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Shedding light on the effects of climate change on the potential distribution of *Xylella fastidiosa* in the Mediterranean basin

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Abstract *Xylella fastidiosa* is a xylem-limited gram-negative bacterium causing a high number of severe diseases to many agricultural and forestry plants. We developed a Maxent model to detect the current and future potential distribution of *X. fastidiosa* in the Mediterranean under climate change. For future projections, we used Hadley Centre's HADGEM2-ES models for four representative concentration pathways (2.6, 4.5, 6.0 and 8.5) and two time periods (2050 and 2070). Maxent models achieved excellent levels of predictive performance as can be seen from AUC, TSS and AUC_{diff} values. The potential distribution obtained for the current time comprises Portugal, Spain, Italy, Corsica, Albania, Montenegro, Greece and Turkey as well as all countries of northern Africa and the Middle East. *X. fastidiosa* is not predicted to change its distribution in the Basin in response to climate change. Our study, however, highlights that *X. fastidiosa* may overcome the current boundaries outside Italy. Given the potentially high risk, we urge that the listed countries consider appropriate and preventive phytosanitary measures to avoid the introduction of the bacterium.

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Introduction

Species distribution models (SDMs) are essential to understand the ecological and evolutionary factors that determine spatial patterns useful for species occurrence (Guisan and Zimmermann 2000). SDMs provide increasingly realistic scenarios to explain the influence of bioclimatic variables on the epidemiology of pathogens, especially in the context of emerging plant diseases (Fabre et al. 2011; Aguayo et al. 2014; Shabani et al. 2014; Bosso et al. 2016). The plant pathogens might have increased their distribution or pathogenic action due to improved environmental conditions for disease development in new regions

(Garrett et al. 2006). SDMs utilize global climate models (GCMs) and gas emission scenarios to assess the current habitat suitability and future habitat ranges of particular species due to the influence of climate change (Ruosteenoja et al. 2003; Rosentrater 2010). They are not intended to provide accurate predictions regarding the future state of the climate system at any given point in time, but to establish the envelope that future climate could conceivably occupy.

While many studies on plant emerging diseases have dealt with the introductions of pathogens in a new area, the impacts of climate change on plant diseases are still poorly studied, especially those caused by pathogenic bacteria, fungi and viruses (Fabre et al. 2011; Aguayo et al. 2014; Shabani et al. 2014; Bosso et al. 2016). *Xylella fastidiosa* (Wells et al. 1987) is a xylem-limited bacterium that affects several economically important plants (Janse and Obradovic 2010; Purcell 2013). Pathogenic strains of *X. fastidiosa* were first recognized in North and South America and Asia in the 1990s. This bacterium was first observed in Europe near Gallipoli (Apulia Region), southern Italy, in October 2013 (Saponari et al. 2013; Cariddi et al. 2014; Loconsole et al. 2014), and since its initial outbreak it has spread across the region causing considerable damage to olive groves (Saponari et al. 2014). *X. fastidiosa* is transmitted by various species of sap-sucking hopper insects and in Apulia it is vectored to olive trees by the spittlebug, *Philaenus spumarius* (Hemiptera: Aphrophoridae) (Saponari et al. 2014).

Hoddle (2004) used *X. fastidiosa* records collected in California to project a distribution model to the rest of the world. The model was developed using the climatic response of this plant pathogen from the native geographic range. The main prediction was that cold temperatures would not allow *X. fastidiosa* to colonize France and the northern and central areas of grape production in Spain and Italy. Bosso et al. (2016) developed a Maxent model for *X. fastidiosa* in Italy based on Apulia records. The Maxent model predicted a high probability of *X. fastidiosa* occurrence in Apulia, Calabria, Basilicata, Sicily, Sardinia and coastal areas of Campania, Lazio and south Tuscany. Precipitation of the driest and wettest months were found to be the main variables influencing model performance. Based on the model predictions, *X. fastidiosa* had a high probability of colonizing areas characterized by: (a) relatively low altitude (0–150 m

a.s.l.); (b) precipitation in the driest month <10 mm, wettest month ranging between 80 and 110 mm and warmest quarter <60 mm; (c) mean temperature of coldest quarter ≥8 °C; (d) agricultural areas comprising intensive agriculture, complex cultivation patterns, olive groves, annual crops associated with permanent crops, orchards and vineyards; forest (essentially oak woodland); and Mediterranean shrubland.

