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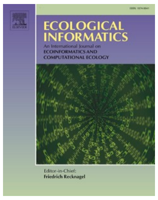

Exploring the main factors influencing habitat preference of *Popillia japonica* in an area of recent introduction

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ABSTRACT

The possibility of establishment of an invasive species in an area of new introduction is influenced by several factors, including weather conditions, soil characteristics, and species spread dynamics. Disentangling the role of multiple variables on habitat preference can provide important elements supporting the management of invasive species. In this work, we present a modelling framework that allows i) the identification of the main drivers influencing the probability of the presence of the invasive pest Japanese beetle *Popillia japonica*, in an area of recent introduction in Northern Italy, and ii) the evaluation of bi-dimensional niches to investigate the non-linear combined effects of couples of variables on the potential distribution of this species. Occurrence records of larval populations sampled between 2017 and 2019 in 8488 sites in Northern Italy were used in the present study. The sample sites were characterised based on a set of explanatory variables related to land use, soil characteristics, meteorological conditions, and infestation history. We performed a stepwise logistic regression analysis for testing the statistical significance of explanatory variables on the occurrence of local larval populations. Then, we implemented a Generalized Additive Model to investigate the bi-dimensional ecological niche determined by the interaction of two variables on the probability of the presence of *P. japonica*. The results highlight the prominent role of soil and weather variables and the infestation history of the species in driving the presence of *P. japonica* larvae. Less acidic soils, especially with sandy-skeletal particles, are preferred. A high density of *P. japonica* larvae is associated with medium content of soil organic carbon in the soil. Long drought periods or high precipitation levels reduce the probability of the presence of the species. Non-linear effects are observed between soil temperature variables and habitat preferences of *P. japonica*. The probability of the presence of *P. japonica* is also related to the number of years since the first occurrence of the species at the site. The results of the present work provide fundamental elements for guiding the assessment of the risk and the management of *P. japonica*.

1. Introduction

The Japanese beetle (JB) *Popillia japonica* Newman (Coleoptera: Scarabaeidae) is a highly polyphagous plant pest, feeding on >300 host plants (EFSA Panel on Plant Health (PLH) et al., 2018; Fleming, 1972). Impacts on plants are caused by both adults and larvae. Adults feed on leaves, flowers, and fruits of wild, cultivated, and ornamental plants (Klein, 2008; Vittum, 2020). The larvae live below ground and feed on the roots of mainly pastures and turfgrasses (EPPO, 2020a; Potter and Held, 2002). Based on the EU Regulation 2019/1702, the JB is listed among the 20 priority pests in the EU. It is also included in the European and Mediterranean Plant Protection Organization (EPPO) A2 list and is considered one of the most serious economic, environmental and social threats (EFSA Panel on Plant Health (PLH) et al., 2018).

The JB commonly shows one generation per year in most of the native and the invaded range. In the cooler areas of its distribution, JB individuals might take two years to complete their life-cycle (Fleming, 1972; Vittum, 1986). Adults are present between June and September (EPPO, 2016; Gilioli et al., 2021). Within their life-span (4–6 weeks) adult females mate and lay around 40–60 eggs belowground,

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preferentially in moist grasslands (Campbell et al., 1989; Potter and Held, 2002). The larvae hatch from the eggs in 10–14 days and pass through three instars. During larval development, individuals can perform vertical movements within the soil to find suitable environmental and trophic conditions (Fleming, 1972; Hawley and Dobbins, 1945; Shanovich et al., 2019).

The JB originated from north-eastern Asia and the far east of Russia. In 1916, the pest was accidentally introduced, invading vast areas of North America and some areas of southern Canada (USDA APHIS, 2022). In Europe, the species was first found in Terceira island (Azores, Portugal) in the early 1970s (EPPO, 2019). Since 2014, the JB has been reported in Northern Italy, between Lombardy and Piedmont Regions (EPPO, 2014; Pavesi, 2014), and in Switzerland since 2017 (EPPO, 2017; EPPO, 2020b). In Italy, despite the timely control actions implemented by the Italian National and the two Regional Phytosanitary Services (EPPO, 2016), the area infested by the species has increased over time, reaching $>$14,000 km^2 in 2021, and currently, the JB is now considered not eradicable in Italy (EPPO, 2020b). In its native range, the JB does not represent a major threat to plants mainly because the presence of co-adapted natural enemies prevents high population densities (Clausen et al., 1927; Kistner-Thomas, 2019). Outside its native range, the species shows a high invasive capacity, representing a potential threat to both cultivated and wild plants.

