and extreme weather events (e.g. drought, frost, storms, and floods) (Schelhaas et al., 2003). Disturbances impact various ecosystem functions, services, and processes such as tree growth and survival, wildlife habitat, recreational use, landscape, and cultural values (Nelson et al., 2017). Furthermore, the frequency and the intensity of damage driven by both the biotic and abiotic factors are being affected by climate change (Rebollo et al., 2024).

Among the pathogens identified in Mediterranean forests, mistletoe (*Viscum album* L.) stands out. It is a hemi-parasitic plant that lives on woody plants, from which it extracts water and minerals, causing stress to the host tree and altering its growth and reproductive capacity (Catarina et al., 2021). Moreover it can cause permanent systemic metabolic changes in the host plant (Lázaro-González et al., 2021). There is a degree of host-species specificity, which has led to three subspecies of mistletoe being differentiated; *V. album subsp. album* parasitises on species of the genera *Salix*, *Populus* and *Acacia*, among others; *V. album subsp. austriacum* parasitises on several coniferous species, especially *Pinus* and less frequently *Larix* and *Picea*; and *V. album subsp. abietis* parasitises on *Abies* (López-Sáez and Sanz De Bremond, 1992).

The plant reproduces from seed, which is mainly carried by birds, the most important being *Turdus viscivorus* L. and *Silvia atricapilla* L (Zuber, 2004). Once the mistletoe plant is fixed and established on the tree, it develops in a dichotomous manner, each bud branching into two branches. This arrangement gives rise to a characteristic hemispherical cluster. It remains on the same host for 25–30 years and its effects are particularly noticeable during periods of drought, as mistletoe

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https://doi.org/10.1016/j.foreco.2025.122566
Received 13 December 2024; Received in revised form 23 January 2025; Accepted 13 February 2025

penetrates the xylem, absorbing water and minerals and exacerbating water stress (Sangüesa-Barreda et al., 2012), which may contribute to tree decline (Gea-Izquierdo et al., 2019). In addition, the weakening of the host facilitates the entry of other pathogens (Sangüesa-Barreda et al., 2012).

Mistletoe is an ecosystem engineer species. Its infection is a dynamic process that can modify stand dynamics over time with progressively increasing infection rates, which can lead to increased tree mortality, and can be summarised in three stages (Griebel et al., 2017) i) at first, the effects of establishment of the hemi-parasitic species are limited to individual branches. Increasing mistletoe load on individual trees will start to show noticeable effects on the host tree after a few years. At this early stage of infection, initial impacts on biodiversity can be observed, as mistletoe mats provide favourable nesting sites and food resources (Griebel et al., 2017). Mistletoe mainly affects dominant or co-dominant trees located at the borders and of greater height (van Halder et al., 2019); ii) In the next stage of infection, seed dispersers spread the infection from highly infected individuals throughout the stand. At this stage, the effects of mistletoe are reflected in the loss of tree growth and vitality by changing canopy conditions because of crown defoliation. This results in increased light penetration and bird activity, which as infection increases, increases the soil microbial community (Mellado and Zamora, 2016). The combination of both factors favours the establishment of seedlings and therefore at this stage an increase in plant cover, species richness and diversity can be observed (Hódar et al., 2018); iii) In a final stage, which can take more than a decade, stands lose resilience and may see increased tree mortality rates either of individual trees or of stands under excessive water stress (Sangüesa-Barreda et al., 2012). The high degree of infection also leads to regeneration problems (Rigling et al., 2010). Therefore, the mortality of multiple trees combined with the loss of reproductive capacity may favour the consolidation and development of thickets resulting in at least temporary replacement (Griebel et al., 2017; Mellado and Zamora, 2017).

The increase of temperature as consequence of climate change may favour a range shift of mistletoe towards higher elevations and northern latitudes (Sangüesa-Barreda et al., 2018). Mistletoe is very sensitive to low winter temperatures, which determine its northernmost range limits. Temperature is the dominant factor influencing the distribution of mistletoe, with summer temperatures above 15°C and winter temperatures not exceeding −7°C (Walas et al., 2022). In fact, this species exhibits a high degree of sensitivity to low winter temperatures, which determine its northmost range limits. However, its distribution is not only limited by climate, but also by the presence of seed-dispersing birds that act as vectors (Sangüesa-Barreda et al., 2018). To date, other studies have linked the following indicators to the dispersal process: (1) bird abundance (García et al., 2018; Ramsauer et al., 2022) (2) bird species richness (García et al., 2013), the richer the community, the greater the diversity of seed rain, leading to greater colonisation and regeneration of species (García et al., 2013; Ramsauer et al., 2022; Rodríguez-Pérez et al., 2017); (3) the specialisation of a bird species (Ramsauer et al., 2022). However, most of the studies addressing the dynamics of mistletoe have been carried out at local scales (Bilgili et al., 2020; van Halder et al., 2019) focusing on its distribution area, whereas information at broader spatial scales, particularly regarding its abundance in areas where the species is already present, is scarce.

The species distribution model (SDM) has become an important analytical tool in conservation and land management (Walas et al., 2022). The SDM consists of one or several statistical algorithms predicting the distribution (actual or potential) of a species based on field observations and auxiliary maps (Hengl et al., 2009). They allow model-based predictions of species occurrence (Lissovsky et al., 2021), thus contributing to the fields of natural resource management, biogeography, and evolutionary ecology (Duarte et al., 2019). Geostatistical techniques have proved suitable for modelling species distributions from point based surveys (Miller et al., 2007). Geostatistical methods are based on statistical models that incorporate spatio-temporal autocorrelation of predicted variables, which is expected in the case of plant presence and abundance due to the continuous nature of ecological factors and processes controlling species distribution (Cressie, 1985). Universal Kriging (UK) is the most commonly used geostatistical technique for modeling species distributions from large-scale forest inventory data (Hernández et al., 2014), as it allows auxiliary variables to be incorporated to explain the underlying trends in the data (Montes and Ledo, 2010).

For more than three decades, the International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP-Forest) has been assessing the condition and development of forest stands according to harmonised methods and protocols for Europe, with an annual periodicity for reviewing and updating information under the European Level I Monitoring Programme (LIMP). The LIMP is a 16 × 16 km network established more than three decades ago and covering the whole of Europe (about 7500 points or plots) with the aim of monitoring the health vitality and biodiversity of European forests (Ferretti, 2013). Therefore, these long-term monitoring networks provide an essential tool to study the distribution and spatial relationship between forest health and the abiotic and biotic driven forest dynamics.

In addition, there are two others forests conditions networks at the Spanish national level: The Phytosanitary Monitoring National Parks Network (NPN), initiated in 1986, and the Forest conditions Damage Networks of the Autonomous Communities (main administrative units in the country; ACN), progressively installed in the Spanish Autonomous Communities since 2000. The installation of both networks has been executed in accordance with a methodology that is analogous to that employed in the ICP Forests, thereby ensuring the harmonisation of these methodologies (Adame et al., 2022).

These three networks together provide large-scale monitoring over time of the most representative forest types, enabling comprehensive studies at national scale of the factors impacting the health and vitality of forests across extensive areas. These databases can also serve as a valuable risk management tools for competent authorities. Mistletoe management is complex, involving a variety of strategies, including biological, chemical, mechanical, and silvicultural methods (Mudgal et al., 2022). Nevertheless, management plans consistently prioritise the characterisation of affected areas as the first line of action.