In the current study we broaden the scope of that analysis and generate models for the entire Mediterranean Basin projecting potential distributions of *X. fastidiosa* in time over different epochs and according to different scenarios of climate change.

Materials and methods

Study area

We included the entire Mediterranean basin territory between latitudes 46°N–22°N and longitudes 14°E–39°E (corresponding to ca. 2,051,000 km^2) in this analysis (Fig. 1).

Selection of *X. fastidiosa* presence records

We extracted *X. fastidiosa* occurrences from the online database set up by the Apulia Region government: http://webapps.sit.puglia.it/freewebapps/Monitoraggio XFSintesi. We used only observations of olive trees infected by *X. fastidiosa* in 2014–2015. The resulting database included 1258 records mostly regarding the southernmost part of Apulia. Records were screened in ArcGis (version 9.2) for spatial autocorrelation using average nearest neighbor analyses and Moran's I measure of spatial autocorrelation to remove spatially correlated data points (e.g. Russo et al. 2014, 2015; Bosso et al. 2016). After this selection, 50 fully independent presence records for *X. fastidiosa* were used to generate SDMs.

Selection of ecogeographical variables

To build SDMs for *X. fastidiosa,* we used a set of 19 Ecogeographical Variables (EGVs). All bioclimatic variables were obtained from the WorldClim database (www.worldclim.org/current) (Hijmans et al. 2001). All variable formats were raster files (grid) with a

Fig. 1 Current species
distribution models (SDMs)
of *X. fastidiosa*. **a** logistic
map; **b** binary map. Logistic
map shows the probability
of presence ranging from 0
(*green*) to 1 (*red*). Binary
map shows theprobability of
presence: 0 (*light grey*); 1
(*dark grey*)
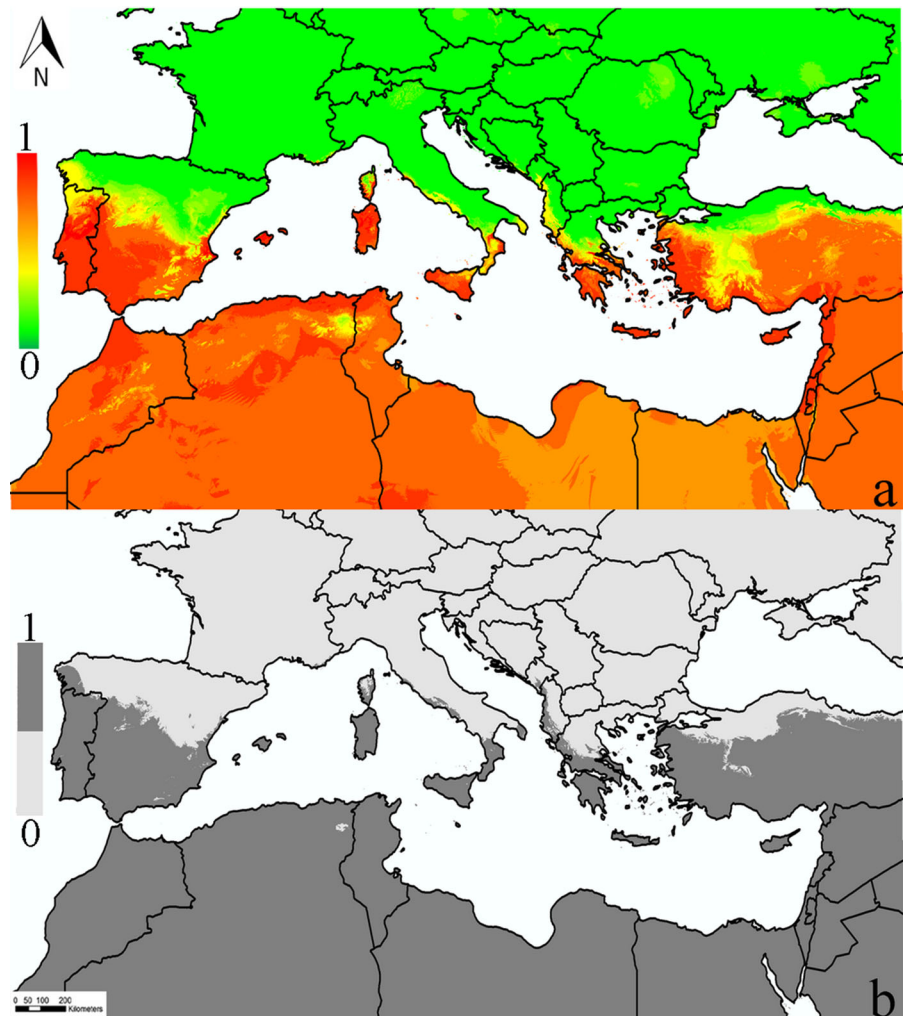
30-arc second resolution (0.93 × 0.93 km =
0.86 km² at the equator). To decrease the number of
variables for the final distribution models, we first
eliminated the highly correlated predictors and
retained those with a Pearson's |r| ≤ 0.80 (Elith et al.
2010). From this first set of predictors, we considered
only those most relevant to the species' ecological
requirements following Hoddle (2004) and Bosso
et al. (2016). This led to a final set of 9 variables
(Table 1) used to model current and future potential
distribution of *X. fastidiosa* in the Mediterranean
basin. We only used bioclimatic variables rather than
other physical environmental or land cover variables
in the model in order to provide an indication of