The assessment of the risks linked to the JB, as well as the definition of specific actions for its management, requires a thorough knowledge of the main variables affecting the life-history and the spatio-temporal population dynamics of the species (Ashraf et al., 2021; Méndez-Vázquez et al., 2019). Many authors investigated the influence of environmental drivers on the life-history strategies, and therefore on the habitat preference of the JB, mainly through laboratory experiments. Being an insect characterised by developmental stages living belowground (eggs, larvae, and pupae) and aboveground (adults), the life-history, occurrence, or abundance of JB is influenced by soil humidity (Allsopp et al., 1992; Fleming, 1972; Ludwig, 1936; Ludwig and Landsman, 1937; Potter et al., 1996), soil texture (Allsopp et al., 1992; Règniére et al., 1979), soil organic matter (Dalthorp, 2004; Dalthorp et al., 2000a; Potter et al., 1996), host plant availability (Hamilton et al., 2007; Whittington et al., 1942), environmental temperature (Fleming, 1972; Ludwig, 1928; Ludwig, 1930; Ludwig, 1932), and land management practices (Szendrei et al., 2005).

However, the current knowledge of the JB biology is mainly based on studies that have investigated the effects of single variables on the life-history, occurrence, or abundance of the species, providing only limited information for the definition of the ecological niche occupied by the JB. Indeed, the ecological niche can be considered as a multidimensional space, where the dimensions represent the different resources and conditions that allow the population to persist (Peterson, 2003). Early modelling attempts to describe a multidimensional ecological niche of the JB have considered climate or climate in combination with anthropogenic factors (Kistner-Thomas, 2019; Zhu et al., 2017). Despite the recognised importance of these two dimensions, some other relevant factors are still missing in the analysis of the ecological niche of the JB, in particular land-use and soil characteristics.

In this paper, we aimed at providing a more complete description of the ecological niche of the JB. We investigated how variables jointly affect the probability of the presence of larval populations of the JB. We considered variables related to land use, soil physical and chemical characteristics, meteorology, and infestation history. The definition of the ecological niche of the JB includes also the investigation of non-linearities in the responses of the species to the variables considered (Jactel et al., 2019; Régnière et al., 2012).

2. Materials and methods

2.1. Data on the larval occurrence

In Lombardy Region (Italy), larvae occurrence data started being collected by the regional Phytosanitary Service in 2015. The sampling protocol has been refined over the years, according to the indications that have been provided over time by international bodies and regional and national legislation. We selected data collected during two monitoring seasons (2017/18 and 2018/19) because it was the largest period of application of the same sampling protocol. Larval samples have been collected through soil coring in 8488 sites within the infested area of the Lombardy Region, following the official procedures reported in EPPO (2016) and the National Legislation (Italian Ministerial Decree *22 January* 2018). A grid of regular hexagonal cells with sides of 1.45 km was superimposed on the infested area. In the cells, the coring was carried out in the springtime, when larvae were in the third and final instar, and mainly in non-irrigated arable land and pasture. In each land-use category, sampling points were randomly selected. At each sampling point, a soil core (20 cm × 20 cm × 20 cm) was extracted using a shovel. For each soil core, the number of JB larvae was counted. Sites were considered positive when at least one larva was found in the soil core.

2.2. Explanatory variables

We considered the factors related to land use, soil characteristics, meteorological conditions, and infestation history as possible dimensions of the niche of JB larvae. The selected explanatory variables are presented in Tables 1 and 2. Land use data, available at a spatial scale of 1:10,000 with a positional accuracy of 5 m (Antenucci et al., 1991), were extracted from the Use of Agricultural Land and Forestry map of the Lombardy region (Destinazione d'Uso dei Suoli Agricoli e Forestali – DUSAF 6, Regione Lombardia, 2018), which is based on the Corine Land Cover classification (Bossard et al., 2000; Büttner, 2014). We focussed on the third level of land use classification. Data on soil depth, soil organic carbon content, soil texture, soil particle size, and soil pH have been extracted from the pedological map of the Lombardy Region, spatial scale 1:250,000 and positional accuracy 25 m (Regione Lombardia, 2013). Data on air temperature, air relative humidity, cumulated rainfall, soil humidity (evaluated at 0–10 cm soil depth), and soil temperature (evaluated at 0–10 cm soil depth) were extracted from the National Centers for Environmental Predictions (National Centers for Environmental Prediction/National Weather Service/NOAA/U.S. Department of Commerce, 2015). Data were re-analysed using the

Table 1
Description of the biologically-relevant indicators used for the exploration of the niche of *P. japonica.*