The overall objective of the study is to assess the dynamics of presence and abundance of *Viscum album subsp. austriacum* (hereafter mistletoe), in their main hosts (*Pinus sylvestris* L., *Pinus pinaster* Ait., *Pinus nigra* Arn. and *Pinus halepensis* L.) in Spain during the period 2005–2020. We also aim to identify the climatic and forest stand composition variables associated with the abundance of this hemi-parasitic species. We expect that, given the observed increment in temperature, the impact of this species during the last years will increase.

2. Materials and methods

2.1. Study area

Spain is characterised by distinct climates, with the Mediterranean being the most common, although other climates such as Alpine, Atlantic and Macaronesian (exclusive for Canary Islands) are also notable. The average annual temperature is around 12.8 ºC (± 2.01) and the average total annual precipitation is 617 mm (± 171) over the study period (2005–2020). The study area focuses on forest stands of *P. sylvestris*, *P. pinaster*, *P. nigra* or *P. halepensis* in the Spanish Iberian Peninsula (southwest Europe). The area under consideration covers approximately 7.5 million hectares, of which 30 % is dominated by *P. halepensis*, 18 % by *P. pinaster*, 17 % is dominated by *P. sylvestris* and 13 % by *P. nigra*. Besides, we have considered mixed stands where the aforementioned target species are present but they are not dominant. These mixed stands represent 21 % of the study area and are mainly

dominant by *P. pinea* L., *Q. ilex* L., *Q. faginea* Lam. and *Q. pyrenaica* Willd. (Fig. 1). All of these species are widespread throughout the country, covering a significant proportion of the Spanish forest area.

2.2. Data bases

2.2.1. Forest conditions damage networks

We used three different data sources to evaluate the dynamics of mistletoe in Spain: i) the European Level I Monitoring Programme of ICP Forests (ICP Forests, http://www.icp-forests.net), ii) the Phytosanitary Monitoring Network of the Forest Stands of the National Parks (NPN) and iii) the Forest conditions Damage Networks of the Autonomous Communities (main administrative units in the country; ACN) (Figure A.1).

The Spanish LIMP network consists of 620 plots in a grid of 16 × 16 km, each with 24 dominant or co-dominant trees sampled. These trees are selected according to strict criteria, embracing the six dominant or codominant trees closest to the center of the plot per quadrant (NE, SE, SW, and NW) (Ferretti, 2013). Tree crown condition (defoliation, crown transparency, and discolouration) and tree damage (agent, affected area, intensity) were assessed once a year from 1986 to 2020. The identification of mistletoe was incorporated in 2005.

The other forest conditions damage Spanish networks studied (NPN and ACN) consist of plots where measurements are taken using comparable field protocols to the ones used in the LIMP network. The ACN includes 2503 plots on an 8×8 km grid and 62,575 trees, while the NPN is limited to 234 plots on a 4 × 4 km grid and 6076 trees. The merging of the three networks provides a harmonised database of 3357 plots and 83,531 trees recorded from 2005 to 2020. These networks consist of a systematic sampling, this sample is representative of the different management options for each species, including wood and fruit production, resin extraction, soil erosion control or biodiversity conservation. Fig. 2 shows the location of the plots in the three forest conditions damage networks with presence of hosts species affected and non-affected by mistletoe. To study the dynamics of presence and abundance of mistletoe in the Spanish forest conditions networks we selected plots in which there was presence at least 10 % canopy cover of the pre-selected pine hosts species (*P. sylvestris*, *P. pinaster*, *P. nigra,* and *P. halepensis)* (Table 1, Table 2, Fig. 2). Additionally, to further investigate the degree of damage at plot level, we calculate the degree of infection (DI) by mistletoe in each plot. DI was defined as the ratio of affected trees (AT), i.e., trees with presence of mistletoe, and the total number of possible hosts (PH) at plot level:

$$DI(\%) = \frac{AT}{PH} \quad (1)$$

2.2.2. Spanish forest Map (SFM)

The Spanish Forest Map (SFM) was used to determine the distribution area of the main hosts species of mistletoe in Spain and consequently to assess the impact of mistletoe on them. The SFM, which is regularly revised, is the main forest mapping resource in the country, providing information on the distribution of Spanish forest stands populations. The SFM provides complete and uniform vector information on the forest structure of each polygon, indicating primary or dominant species (up to three), cover and development stage among other characteristics. The most recent SFM was used, i.e. SFM25 (minimum polygon size of 1 ha) with a scale of 1:25.000 for the regions already available at that scale (64 % of the area), and SFM50 (minimum polygon size of 2.5 ha) with a scale of 1:50.000 for the rest.

The distribution area of *P. sylvestris*, *P. pinaster*, *P. nigra,* and *P. halepensis* was determined by identifying SFM areas in which one of these four pines were presented as a main or secondary species (with at least 10 % presence in the canopy cover). These areas include both monospecific and mixed stands. A monospecific stand is defined as an area where 70 % or more of the total canopy cover is composed of a single species, and the rest are defined as mixed stands where the host species of the study is present as an accompanying species.

2.2.3. Climatic information

Climatic data from meteorological stations belonging to the Spanish State Meteorological Agency (www.aemet.es) were used to analyse the degree of mistletoe infection. The data recorded cover the period 1990–2020 and include 2106 temperature and 3581 precipitation readings. The climatic variables considered as potential explanatory factors are seasonal and annual mean temperatures and seasonal and annual precipitation. Seasonal and annual precipitation was averaged

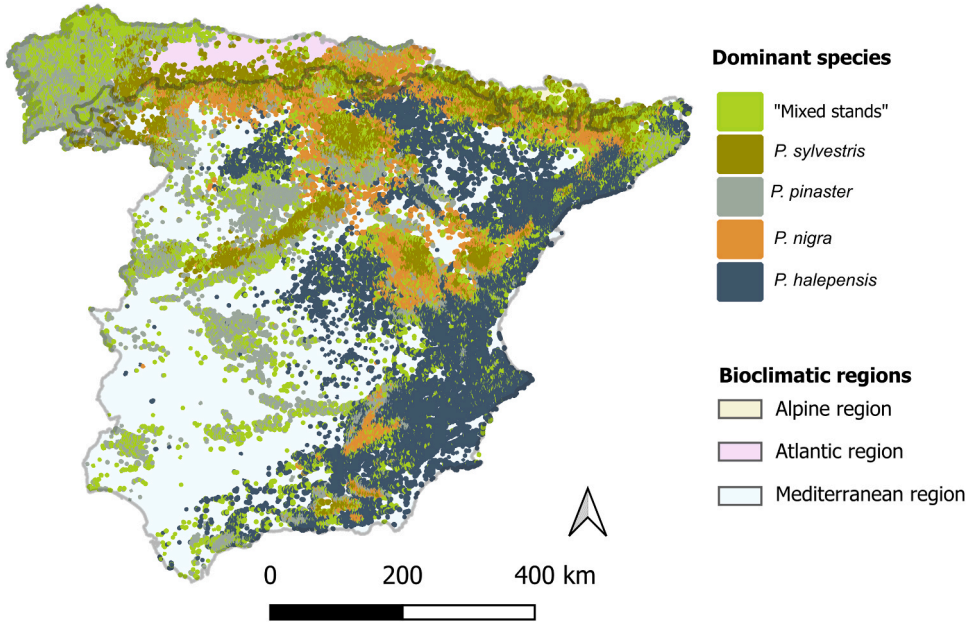

Fig. 1. Spatial distribution of potential mistletoe host pine species. The dominant species refers to dominance of stands where at least 10 % of the area is occupied by one of the four mistletoe hosts (*P. sylvestris, P. pinaster, P. nigra or P. halepensis*). Mixed stands means that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species, these are mainly dominant by *P. pinea, Q. ilex, Q. faginea, and Q. pyrenaica.*