Table 1 List of ecogeographical variables used for this study,
type and measurement unit

| Type	Ecogeographical variable	Unit
Climatic	Annual mean temperature	°C
	Mean temperature of wettest quarter	°C
	Mean temperature of driest quarter	°C
	Mean Temperature of warmest quarter	°C
	Mean temperature of coldest quarter	°C
	Precipitation of wettest month	mm
	Precipitation of driest month	mm
	Precipitation of warmest quarter	mm
	Precipitation of coldest quarter	mm

changing climatic suitability assuming all else remains equal (e.g. Porfirio et al. 2014).

Maximum entropy models

To model *X. fastidiosa* distribution we employed Maxent ver. 3.3.3 k (http://www.cs.princeton.edu/~schapire/maxent) (Phillips et al. 2006). This algorithm usually results in good predictive models compared with other presence-only models and is especially suited to deal with scarce presence-only data (e.g. Elith et al. 2006). Because it is based on a generative approach, rather than a discriminative one, this technique performs well when the amount of training data is limited. Moreover, it has a good ability to predict new localities for poorly known species (Rebelo and Jones 2010; Bosso et al. 2013; Russo et al. 2015). To build the models, we used the presence records of *X. fastidiosa* selected as described above and the EGVs listed in Table 1. In the setting panel we selected the following options: random seed; remove duplicate presence records; write plot data; regularization multiplier (fixed at 1); 1000 maximum iterations; and 50 replicate effects with bootstrap-replicated run type. A set of 10,000 background points was randomly placed over the Apulia region. A cross-validation of the models was implemented by randomly extracting 70 % of records

Fig. 3 Maxent species distribution outputs for *X. fastidiosa* ▶ obtained with HadGEM2-ES (HG) models for four representative concentration pathways (RCPs) (RCPs 2.6, 4.5, 6.0 and 8.5) and scenarios for 2050 (50). Logistic maps show the probability of presence ranging from 0 (*green*) to 1 (*red*). Binary maps show the probability of presence: 0 (*light grey*); 1 (*dark grey*). **a** HG-RCP2.6-50 logistic map; **b** HG-RCP2.6-50 binary map; **c** HG-RCP4.5-50 logistic map; **d** HG-RCP4.5-50 binary map; **e** HG-RCP6.0-50 logistic map; **f** HG-RCP6.0-50 binary map; **g** HG-RCP8.5-50 logistic map; **h** HG-RCP8.5-50 binary map