Indicator	Units	Description
R	mm	Cumulative rainfall
RH	Number (proportion)	Average air relative humidity
T^{air}	°C	Average air temperature
T^{soil}	°C	Average soil temperature
T^{soil}_{min}	°C	Average minimum soil temperature
T^{soil}_{max}	°C	Average maximum soil temperature
W^{soil}	Number (proportion)	Average soil water content
HW^{soil}_{dry}	Number of hours	Number of hours in which soil water content is lower than 15%
DD^{soil}_{cool}	Degree-day	Cumulated cooling degree days calculated for soil temperatures lower than 10 °C
DD^{soil}_{warm}	Degree-day	Cumulated warming degree days calculated for soil temperatures between 15 °C and 28 °C
HT^{soil}_{cold}	Number of hours	Sum of the number of hours in which soil temperature is below 10 °C
HT^{soil}_{warm}	Number of hours	Sum of the number of hours in which soil temperature is above 28 °C

Table 2
List of explanatory variables used in the exploration of the niche of *P. japonica* in Lombardy. The table reports the mean (± SD) and the range for quantitative variables and the frequency distribution for categorical variables calculated for each sampling site.

Explanatory variables	Frequency distribution	Mean (± SD)	Range [minimum, maximum]
LAND USE			
Land-use category (categorical)			
Non-irrigated arable land	66.91%		
Pastures	27.65%		
Others	5.44%		
SOIL			
Soil organic carbon content(categorical)			
Low (<1%)	60.13%		
Medium (1%–2%)	29.21%		
High (>2%)	10.66%		
Soil useful depth (cm) (numerical)		93.21 (±52.54)	[20−201]
Soil texture (categorical)			
Sandy-loam (SaLo)	69.77%		
Loamy-sand (LoSa)	19.79%		
Silt-loam (SiLo)	4.88%		
Loam (Lo)	4.65%		
Sand (Sa)	0.91%		
Soil particle size (categorical)			
Coarse-loamy (CL)	53.16%		
Loamy-skeletal (LS)	20.86%		
Sandy-skeletal (SS)	11.29%		
Sandy (S)	9.41%		
Others (O)	5.28%		
Soil pH (numerical)		6.16 (±0.59)	[4.9–7.3]
T^{soil} (numerical)		11.55 (±1.75)	[0.79–15.25]
T^{soil}_{min} (numerical)		8.57 (±1.3)	[0.60–11.55]
T^{soil}_{max} (numerical)		15.35 (±2.46)	[1.01–20.39]
W^{soil} (numerical)		0.36 (±0.07)	[0.26–0.95]
HW^{soil}_{dry} (numerical)		295.72 (±392.32)	[2.00–2391.5]
DD^{soil}_{cool} (numerical)		788.40 (±234.30)	[399.7–2648.9]
DD^{soil}_{warm} (numerical)		624.00 (±160.41)	[23.88–997.77]
HT^{soil}_{cold} (numerical)		3156.00 (±489.35)	[2165.0–6302.0]
HT^{soil}_{warm} (numerical)		288.79 (±127.82)	[5.45–634.95.8]
METEOROLOGICAL			
R (numerical)		321.92 (±151.12)	[22.06–547.0]
RH (numerical)		0.52 (±0.03)	[0.42–0.62]
T^{air} (numerical)		22.23 (±0.85)	[20.01–24.62]
LOCATION INFESTATION HISTORY			
Years passed since the first infestation (numerical)		1.33 (±0.67)	[0–3]

Weather Research and Forecasting (WRF) model (version 4.02), a mesoscale numerical weather prediction framework based on a grid system (Powers et al., 2017; Wang et al., 2018), to obtain high spatial (2 × 2 km) and temporal (hourly time-step) resolution data. Finally, an inverse weighted distance interpolation has been carried out on WRF results to obtain point-based estimates. These estimates have been used to calculate the biologically-relevant indicators for our study, as detailed in Table 1. The reference time interval of each indicator was selected according to the biological cycle of the species at the site of the study (Fig. SM-1). Soil temperature influences the survival of eggs, larvae, and pupae in the soil, so we considered the period September–May for soil temperature indicators. Soil humidity influences the adults' choice of oviposition sites between June and August, and the survival of eggs and larvae in the soil between September and May. For this reason, we considered the June–May period for soil humidity indicators. Weather influences the survival and fecundity of adults, so we computed weather-related indicators (cumulative rainfall, average relative humidity, and average air temperature) during a time interval including the whole adult flight period. To account for the local infestation history of the JB, we have also included in the model the number of years since the first infestation of the species on the site, estimated on the basis of the monitoring data collected by the Lombardy regional Phytosanitary Service.