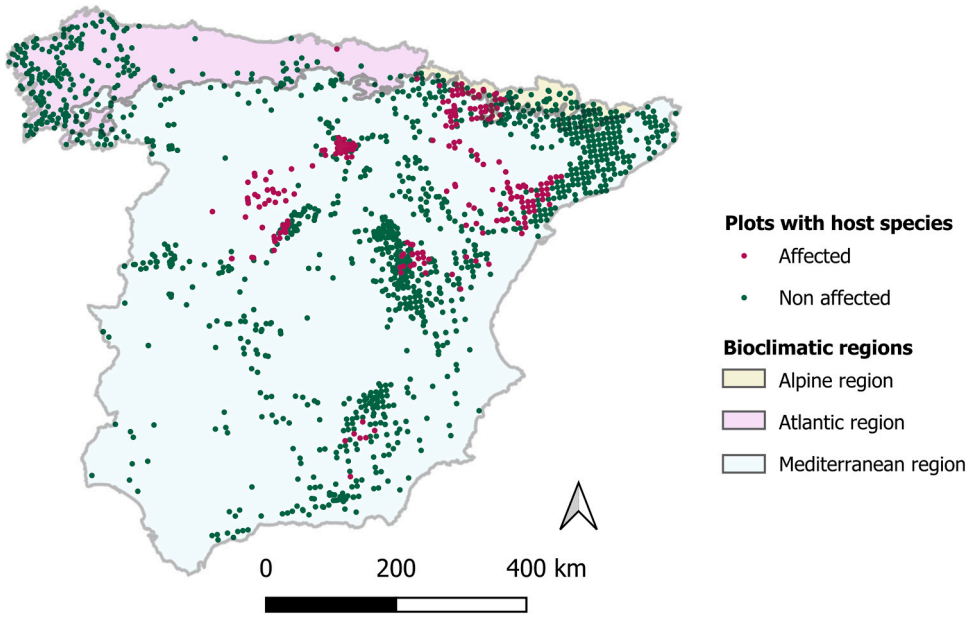

Fig. 2. Distribution of plots with hosts (*P. sylvestris, P. pinaster, P. nigra and P. halepensis*) non-affected and plots with pine trees affected by mistletoe in Spanish peninsular forests in the period 2005 – 2020 registered by the three forest conditions damage networks studied.

Table 1
Number of plots and number of trees assessed in the IPC-Forest damage network, the National Parks networks (NPN), and the Autonomous Communities network (ACN) in the period 2005–2020 in which host trees are present (PH) and which are affected by mistletoe (AT).

	With presence of hosts (PH)				Affected by mistletoe (AT)			
Network	Plots	%	Trees	%	Plots	%	Trees	%
ICP-Forests	292	19	9350	24	52	22	572	24
ACN	1179	76	26549	69	180	75	1771	73
NPN	71	5	1928	5	8	3	77	3
Total	1542	100	38639	100	240	100	2420	100

Table 2
Number of plots and percentage with host species and those affected by mistletoe in the period 2005–2020 by dominant specie. The dominant species represents the dominance of stands where at least 10 % of the surface area is occupied by one of the four mistletoe hosts (*P. sylvestris, P. pinaster, P. nigra or P. halepensis*). Mixed stands means that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species, these are mainly dominant by *P. pinea, Q. ilex, Q. faginea and Q. pyrenaica.*

Dominant specie	Number of plots with hosts species	%	Number of affected plots	%
P. sylvestris	385	25	61	25
P. pinaster	321	21	108	45
P. nigra	265	17	27	11
P. halepensis	330	21	24	10
"Mixed stands"	241	16	20	8
Total	1542	100	240	100

for each time point, taking into account 1) the reference year and 2) the five preceding years. A total of 15 seasonal/annual climate variables were obtained. Spatio-temporal UK models as described in the following sections, incorporating altitude as well as X and Y coordinates as auxiliary variables, were used to interpolate the climate variables at the sampling points of the damage networks and at the centroids of the SFM polygons. The auxiliary variables with $p < 0.05$ were included in the model. When none of the auxiliary variables were significantly related to the response, Ordinary Kriging (OK), which retrieves predictions based only on geographic variables observations, was used instead of UK.

2.3. Mistletoe distribution modelling

The prediction model for DI of mistletoe was developed in two phases. Firstly, we predicted the species distribution by fitting an OK space-time model where the target variable was the indicator variable of presence/absence of mistletoe in the plot. Mistletoe presence was considered when this species occurred in at least one of the sampled trees in a plot. We used the full array of plots (PH) (Table 1) in this analysis. Kriging techniques predict the value of $Z(s_0, t_0)$ at an unsampled location s_0 and a time-point t_0 based on the values of $Z(s_1, t_1)$, $Z(s_2, t_2)$, …, $Z(s_n, t_n)$ at n observation points. The value prediction $p(Z,s_0, t_0)$ of the variable Z at point s_0, t_0 is then performed by estimating the optimal weights λ_i for each observation while considering the autocorrelation structure of the variable (Armstrong et al., 1998; Oliver and Webster, 2015):

$$p \quad (Z, \quad s_0, t_0) = \quad \sum_{i=1}^{n} \lambda_i \bullet Z(s_i, t_i) \tag{2}$$

The autocorrelation structure of the observations can be represented abstractly by the empirical semi-variogram or variogram $\gamma(h_s,h_t)$. This is defined as half the expected squared difference between paired (intrinsic) random functions (Matheron, 1973) at a distance d (Atkinson and Lloyd, 2007; Goovaerts, 1997). Modelling of the variogram $\gamma(h_s,h_t)$ is required to estimate the optimal weights λ_i. We utilised the generalized product-sum model (De Iaco et al., 2002) to model the spatio-temporal variograms. The spherical variogram model was selected for both the spatial and the temporal components after visual inspection of the empirical variogram. Weighted Least Squares (Cressie, 1985) was used to fit the OK variogram parameters. We then predicted the probability of mistletoe presence in the polygons of the SMF in 2005, 2010, 2015, and 2020 to assess possible changes in mistletoe distribution over the monitored period.

To back-convert the continuous values predicted by the OK model into mistletoe presence/absence maps, we used a cutoff point obtained (known as optimal operating point) from the Receiver Operating Characteristic curve. This point reflects the decision threshold that optimises the performance of the model in terms of maximizing sensitivity, calculated through the True Positive Ratio, and 1 – specificity, calculated through the False Positive Ratio (Valavi et al., 2022). In this way,

polygons with predicted values above the threshold (optimal operating point) (Fig. 2) are classified as areas with mistletoe, while those with values below the threshold are classified as areas without the hemi-parasitic plant.