for training and the remaining 30 % to test the model. The procedure was repeated 20 times. The average final map obtained had a logistic output format with suitability values from 0 (unsuitable habitat) to 1 (suitable habitat). The 10th percentile (the value above which the model classifies correctly 90 % of the training locations) was selected as the threshold value for defining the species' presence. This is a conservative value commonly adopted in species distribution modelling studies, particularly those relying on datasets collected over a long time by different observers and methods (e.g. Rebelo and Jones 2010; Bosso et al. 2013; Russo et al. 2015). This threshold was used to reclassify our model into binary presence/absence maps. The model was projected to the entire Mediterranean basin. In order to project the models calibrated in Apulia over
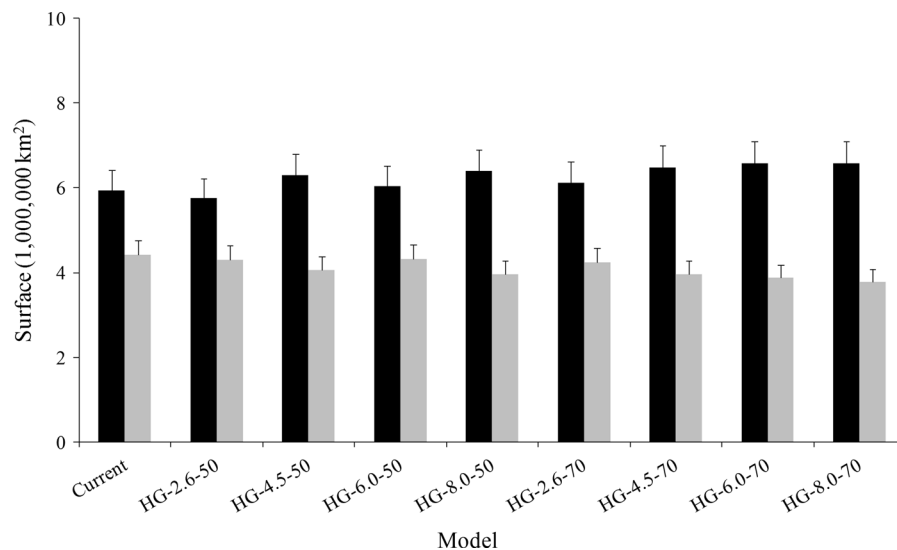