2.3. *Statistical models*

2.3.1. *Logistic regression model*

We performed a Logistic Regression Model (LRM) to investigate the relationship between selected explanatory variables and the probability of the presence of JB larvae (response variable). Firstly, we assessed the correlation between the explanatory variables with Pearson's linear correlation coefficients. When the correlation coefficient was >90% (in absolute terms), the variable with the highest overall correlation profile was excluded from the analysis. In the second step, we evaluated the inclusion of interaction factors which allow the effect of a variable to be modelled when it depends on the values assumed by another explanatory variable. This evaluation was based on the results of the descriptive statistics. Finally, we applied the full stepwise procedure to select the most statistically significant explanatory variables according to the Akaike Information Criteria (AIC) (Atkinson, 1980; Harrell, 2015)., we performed a K-fold cross-validation procedure (cv.glm function of 'boot' R package version 1.3–20) to validate the results of the logistic regression model. We used accuracy (percentage of correctly classified elements), sensitivity (true positive rate), specificity (true negative rate), and balanced accuracy (Allouche et al., 2006; Duque-Lazo et al., 2016; Freeman and Moisen, 2008; García et al., 2009; Giannini et al., 2013; Miller, 2010) to evaluate the performance of the logistic model. Considering the unbalanced dataset (positive sites are <13% of the total points sampled, see Table 3), we chose to select the best trade-off between specificity and sensitivity on the ROC (Receiver Operating Characteristic) curve (roc function of 'pROC' R package) as classification cut-off for the confusion matrix (Freeman and Moisen, 2008; Weiss and Provost, 2001).

2.3.2. *Generalized additive model*

The Generalized Additive Model (GAM) (Hastie and Tibshirani, 1990; Heikkinen et al., 2007) allows fitting both linear and complex additive response curves. We applied a GAM model to predict the response variable (presence/absence of JB larvae in a soil core) based on the explanatory variables that resulted as significant in the LRM. GAM was developed with the gam function of mgcv R package (Wood, 2017), using a logit link function (family binomial). The goodness of fit of the GAM is evaluated with the QQ-plot (quantile-quantile plot) of residuals (Wilk and Gnanadesikan, 1968). Furthermore, to investigate in more detail the nonlinear joint effects of explanatory variables on the probability of the presence of the JB, we estimated the probability of the

Table 3
Distribution of coring sites in the area of recent invasion in the Lombardy Region (Italy). Sites are divided by sampling season, and presence/absence of *P. japonica* larvae.

Sampling season	Sampling period	Number of sites	Number of sites with *P. japonica* larvae (%)	Number of sites without *P. japonica* larvae (%)
2016/17	Spring	5728	485 (8.47%)	5243 (91.53%)
2017/18	Spring	2760	397 (14.38%)	2363 (85.62%)
Total		8488	882 (10.39%)	7606 (89.61%)

presence of JB larvae by combining the values of couples of explanatory variables, keeping the values of the other explanatory variables fixed.

3. Results

The descriptive statistics of the explanatory variables are reported in Table 2 in terms of mean and standard deviation (for quantitative variables) or frequency distribution (for categorical variables). The numbers of coring points (overall, positive and negative sites) per sampling season are reported in Table 3. The frequency of samples with at least one JB larva almost doubled in one year, from 8.5% in 2017 to 14.4% in 2018.

The correlation matrix of environmental variables (Fig. 1) showed clusters of variables with a very high correlation (>90%). We excluded from the LRM the variables with the highest linear correlation coefficients: T_{min}^{soil}, T_{max}^{soil}. From the descriptive statistics (see Figs. SM.2 and SM.3), it emerged that levels of soil organic carbon and soil pH are influenced by soil texture and particle size. For this reason, we included the corresponding interaction factors in the regression model.

3.1. Results of the logistic regression model

Based on the stepwise procedure, 11 explanatory variables and two interaction terms have been selected by the LRM (Table 4). The estimated coefficients for the soil organic carbon content should be interpreted according to the reference category, i.e. medium level of soil organic carbon content. Thus, the expected probability of finding JB larvae is lower in soils with low or high levels of soil organic carbon content than in soils with a medium level of organic carbon content. The coefficient associated with the interaction term ‘Soil pH: soil particle size=CL’ reduces the effect of soil pH on the probability of finding JB larvae in Coarse-loamy soils compared to other types of soil particle size. The coefficient associated with the interaction term ‘Soil pH: soil particle size=SS’ magnifies the effect of soil pH on the response variable, whereby the probability of finding JB larvae strongly increases with increasing pH in Sandy-skeletal soils compared to other types of soil particle size. According to the ROC curve (Fig. 2), the best trade-off between sensitivity and specificity (highlighted with a red star in Fig. 2) is obtained with a cut-off value equal to 0.13. The evaluation metrics, computed based on this cut-off, show a good fitting of the LRM to the observed data (Fawcett, 2006). In particular, LRM correctly classified 82.3% of the overall sites (accuracy), 83.1% of the positive sites (sensitivity), and 75.3% of the negative sites (specificity). Balanced accuracy is equal to 79.2%.