Leave-one-out cross validation was carried out in order to validate the OK model. Due to the low inter-annual variance, when predicting the value during the cross validation, the entire temporal series corresponding to each predicted observation point was excluded from the sample. The discriminative power of the model was evaluated using the area under the precision-recall curve (AUC_{PR}) statistic, which measures the performance of a classificatory model in terms of its ability to maximise both precision and recall simultaneously. The precision-recall curve is considered an effective diagnostic for imbalanced binary classification models. A value of 1 is indicative of a perfect model, whereas a value of 0.5 is indicative of a model that is no better than a random choice.

Additional statistical metrics for evaluating the predictive efficacy of classification models include the Matthews correlation coefficient, which assesses the quality of a binary classification by considering the four values of the confusion matrix. It takes values between −1 and 1. A value of 1 indicates a perfect prediction, −1 indicates an incorrect prediction, and 0 indicates a random outcome. Finally, the kappa coefficient indicates the 'goodness-of-prediction' over chance. It takes values from 0 to 1, and a value of 0.61–0.8 is considered a good prediction, while a value of 0.81–1.00 is considered a very good prediction.

2.4. Degree of infection prediction

In the second phase, we adjusted an UK model for DI including climatic data as auxiliary information and the dominant species as a categorical variable. Considering that forest types are mainly defined by the dominant species and that the UK model takes into account both the effect of the dominant species through the categorical auxiliary variable and the spatial proximity of nearby plots of the same or different species, provide a suitable approach for modelling the degree of mistletoe infection in areas where species are intermixed. In UK models, the mean E(Z(s, *t*)) is composed of a deterministic drift that can be explained by an unknown linear combination of $p + 1$ spatially structured auxiliary variables (usually denoted as $f_k(s, t)$) that are known at both sampled and unsampled locations, and a spatially correlated random process δ(s, *t*) (Montes and Ledo, 2010):

$$Z \quad (s_0, t_0) = \quad \sum_{K=0}^{p} \beta_k f_k(s_0, t_0) + \delta_0(s_0, t_0) \tag{3}$$

Several methods can be employed to determine the variogram parameters and β_k coefficients. Iteratively Reweighted Generalised Least Squares, as described by Neuman and Jacobson (1984), was selected to jointly estimate the variance-covariance matrix and β_k coefficients of the auxiliary variables. We employed the generalized product-sum model and spherical variograms for both temporal and spatial components and assumed a shared nugget effect for both components.

Due to the importance of the host species in the spread of mistletoe spreading, dominant pine species was included as categorical auxiliary variable in the model. This categorical variable was introduced in the kriging equations as p-1 (were p is the species number) dummy variables, thus establishing a different trend function intercept depending on the dominant species. Different combinations of uncorrelated climatic auxiliary variables were tested. In order to assess the significance of β_k coefficients of the auxiliary variables p-values were calculated (Moreno-Fernández et al., 2016). For this model, we filtered out the plots affected by mistletoe (AT, Table 1). Then, we predicted the DI of the species in the polygons of the SFM where OK prediction of the mistletoe presence indicator surpass the model operating point. In order to analyse the effect of climate variables on degree of mistletoe infection we used block kriging (Hernández et al., 2014) to obtain the mean prediction and kriging variance by dominant species and also i) total annual rainfall averaged for the previous 5 years and ii) mean temperature.

Leave-one-out cross-validation was employed to evaluate the performance of the UK model in terms of bias and predicted variance. A random sample of 100 points was selected from the data set for the cross-validation of the UK model. Due to the low inter-annual variance, when predicting the value during the cross validation, the entire temporal series corresponding to each predicted observation point was excluded from the sample.

Finally, mistletoe damage degree maps were created for the centroids of the SFM polygons for 2005, 2010, 2015, and 2020. These maps show the spatiotemporal dynamics of the mistletoe distribution and the impact in stands where *P. sylvestris, P. pinaster, P. nigra* and *P. halepensis* are present in Iberian Peninsula. To facilitate the representation of the spatio-temporal dynamics of the degree of infection, we grouped this index into four classes; the first one (DI1) representing slight infection of between 1 % and 25 %, class 2 (DI2), moderate infection of between 26 % and 50 % of the affected trees, class 3 (DI3), moderate-high infection of between 51 % and 75 % of the affected trees and class 4 (DI4) severe infection, of between 76 % and 100 % of the affected trees.

Considering that forest types are mainly defined by the dominant species and that the UK model takes into account both the effect of the dominant species through the categorical auxiliary variable and the spatial proximity of nearby plots of the same or different species, providing a suitable approach for modelling the degree of mistletoe infection in areas where species are intermixed.

The geostatistical analyses were conducted using MatLab® software developed by the authors and freely available by contacting the corresponding author, and raster calculations and map drawings were carried out using QGIS 3.34.3.

3. Results

3.1. Spatial distribution of mistletoe

The results from the exploratory data analysis (Table 2) show that, of the total plots used in the study, 25 % are dominated by *P. sylvestris*, 21 % by *P. pinaster* and *P. halepensis* respectively, 17 % by *P. nigra*, and 16 % correspond to mixed stands. Mistletoe is present in 45 % of the plots dominated by *P. pinaster*, followed by 25 % in plots dominated by *P. sylvestris*. It is also found in 11 %, 10 %, and 8 % of the plots dominated by *P. nigra*, *P. halepensis*, and mixed stands, respectively.

The mistletoe variogram for the distribution of mistletoe exhibit moderate spatial variability (spatial sill = 0.0581) extending over considerable distances (spatial range 1704 km), whereas temporal variability was practically negligible (temporal sill = 0.000, time range = 0.7724). This indicates that the spatial distribution of the target species remained quite stable over the study period. With regards to model validation, cross-validation statistics indicate a robust model, exhibiting excellent performance in terms of classification and discrimination of mistletoe presence, contingent on the accuracy measures employed in the analysis (Fig. 3).

Having predicted the presence of mistletoe in the polygons, we found that overall, 87 % of the forest pine area is free of mistletoe. Within the affected distribution area, the Alpine region has the highest percentage of area affected, followed by the Mediterranean region, with no records in the Atlantic region. In terms of area, the Mediterranean region accounts for the most. When analysing the distribution according to the dominant species in the forest stands, *P. sylvestris* has the highest percentage of affected area (22 %), followed by stands dominated by *P. halepensis* (14 %) and *P. pinaster* (12 %), with hardly any presence in stands dominated by *P. nigra* (5 %) (Table 3, Fig. 4).