Fig. 2 Suitable (*black bars*) and unsuitable (*grey bars*) surface areas (in km^2) for *X. fastidiosa* in the Mediterranean Basin. Future projections were obtained with HAdGEM2-ES (HG) models at four representative concentration pathways (RCPs) (RCPs 2.6, 4.5, 6.0 and 8.5) and two time periods: 2050 (50) and 2070 (70). *Error bars* represent Standard Deviation. No significant difference was detected across different scenarios and time steps
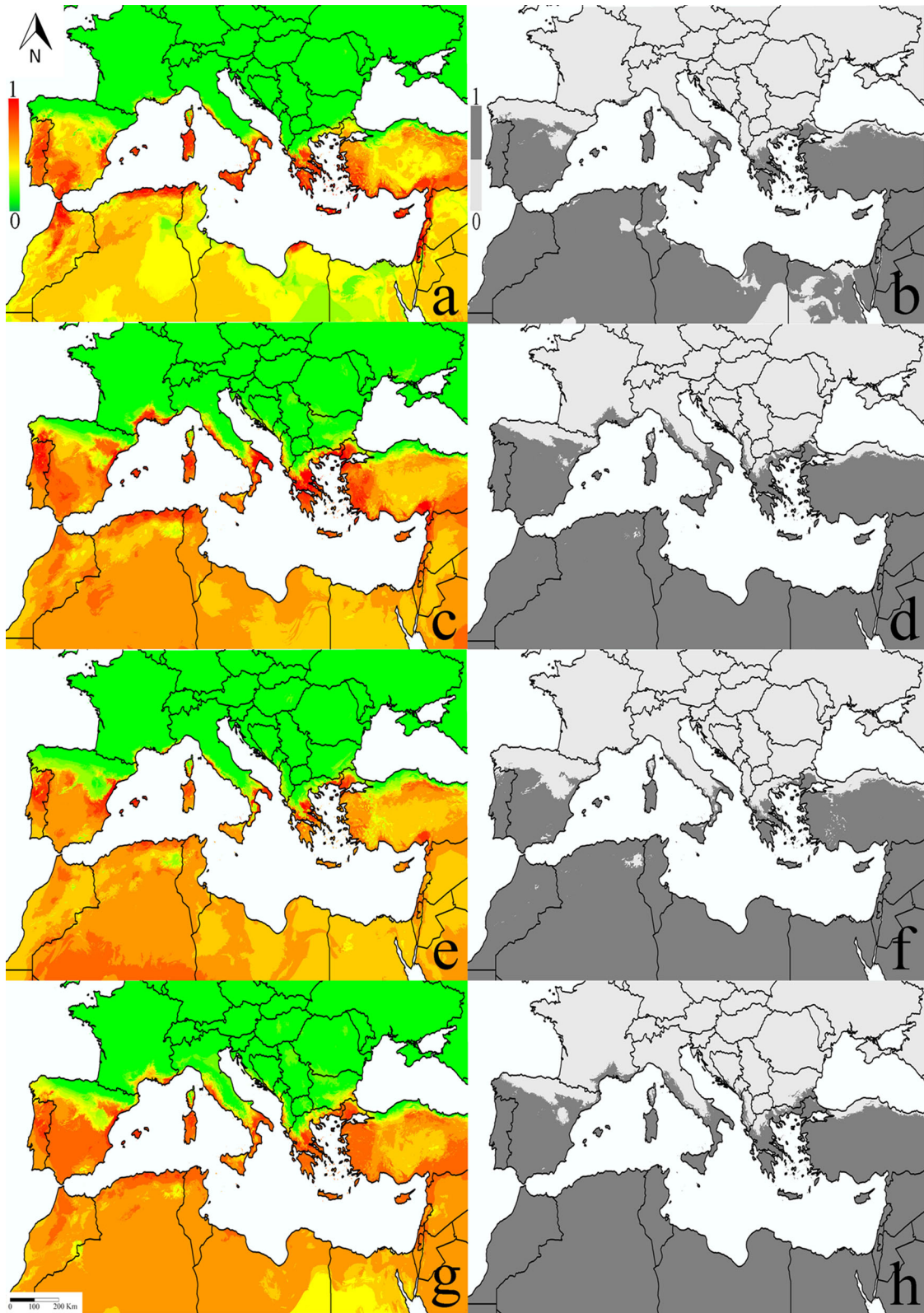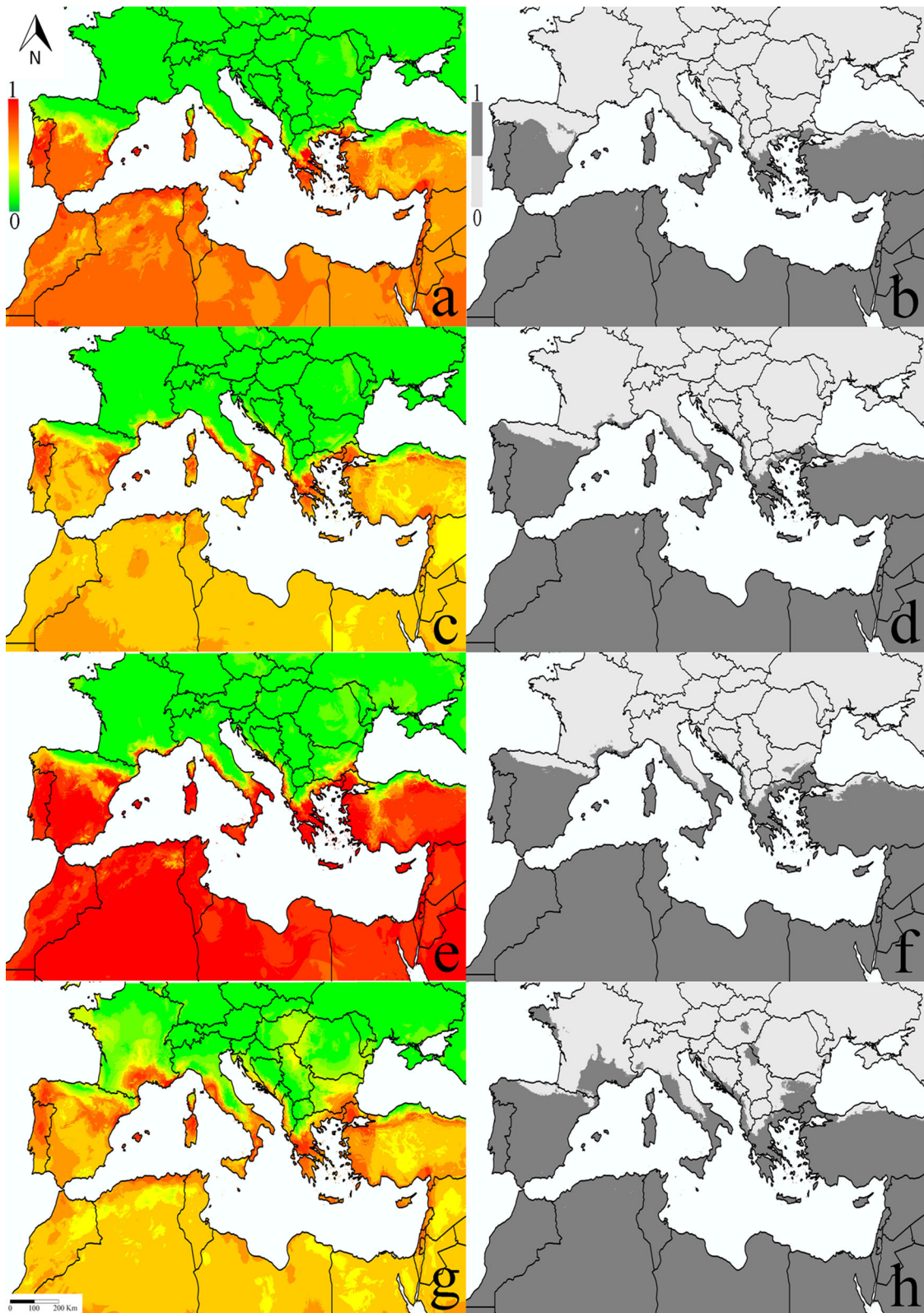
◀ **Fig. 4** Maxent species distribution outputs for *X. fastidiosa* obtained with HadGEM2-ES (HG) models for four representative concentration pathways (RCPs) (RCPs 2.6, 4.5, 6.0 and 8.5) and scenarios for 2070 (70). Logistic maps show the probability of presence ranging from 0 (*green*) to 1 (*red*). Binary maps show the probability of presence: 0 (*light grey*); 1 (*dark grey*). **a** HG-RCP2.6-70 logistic map; **b** HG-RCP2.6-70 binary map; **c** HG-RCP4.5-70 logistic map; **d** HG-RCP4.5-70 binary map; **e** HG-RCP6.0-70 logistic map; **f** HG-RCP6.0-70 binary map; **g** HG-RCP8.5-70 logistic map; **h** HG-RCP8.5-70 binary map