3.2. Results of the generalized additive model

The GAM confirmed the statistical significance for all explanatory variables used in the LRM, except for the average soil temperature. Results of the GAM have been used to explore bi-dimensional niches of JB. All the interactions between couples of explanatory variables have been tested. In Fig. 3, we reported the graphs for the relationships that showed a greater degree of non-linearity and a high impact on the expected probability of finding JB larvae at the site. In the supplementary

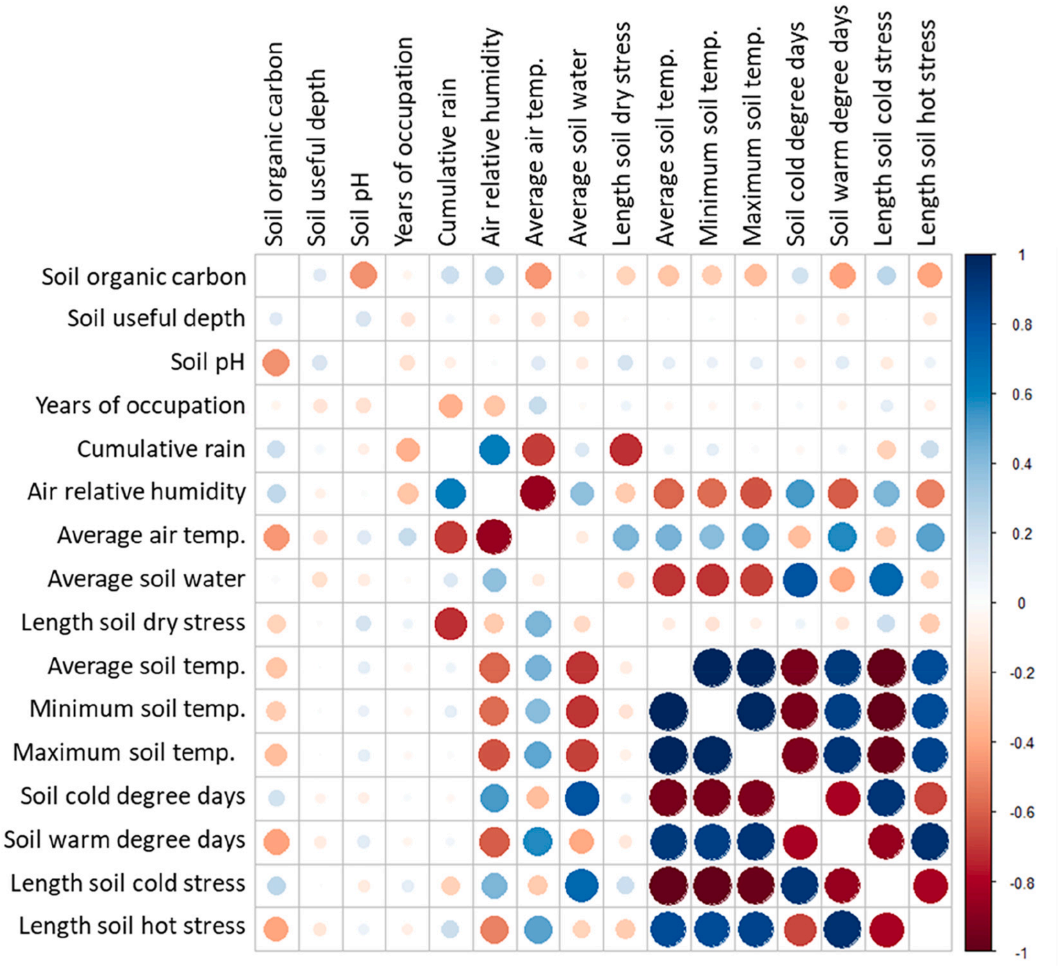

Fig. 1. Matrix of Pearson correlation coefficients for the quantitative explanatory variables used in the exploration of the ecological niche for *P. japonica* in the Lombardy region (Italy).

Table 4

Results of the logistic regression model applied for investigating the probability of the presence of larvae of *P. japonica* in the area of recent invasion in Lombardy Region (Italy). The table reports the estimated coefficients, the standard errors and the significance of the explanatory variables.