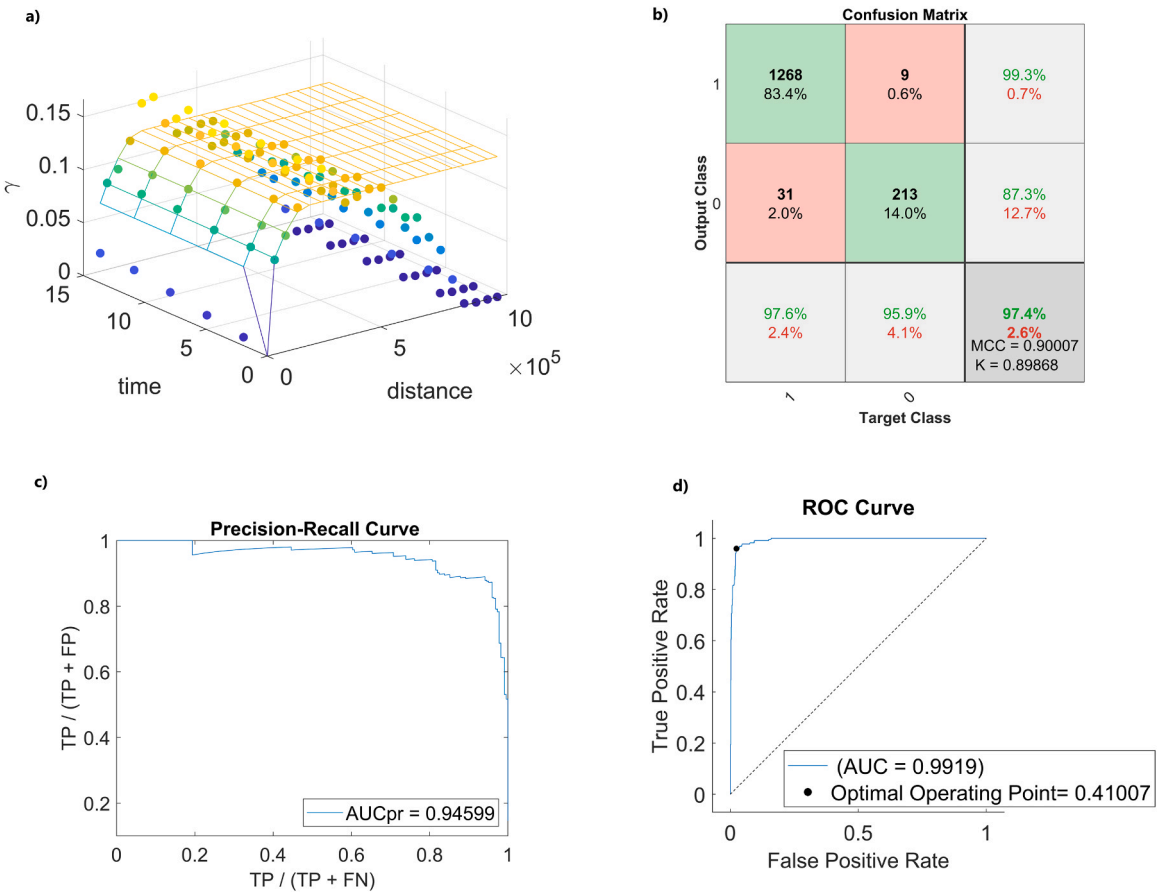

Fig. 3. Ordinary kriging models, parameters of variogram and cross validation. a) variogram; b) matrix confusion; c) precision recall-curve; d) ROC curve. AUCpr: Area Under the precision-recall curve, AUC: Area under the receiver operating characteristic curve, k: kappa coefficient, MCC: Matthews coefficient correlation.

Table 3
Spatial distribution of mistletoe according to dominant species by bioclimatic areas. Mixed stands means that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species. Naff: non-affected areas; Aff: affected areas.

Dominant species		Alpine Area		Atlantic Area		Mediterranean Area		Total	
		(ha)	(%)	(ha)	(%)	(ha)	(%)	(ha)	(%)
P. sylvestris	Naff	152,512.80	75	94,598.53	100	758,839.48	77	1,005,950.81	78
	Aff	51,493.43	25	0.00	0	232,216.41	23	283,709.84	22
P. pinaster	Naff	220.51	100	363,040.21	100	861,390.86	84	1,224,651.58	88
	Aff	0.00	0	0.00	0	168,094.29	16	168,094.29	12
P. nigra	Naff	7890.85	79	18,426.41	100	933,797.11	95	960,114.37	95
	Aff	2158.73	21	0.00	0	45,912.70	5	48,071.43	5
P. halepensis	Naff	171.66	100	4.29	100	1,960,498.03	86	1,960,673.98	86
	Aff	0.00	0	0.00	0	316,864.27	14	316,864.27	14
"Mixed stands".	Naff	81,811.66	83	354,474.53	100	1,035,733.00	89	1,472,019.19	91
	Aff	17,071.55	17	0.00	0	124,994.66	11	142,066.21	9
TOTAL	Naff	242,607.48	77	830,543.97	100	5,550,258.48	86	6,623,409.93	87
	Aff	70,723.71	23	0.00	0	888,082.33	14	958,806.04	13

3.2. Evolution of degree of mistletoe infection

Based on prior exploratory analyses (Table 4), dominance of each of the four host species (as dummy variables), mean annual temperature, and averaged total precipitation in the five preceding years were selected as auxiliary variables (M5). The dummy variables indicating pine-species dominance were significant at $p < 0.0001$ for all the models tested.

The coefficient of the explanatory variables is negative for the rainfall and positive for the temperature (Table 5), indicating a positive relationship between degree of infection by mistletoe and less humid and warmer conditions.

With regard to the total distribution of mistletoe without distinguishing between dominant host in the stand, it can be seen that the area corresponding to moderate-high and severe damage classes increases and the area corresponding to light and moderate damage classes decreases (Fig. 5.a). Throughout the study period, the area in which there is moderate damage predominates and is also the damage class which the proportion remains the most stable. The variation throughout the study period by damage-degree class reveals a decrease of 18.2 % in class 1, a decrease of 2 % in class 2, an increase of 15 % in class 3 and an increase of 5.2 % in class 4.

In the Fig. 5b-f, the temporal evolution of the variation in the different degree infection classes is shown according to the dominance

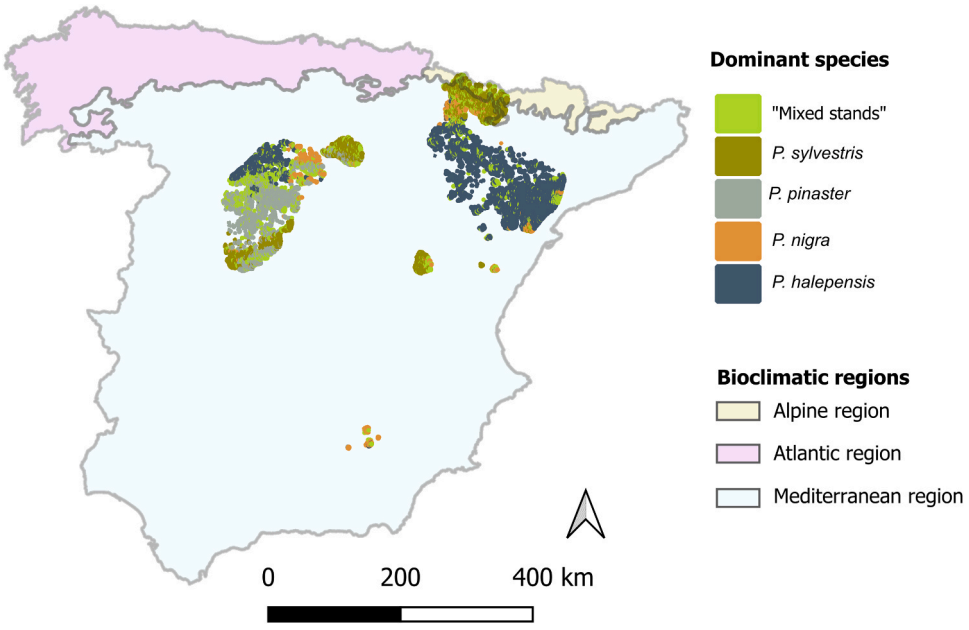

Fig. 4. Mistletoe spatial distribution by affected dominant host species. Dominant species refers to the dominance in stands where at least 10 % of the surface area is occupied by one of the four mistletoe hosts (*P. sylvestris, P. pinaster, P. nigra or P. halepensis*). Mixed stands means that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species, these are mainly dominant by *P. pinea, Q. ilex, Q. faginea and Q. pyrenaica.*