the Mediterranean basin territory, the variables in the projection area must meet a condition of environmental similarity with the environmental data used for calibrating the model. Therefore, we first ascertained that this condition occurred by inspecting the Multivariate Environmental Similarity Surfaces (MESS) generated by Maxent (Elith et al. 2010). Finally, we analyzed the MoD map to detect the most dissimilar variables between the training area and suitable projection area of *X. fastidiosa* in the Mediterranean basin, at current time as well as under different climate scenarios i.e., the variables that are furthest outside their training range (Elith et al. 2010).

SDMs of *X. fastidiosa* under climate change

Future climate projections of *X. fastidiosa* were derived from one GCM for four representative concentration pathways (RCPs) (RCP 2.6, 4.5, 6.0 and 8.5) and over two time periods: 2050 (average for 2041–2060) and 2070 (average for 2061–2080). RCPs are greenhouse gas concentration trajectories adopted by the IPCC for its fifth Assessment Report in 2014 (Rogelj 2013). The CO_2-equivalent concentrations are 490, 650, 850 and >1370 ppm, for RCP 2.6, 4.5, 6.0 and 8.5, respectively (Meinshausen et al. 2011). The GCMs data were obtained from World-Clim-Global Climate Data (http://www.worldclim.org/cmip5_30s). Hadley Centre's HADGEM2-ES (HG) model offers the best performance for the Mediterranean basin (Brands et al. 2011, 2013; Nabat et al. 2013; Mariotti et al. 2015). All Maxent parameters to model *X. fastidiosa* under climate change were the same as described above.