Explanatory variables	Coefficient estimated	Standard error	$Pr(>\|z\|)$
Intercept	91.634	9.649	< 0.001
Soil organic carbon - low	−1.703	0.179	< 0.001
Soil organic carbon - high	−1.257	0.232	< 0.001
Soil texture = LS	−2.746	0.319	< 0.001
Soil pH	0.448	0.196	0.023
Soil pH: soil particle size = CL	−0.133	0.021	< 0.001
Soil pH: soil particle size = SS	0.215	0.032	< 0.001
Soil depth	−0.012	0.001	< 0.001
R	−0.009	0.001	< 0.001
HW_{dry}^{soil}	0.0004	0.0002	0.04
T^{soil}	−4.531	0.440	< 0.001
HT_{cold}^{soil}	−0.016	0.002	< 0.001
DD_{cool}^{soil}	0.005	0.001	< 0.001
DD_{warm}^{soil}	0.011	0.001	< 0.001
Years passed since the first local infestation	1.582	0.079	< 0.001

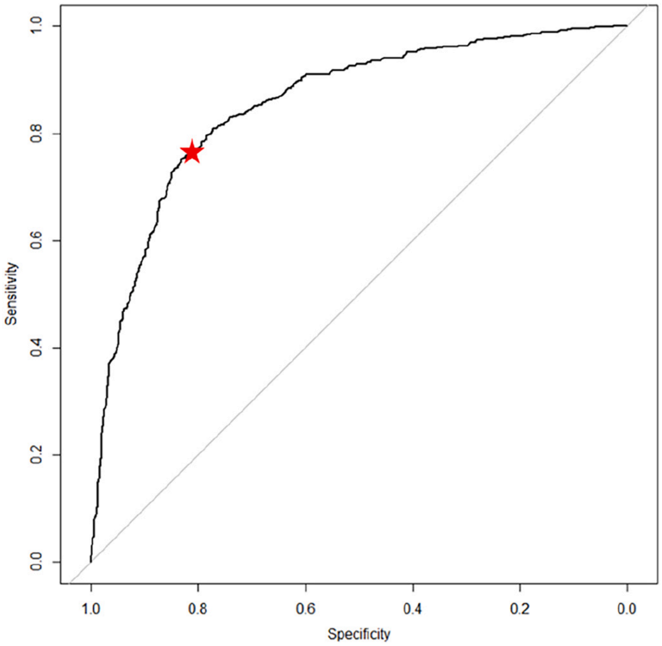

Fig. 2. Receiver Operating Characteristic (ROC) curve for selecting the optimal classification cut-off between the probability of correctly predicting sites with the presence of JB larvae conditional on positive sites and the probability of correctly predicting sites with the absence of JB larvae conditional on negative sites. The red star represents the best trade-off between sensitivity and specificity identified in the analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

materials, graphs are available for bivariate analyses for which the probability of the JB presence reached at least 50% once. In Fig. 3, plots A and B, the combined effects of soil temperature and the infestation history on the probability of the presence of the JB larvae (defined as suitability) are shown. The suitability is quite high (> 80%) in areas characterised by relatively cool soils (DD_{cool}^{soil} between 1800 and 2500) and where the JB infestation began at least two years earlier. This result is in agreement with what can be expected during an ongoing invasion process. Non-linear effects on the suitability of the JB larvae are observed when considering the combined influence of soil humidity and soil temperature (Fig. 3 C and D). The probability of the presence of JB is higher (> 50%) in areas characterised by cool soils (DD_{cool}^{soil} between 2100 and 2300) and dry periods of medium duration (HW_{dry}^{soil} between 800 and 1100). Extreme soil humidity ($HW_{dry}^{soil} > 2{,}000$ or $HW_{dry}^{soil} < 100$) and soil temperature ($DD_{cool}^{soil} > 2{,}600$ or $DD_{cool}^{soil} < 1500$) conditions are unsuitable for the presence of the species. In Fig. 3, plots E and F, we showed the influence of cumulated cool degree days (DD_{cool}^{soil}) and soil depth on the JB presence. In particular, GAM estimated a high (> 50%) probability of finding JB larvae in shallow soils (< 25 cm depth) with DD_{cool}^{soil} ranging between 2100 and 2300. Soils characterised by useful depth higher than 120 cm and with DD_{cool}^{soil} lower than 1400 or higher than 2200 were found to be less suitable for the JB. The GAM results highlight the non-linearity of the effects of temperature on the JB habitat suitability.

4. Discussion

Disentangling the combined effects of several factors on the probability of the presence of a pest is fundamental for the assessment of the risks and the implementation of pest management strategies (Jeschke and Strayer, 2008; Peterson, 2003; Roura-Pascual et al., 2011). We aimed at identifying the influence of multiple variables related to land use, soil characteristics, weather, and infestation history on the probability of the presence of JB larvae in an area of recent invasion in Northern Italy.