Table 4
Variogram parameters and cross-validation statistics for final model selection. The auxiliary variables are composed of a three-character code, the first character refers to the climatic variable (T: temperature, R: rainfall); the second to the reference year (0: reference year, 5: averaged for the previous 5 years); and the last to the season (A: annual, Sm: summer, Sp: spring). Significant explanatory variables: * <0.01, * *< 0.001, * ** <0.0001.

		Variogram parameters						Cross-validation statisctics		
Models	Auxiliary variables	XYt Nugget	XY Partial Sill	XY Range	t Partial Sill	t Range	Scale coefficient	Root mean square error	Bias	Squared Error/Kriging Variance
M1	TA0 *** , RA0 *	591.94	157.93	656,897.69	40.77	15.00	0.00	0.6246	0.0209	0.8255
M2	TA0 * **	602.25	195.19	656,897.67	27.93	15.00	0.00	0.6164	0.0388	0.8291
M3	TSm0 * **	610.99	190.80	656,897.65	16.43	15.00	0.00	0.5735	0.0899	0.6140
M4	TA0 * ** , RSp0 *	587.15	194.94	656,897.69	28.02	15.00	0.00	0.5404	0.0139	0.6396
M5	TA0 * ** , RA5 *	594.24	160.83	656,897.69	35.41	15.00	0.00	0.5449	0.0176	0.6429
M6	TA0 * ** , RSp5 *	600.64	216.30	656,897.69	53.99	5.13	0.00	0.5521	−0.0159	0.6644

Table 5
Coefficients of the explanatory variables of the UK model for the degree of mistletoe infection (DI).

Explanatory variables		coefficient
Dominant	*P. sylvestris*	22.551828
	P. pinaster	22.749674
	P. nigra	−1.041476
	P. halepensis	−0.438802
	"Mixed stands"	31.755845
Annual mean rainfall 5 years prior to the reference year		−0.02182
Annual temperature of the reference year		3.5974272

of each host species. In the stands dominated by *P. sylvestris*, the largest proportion of the area exhibits moderate and moderate-high damage, with a notable 34.5 % increase in moderate-high damage between 2005 and 2020. In stands dominated by *P. pinaster*, areas with moderate-high damage predominate, with a notable 14.7 % increase in the proportion of area with severe damage. In stands dominated by *P. nigra*, most of the area shows mild to moderate damage; however, the significant increase in the area with moderate damage, from 17 % in 2005 to 49 % in 2020, represents the largest increase, a trend also observed in stands dominated by *P. halepensis*. Lastly, mixed stands show the highest proportion of severe damage, reaching 24.2 % in 2020. If the areas with moderate-high damage are included, the proportion of affected area reaches nearly 88 %.

Finally, the UK prediction maps (Fig. 6) reveal a significant shift in the prevalence of mistletoe infection over the course of the study period. The upper part of the figure illustrates the distribution of mistletoe presence in host stands, while the lower part depicts the evolution of the degree of infection over the entire study period (2005–2020), with a zoom-in on each affected area.

The block kriging predictions according to the infection degree and the mean temperature showed similar trends for the different dominant species: the higher the temperature, the greater the degree of infection (Fig. 7a), with significant differences between the temperature range limits. Conversely, the lower the five-year averaged annual rainfall, the greater the degree of infection (Fig. 7b).

4. Discussion

This study proposes a spatio-temporal approach to identify the climatic variables associated with the distribution dynamics of mistletoe

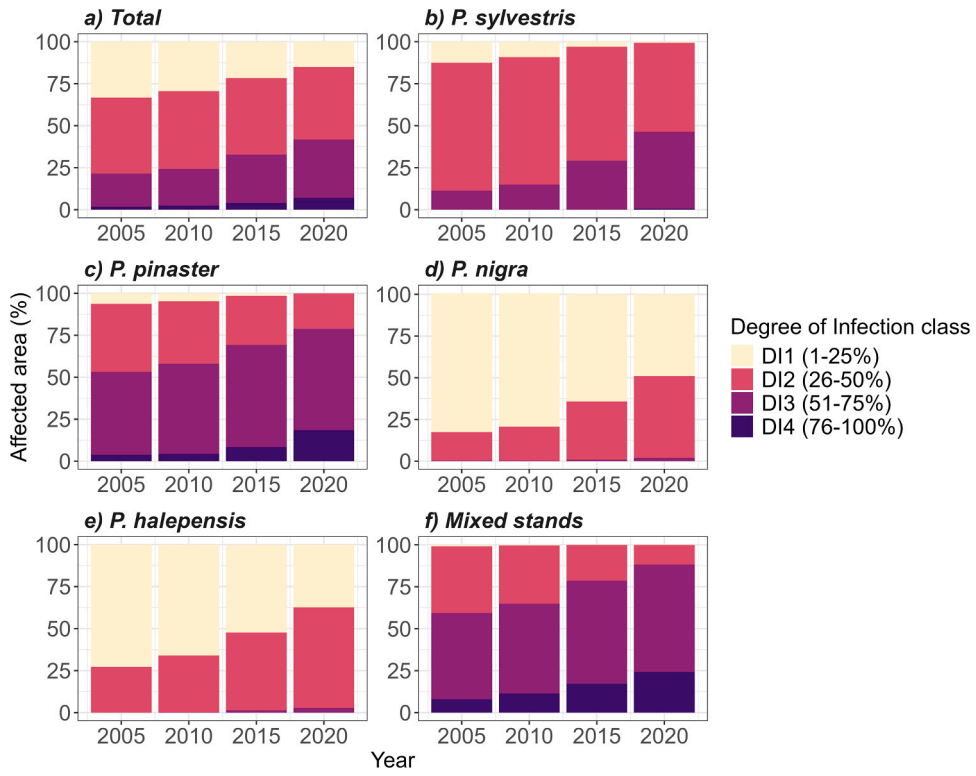

Fig. 5. a) Affected area (%) by degree of infection class from UK prediction for the overall mistletoe distribution. b) Affected area (%) by dominant specie. DI: Degree of infection. Mixed stands means that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species.

considering its presence and level of infestation in Spanish pine forests between 2005 and 2020. Geostatistical techniques allow for the spatial modelling of regionalized variables from a set of observations irregularly distributed across space and time (Matheron, 1973). Previous distribution modelling through indicator kriging enhances the assessment of the effect of environmental factors on mistletoe infection degree by eliminating the observation points outside the distribution area from the UK sample (Montes et al., 2005).