Statistical analysis

We used ANOVA to compare the mean (n = 20 replicates) suitable and unsuitable areas for *X.*

fastidiosa for the current time with those (n = 20) generated for each of the climatic scenarios. The analysis was done on binarized distribution maps. Tests were carried out in XLSTAT version 2013.1. and significance threshold set at $p < 0.05$.

Model validation

We tested the predictive performance of the models with different methods: the receiver operated characteristics, analyzing the area under curve (AUC) (Fielding and Bell 1997); the true skill statistic (TSS) (Allouche et al. 2006); and the minimum difference between training and testing AUC data (AUC_{diff}) (Warren and Seifert 2011). Such statistics were averaged across the 20 replicates run on the 70 % (training) versus 30 % (testing) dataset split. These model evaluation statistics range between 0 and 1 (AUC and AUC_{diff}) and between −1 and 1 (TSS): excellent model performances are expressed respectively by AUC and TSS values close to 1 and AUC_{diff} close to 0.

Results

SDMs of *X. fastidiosa* and model validation

Our models showed high levels of predictive performances as can be seen from the values of AUC (training, 0.971 ± 0.030; test, 0.952 ± 0.039), AUC_{diff} (0.019 ± 0.001) and TSS (0.854 ± 0.024). The model achieved a 1.82 regularized gain value indicating an excellent fit with occurrence data. Five variables contributed to a total 95 % of model prediction. The analysis of single variable contributions showed that precipitation during driest (30.7 %) and wettest (30.3 %) months were the main factors influencing model performance. Precipitation of driest quarter and mean temperature of coldest and warmest quarter provided a total contribution of 35.1 %. Based on the model's predictions, *X. fastidiosa* has a greater probability (>0.7) of occurring in areas characterized by low precipitation in the driest month (<10 mm) and in the driest quarter (<60 mm), medium precipitation in the wettest month (80–110 mm), and mean temperature >8 °C and >22 °C in the coldest and warmest quarters, respectively. The current potential distribution comprises Portugal, Spain, Italy, Corsica, Albania, Montenegro, Greece and Turkey as well as all

countries of northern Africa and the Middle East (Fig. 1a, b). Its northernmost geographic limits correspond to Portugal, Spain, Corsica, southern Italy, Montenegro, Albania, southern Greece and Turkey. We rejected the hypothesis that potential distribution of *X. fastidiosa* is significantly affected by climate change in the Mediterranean basin for all HG scenarios: precisely, for neither of the HG models used in this study, we recorded significant changes in habitat suitability (Fig. 2, ANOVA: F = 1.56, n.s.; Figs. 3, 4). MESS analysis indicated that the central and southern Mediterranean basin had moderate (values around to 0) to high (positive values) environmental similarity with the training area. The MoD map showed that the variables with the highest contribution useful to detect the potential distribution of *X. fastidiosa* were similar between the training and suitable projection areas in the Mediterranean basin at current and future times (Fig. S1).

Discussion

Model performance and limitations

Both current and future potential distribution models that we generated for *X. fastidiosa* in the Mediterranean showed considerable power, mainly supported by the high gain value (1.8) achieved. AUC values such as those we obtained (>0.9) are among the highest reported for published models (e.g.: Rebelo and Jones 2010; Domíguez-Vega et al. 2012; Russo et al. 2014; Di Febbraro et al. 2015), and demonstrate a very high predictive capacity (Elith et al. 2010). This was further supported by AUC$_{diff}$ and TSS values (Russo et al. 2014, 2015).

Although our models provided a strong statistical validation and robust maps of *X. fastidiosa*' potential distribution, we are aware that some limitations may arise from not considering "realized niche" predicting factors, such as biotic interactions as well as plant-pathogen-antagonist interactions. Furthermore, our model did not take into account the potential distribution of the bacterium's vector and land cover dynamics. Actually, *P. spumarius* is the known vector of *X. fastidiosa* in Italy (Saponari et al. 2014). This insect is widespread in the Mediterranean Basin and is considered ecologically flexible (Halkka et al. 1967) thus its presence in the model is not expected to

represent a constraint for the habitat suitability prediction of *X. fastidiosa*. Moreover, future projections of models such as ours inevitably disregard the effects of land use modifications, given the inherent uncertainty in predicting changes in the physical environmental or land cover. Still, our models, developed for a vast geographical area, can surely help detect the influence of factors acting on a broad spatial scale such as bioclimatic variables on species' spatial patterns.