According to LRM results, JB larvae show a preference for less acidic soils, especially in combination with soils characterised by sandy-skeletal particles. The effect of soil pH is less important in coarse-loamy particle size. This result is in partial disagreement with Fleming (1972) and Potter et al. (1996) that reported a decrease in the density of the grubs with the increment of pH. Our results confirm that the relationship between pH and suitability is non-linear and is strongly influenced by soil particle size (Fig. SM.4-j). Focusing on soil texture, the probability of finding JB larvae in sites with loamy sand soils is considerably lower than that calculated in soils with other textures, keeping fixed all other explanatory variables. This result is in agreement with previous scientific evidence reported in Hawley and Dobbins (1945) and Règniére et al. (1979). Both extremely high and extremely low levels of soil organic carbon are associated with the low density of the JB larvae. This result is in agreement with Dalthorp et al. (2000b) that reported a positive relationship between medium levels of organic matter content in soils and grub density, confirming the non-linearity between suitability and soil organic carbon. The lower suitability of soils with high levels of organic content also emerges from the work of Szendrei et al. (2005).

The JB larvae showed high sensitivity to soil water content. This was evidenced by the negative effects of the cumulative rainfall (that is a proxy of water input in soil) and the positive effects of HW_{dry}^{soil} on the presence of larvae. These results seems partially in contrast with those of Dalthorp (2004), Fox (1939) and Hawley (1949), who reported a negative association between drought and larval population abundance. However, the GAM results provide more insights into the role of drought