Our mistletoe infection degree maps provide information about the areas and species most severely affected and those with the highest rates of mistletoe spread. Community-scale changes can be accentuated in communities where keystone organisms or important dominant species serve as primary hosts (Bruno et al., 2007; Dobson and Hudson, 1986; Minchella and Scott, 1991). Our results indicate that *P. sylvestris* and *P. pinaster* are the main affected species. Previous findings indicate that mistletoe is impacting the growth of these species (Gea-Izquierdo et al., 2019). The presence of mistletoe can also accelerate species succession within these pine-dominated communities, resulting in higher taxonomic diversity when dominant species are preferred as hosts (Mellado and Zamora, 2017). However, our results indicate that mixed stands have the highest coefficient, which suggests that these forest types are the ones most affected, probably due to the higher diversity of birds in these forests as argued by other authors (García et al., 2013; Ramsauer et al., 2022; Rodríguez-Pérez et al., 2017). In these stands, mistletoe grows on non-dominant species and, therefore, mistletoe impact may result in lower diversity because of the degradation of companion species (Gibson and Watkinson, 1992). Moreover, some authors also claim that mistletoe, being dependent on a network of other organisms (including pollinators, seed dispersed, and hosts), can be used as a bioindicator of ecosystem health (Crates et al., 2022).

The majority of the variability of the mistletoe presence indicator is associated with the spatial sill in the ordinary kriging variogram, which results in a stable area of mistletoe presence accounting for 13 % of pine forests in Spain during the study period. It must also be taken into account that the presence of mistletoe requires a host and a seed dispersal vector, in this case birds (Walas et al., 2022). Therefore, mistletoe distribution is closely tied to that of its hosts and dispersal vectors. A strong link between bird mobility and the dispersal process has been demonstrated (Ramsauer et al., 2022), and bird abundance is strongly related to the seed dispersal of this species (García et al., 2018) and similar parasitic plants (Wilson et al., 2014). The high spatial autocorrelation along with reduced temporal variability could be explained by the fact that mistletoe remains on the same host for several years, exerting direct and spatially concentrated effects (Mellado and Zamora, 2017). The distribution of mistletoe in Iberian pine stands is mainly constrained to Inner Spain and southern high-mountain forests. In particular, (Walas et al., 2022) found a shift of this species towards northern and eastern Europe and a retraction of southern populations subjected to warmer conditions. Other studies have found an upward elevation shift in mistletoe distribution in response to increasing winter temperatures (Dobbertin et al., 2005; Tikkanen et al., 2021; Varga et al., 2014).

In addition, there are additional constraints on mistletoe expansion in Mediterranean areas, drought stress being an important limitation to mistletoe expansion near its ecological or thermal distribution limits where, conversely, high levels of mistletoe infestation are reached (Sangüesa-Barreda et al., 2018). This is also supported by our results on the UK mean function and UK block kriging results, which show increasing infection degree with warmer and drier climate conditions. These conditions are harmful for the health status of the host species (Camarero et al., 2015) and, consequently, may both facilitate the development of epiphytic species and their impact. However, extreme drought periods have been shown to reduce the occurrence of other epiphytic species (e.g., *Amyema miquelii*) in *Eucalyptus* species (Griebel et al., 2022).

Annual precipitation averaging over the five previous years captured the effect of water stress on mistletoe infection better than the single reference year values, due to the great inter-annual rainfall variability.

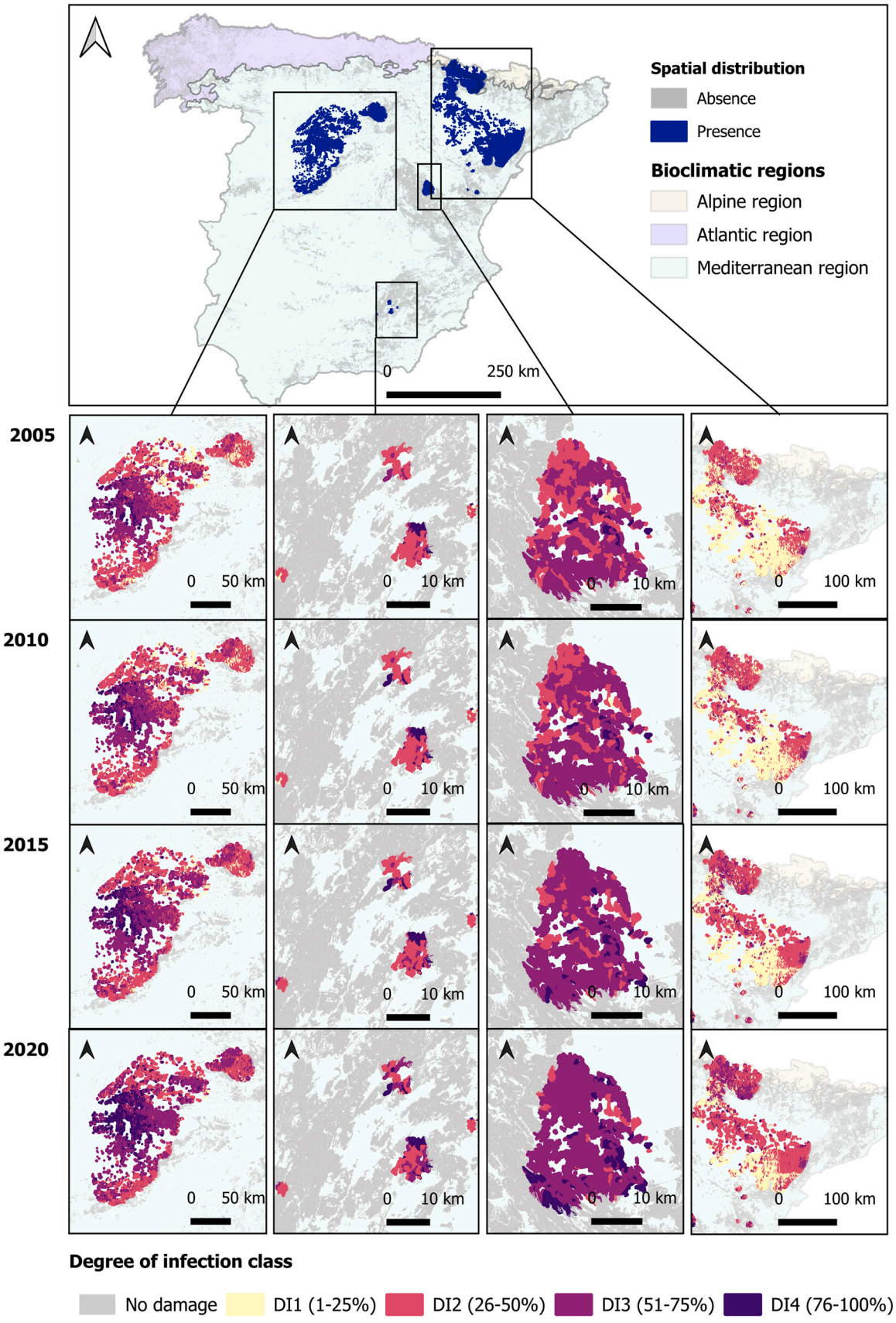

Fig. 6. Spatial distribution (absence /presence) of mistletoe (upper) and its evolution degree infection between 2005 and 2020 (lower). DI: degree of infection.