Predicting the potential distribution of *X. fastidiosa* in the Mediterranean basin

X. fastidiosa seems to be a pathogen potentially threatening plants throughout the Mediterranean basin currently and in the future. The main reason for the exclusion of *X. fastidiosa* from central and northern European countries is cold stress that can affect both the bacterium and its vector (Halkka et al. 1967; Ejere and Okpara 2010). In agreement with the results obtained using CLIMEX by Hoddle (2004), our model confirms that the Mediterranean climate can be particularly favourable for *X. fastidiosa*. Purcell (1997) and Hoddle (2004) predicted that the bacterium could colonize the Italian central and southern areas whose climatic regime is especially favourable for its vector. In contrast, cold stress would not allow the bacterium to spread in the grape-growing provinces of Northern Italy, Burgundy and Champagne regions of France, Central and Northern region of Spain and Baltic region. However, under the scenarios RCP 4.5, 6.0 and 8.5 (Figs. 3c–h, 4c–h), also some areas of France may be suitable for *X. fastidiosa*. As found for North America, our model predicted a preference for internal and coastal areas with mild winters at low altitudes. For instance, in the USA, *X. fastidiosa* occurs in areas whose winter temperatures are $\geq 1-4$ °C (Purcell 1997). In contrast, it appears less harmful where winter is colder, such as at higher altitudes, because freezing events can strongly decrease *X. fastidiosa* viability (Hopkins and Purcell 2002; Hoddle 2004). Specifically, Lieth et al. (2011) found that temperatures <6 °C may kill this pathogenic bacterium.

According to our results, climate change would not affect the future potential distribution of *X. fastidiosa*

significantly for all HG models, regardless of the time and greenhouse scenarios selected. This is because the Mediterranean basin is already potentially suitable for *X. fastidiosa* and such suitability cannot increase further because the spatial distribution of values for the variables that contribute the most to the model does not change sufficiently under any of the scenarios or time steps used (Fig. 1a, b). Similarly, Fabre et al. (2011) reported the main EGVs influencing *Diplodia pinea* presence in France were, besides host species presence (essentially *Pinus pinaster*, *Pinus nigra* and *Pinus sylvestris*), winter temperature and summer rain, both of which are positively correlated with cone colonization. The climate became more favourable to *D. pinea* presence over the last 15 years compared with the previous 30 years. By contrast, future climatic changes over the next 60 years should have far less impact on *D. pinea* (Fabre et al. 2011) as well as for *X. fastidiosa* (this study).

Cold stress also seems to limit the distribution of *Phytophthora alni* in the Mediterranean basin. Aguayo et al. (2014) showed that the climate of south western France was much more favourable to *P. alni* than that of the northeast, because it seldom limited the overwintering of the pathogen. On the other hand, Shabani et al. (2014) predicted an increase of suitable areas for *Fusarium oxysporum* in Europe with a northerly shift of that pathogen in the future. This projection was supported by the two GCMs used by Shabani et al. (2014) which indicate that about 700 million ha in Europe will be at high risk of being affected by the fungus by 2050 and 2100 respectively.

A fundamental requirement for the establishment of any species outside its native range is that the recipient location must have a climate comparable to that of the invader's original range. *X. fastidiosa* is therefore a real emerging threat for Italy and the entire Mediterranean basin, not only for the grapevine (Hoddle 2004) and olive groves (Saponari et al. 2014), but, in principle also for stone fruits and citrus cultivation as well as Mediterranean shrubland (Janse and Obradovic 2010). Our work highlights that while climate change is unlikely to affect the future distribution of *X. fastidiosa*, a vast area of the Mediterranean Basin is exposed to a great risk given its high suitability so the countries involved should be targeted with appropriate phytosanitary preventive measures to avoid the spread of the bacterium.

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