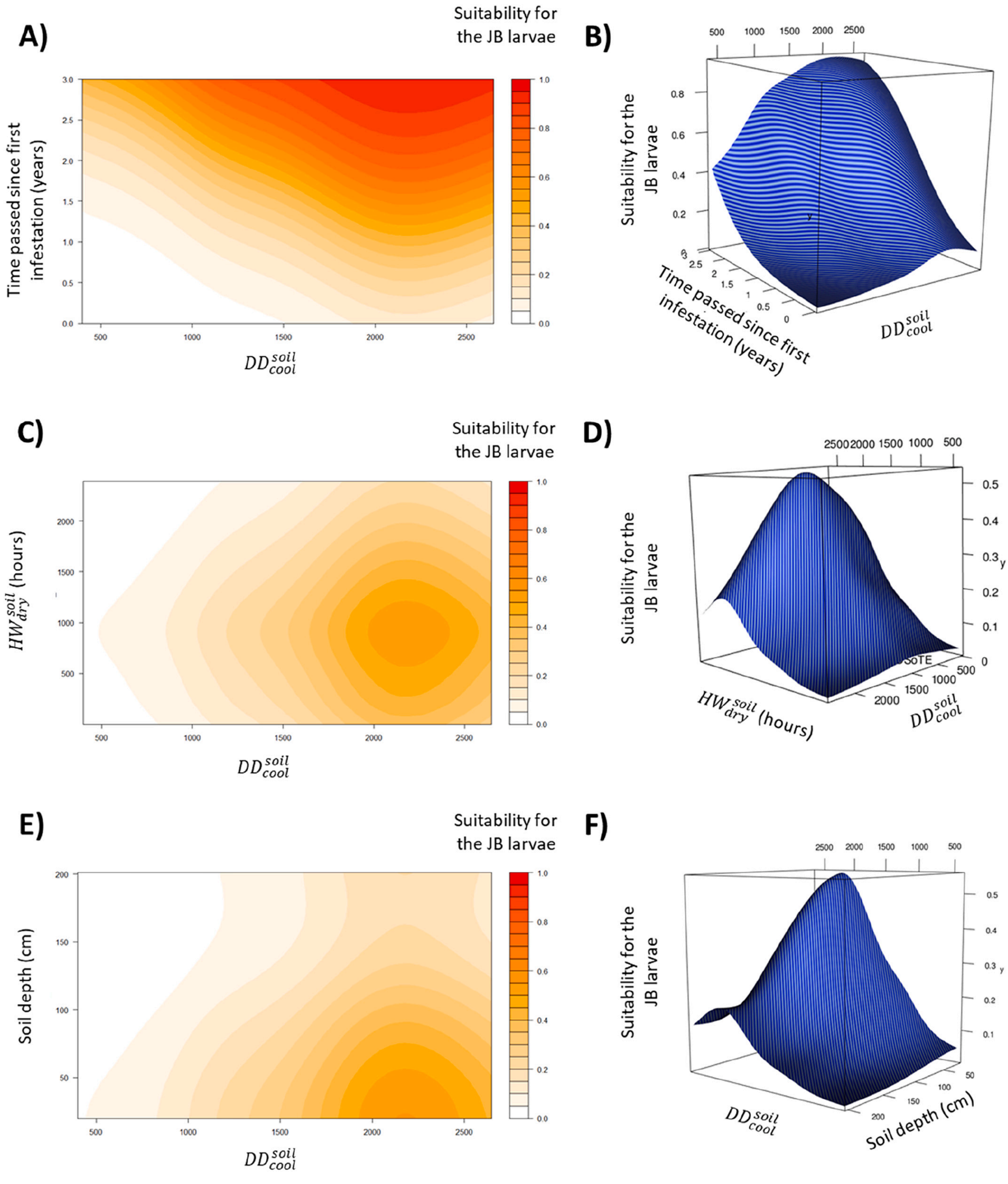

Fig. 3. Estimated probabilities of the presence of *P. japonica* larvae based on the values assumed by the DD_{cool}^{soil} - 'Time passed since first infestation' (plots A and B), DD_{cool}^{soil} - HW_{dry}^{soil} (plots C and D), and DD_{cool}^{soil}- 'Soil depth' (plots E and F), keeping fixed the values of the other explanatory variables. The left plots (A, C, and E) represent the *P. japonica* suitability in a bi-dimensional space, where the probability of the presence of the JB larvae is represented by a colour gradient. The right plots (B, D, and F) show the suitability in a three-dimensional space, where the two explanatory variables are represented on the X-axis and Y-axis and the probability of the presence of *P. japonica* larvae is represented on the vertical (Z) axis.

on the probability of the presence of JB larvae. Both extreme high and extremely low soil humidity and soil temperature conditions are unsuitable for the presence of the species. Many authors reported that drought periods negatively influence the survival and the presence of JB immature stages (Allsopp et al., 1992; Kistner-Thomas, 2019; Potter and Held, 2002). With this work, we provide further elements to the knowledge on the relationship between soil humidity and JB suitability, showing that also excessive soil wetness might hinder the presence of the species. This phenomenon might be explained by the increased mortality of eggs and young larvae due to high soil wetness (Potter et al., 1996; Régnière et al., 1981).

A strong negative relation between soil temperature and the probability of the presence of JB larvae has been observed. This result can be partially explained by the potential negative effects of high temperatures on larval survival and adult oviposition preferences, as reported in Dalthorp et al. (2000a), Fleming (1972), and Potter and Held (2002). Both DD_{cool}^{soil} and DD_{warm}^{soil} positively influence the presence of larvae. However, also long periods characterised by low soil temperatures ($<$ 10 °C), expressed by the variable HT_{cold}^{soil}, are negatively related to the presence of the JB. Despite the capacity of JB larvae to withstand cold weather conditions (Fleming, 1972; Ludwig, 1928), our results show possible negative effects of long exposure to cold temperatures on grub density, as observed by Ludwig (1930). More information on the role of temperature is provided by the GAM results. We observed a non-linear effect between DD_{cool}^{soil} and the probability of presence of the pest. Our results suggest that moderately long periods of cold soil conditions can favour the presence of the JB, while extremely long or short periods of cold soil conditions can hinder the presence of the pest.

The results presented in this work can support the definition of suitable strategies for the management of JB populations. Our findings can be used to develop risk maps to guide surveillance efforts and prioritize intervention in high-risk areas (European Food Safety Authority (EFSA) et al., 2019). For instance, high-risk areas can be targeted by preventive agronomic, biological, and chemical control actions to reduce the impacts of the pest on crops (Santoiemma et al., 2021). Different management strategies are currently being tested, including the use of nematodes as biotic control agents (Mori et al., 2022; Torrini et al., 2020) or innovative techniques for the injection of insecticides into the soil without severely affecting the plant root system. Furthermore, results can support the identification of suitable land management strategies to reduce the potential impact of the pest on suitable hosts (e.g., cropping-plan decision-making, use of organic fertilisers, soil management practices).

The availability of longer time series data on habitat suitability of PJ could improve the reliability of the results we have obtained for the benefit of risk management decisions making. During the establishment phase the pest could be under the influence of a set of factors that could change in the medium- and long-term. For example, we expect that long-term studies make it possible to assess the effect of the biotic relationships of the JB population with local communities that could act as natural control agents.

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CRediT authorship contribution statement

A. Simonetto: Conceptualization, Data curation, Formal analysis, Methodology, Statistical analysis, Software, Validation, Visualization, Writing – original draft. **G. Sperandio:** Conceptualization, Data curation, Methodology, Validation, Writing – original draft. **A. Battisti:** Investigation, Writing – review & editing. **N. Mori:** Investigation, Writing – review & editing. **M. Ciampitti:** Methodology, Resources, Writing – review & editing. **B. Cavagna:** Resources, Writing – review & editing. **A. Bianchi:** Resources, Writing – review & editing. **G. Gilioli:** Conceptualization, Methodology, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

All authors have no competing interests to declare.

Data availability

The authors do not have permission to share data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2022.101749.

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