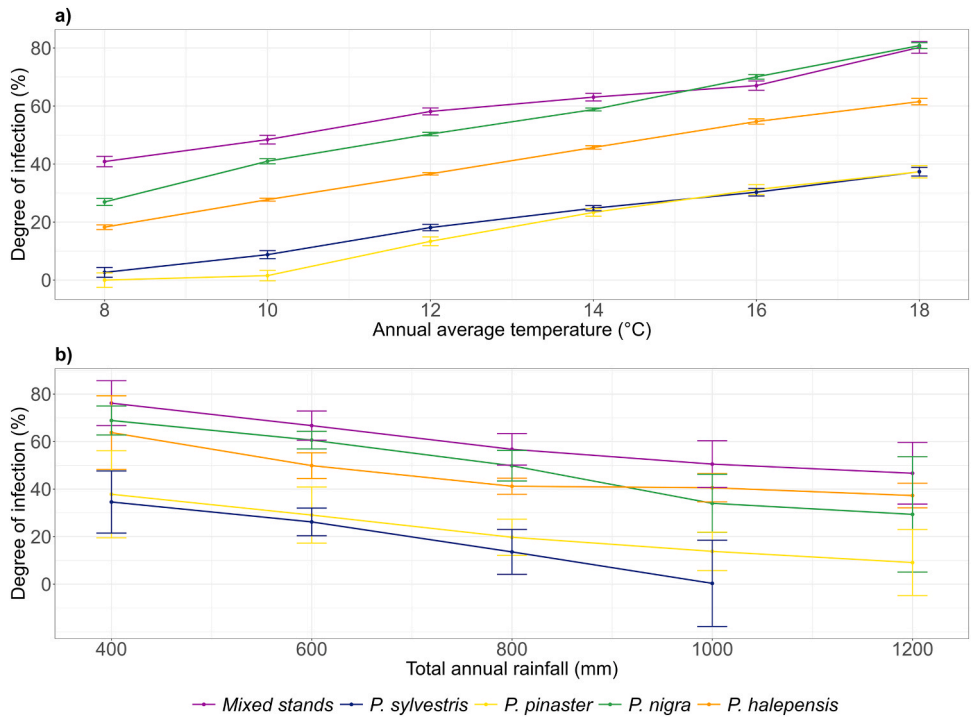

Fig. 7. Degree of infection trends by a) annual average temperature (ºC) and b) annual average rainfall for five years prior to reference year (mm) and dominant species. Mixed stands refers that at least one of the four hosts has at least 10 % of trees in that stand but none of them occupies the main species.

Regarding the effect of other climatic variables on the spread of mistletoe, spring rainfall showed significant positive effect on the degree of infection, suggesting that summer drought may favour mistletoe spread, although this variable was not included in the final model. The proportion of area affected by increasing severity increased during the study period, which might be related to increasing temperatures and severe droughts. This rise in the proportion of area affected by increasing severity is observed when analyzed for each dominant species in the forest stand and regardless of the dominant species.

Moreover, subtle changes in mistletoe distribution may be missed due to the low sampling intensity of the ICP-Forests grid (16 ×16 km), which in our approach is increased by two additional damage networks that aggregate information on forest vitality status following ICP field methods and harmonisation of field teams on an annual basis: the regional networks and the National Parks network. The advantage of ICP is that the data are always collected in the same season of the year (summer) and with a harmonised methodology across the EU, avoiding bias due to seasonal effects on visual assessment. In contrast to Spanish National Forest Inventory, where mistletoe damage data are also collected but the plot revisiting period is quite long (ca 10 years) and data collection does not always take place at the same time of the year (Alberdi et al., 2017). The difficulty of detecting mistletoe in large trees in the early years would be another limitation for early detection of distribution shifts. In this regard, recent advances have been proposed to monitor and manage mistletoe with unmanned aerial vehicles (Krasylenko et al., 2023; Miraki et al., 2021).

Another limitation of this study is the lack of plot-level information on the specific management practices applied to the forests where the plots are located. However, since the distribution of these plots is based on systematic sampling, it can be argued that the management variable is implicitly accounted for in the model. This is because the sampled plots are representative of the different management options for each species, including wood and fruit production, resin extraction, soil erosion control or biodiversity conservation. Consequently, the potential impact of forest management on mistletoe infestation is indirectly reflected in our estimations.

Although some stand features such as density, age or allometric properties have found to be related to infestation of mistletoe (Tymińska-Czabańska et al., 2024) or other epiphytic species (Sayad et al., 2017), ICP data do not include these forest features, so we did not include them as auxiliary variables. Future research should focus on stand structure effects on mistletoe infection to design mitigation strategies in areas with higher infection levels.

Finally, the different levels of infection identified may be related to the stages of infection dynamics described by Griebel et al., (2017). Although the first two stages even favour the biodiversity of the stand, it could be a good time to intervene before entering the third stage, where the damage caused by mistletoe jeopardize tree stand vitality and their future perspectives. Optimizing mistletoe control practices in space and time could turn mistletoe into a good ally for forests, providing them with biodiversity benefits in the early stages of infection and economic valorisation before it causes health damage to the stands. An accurate mapping of infection stages or levels of infection allows the best moment for intervention to be determined in management plans.

5. Conclusion

Our results indicate that the distribution area of mistletoe in Spain has remained quite stable since 2005, but the degree of infection has increased during this period. The degree of infection increases as temperature increases and precipitation in the prior years the reference year decreases. Therefore, predicted changes in climatic conditions could alter the impact of this hemi-parasitic species, increasing the intensity of damage in warmer and driest areas where it is already present. This study establishes a methodology to produce continuous spatial coverage prediction of the intensity of mistletoe damage in the pine forests of the Iberian Peninsula, generating maps of the distribution and intensity of damage, thus enabling the development of control programmes and the monitoring of forest ecosystems health.

CRediT authorship contribution statement

Moreno-Fernández Daniel: Writing – review & editing, Supervision. **Suárez-Herrera Sira:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Adame Patricia:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Montes Fernando:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis. **Oliveira Nerea:** Writing – review & editing. **Hernández-Mateo Laura:** Writing – review & editing. **Alberdi Iciar:** Writing – review & editing, Conceptualization. **Cañellas Isabel:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Isabel Canellas reports financial support was provided by Spain Ministry for the Ecological Transition and Demographic Challenge. Fernando Montes reports financial support was provided by Spain Ministry of Science and Innovation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the National Parks Autonomous Agency and the Spanish Autonomous Communities (Junta de Andalucía, Gobierno de Aragón, Govern Illes Balears, Gobierno de Cantabria, Generalitat de Catalunya, Castilla la Mancha, Junta de Castilla y León, Junta de Extremadura, Xunta de Galicia y Comunidad de Madrid, who have provided us with the regional data network data for this study. And we wish to thank Adam Collins for revising the English grammar. This work has been funded by the MITECO2023-AF project. 20234TE004 Scientific bases of forest information based on the National Forest Inventory and the PID2020–119204RB-C21 project supported by the Spanish Ministry of Science and Innovation.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122566.

Data availability

The authors do not have permission to share data.

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