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The Spread of the Japanese Beetle in a European Human-Dominated Landscape: High Anthropization Favors Colonization of *Popillia japonica*

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Abstract: The impact of invasive species is not limited to the loss of biodiversity; it also represents significant threats to agriculture on a global scale. The Japanese beetle *Popillia japonica* (native to Japan but an invasive agricultural pest in North America) recently occurred in the Po plain (Italy), one of the most cultivated areas in southern Europe. Thus, our aims were to identify (i) the main landscape predictors related to the occurrence of the Japanese beetle and (ii) the areas of potential invasion of the Japanese beetle in the two Northern Italian regions in which this invasive species currently occurs, Piedmont and Lombardy. Specifically, we combined Japanese beetle occurrences available in the citizen science online platform iNaturalist with high-resolution landscape predictors in an ensemble approach and averaged the results of Bayesian generalized linear and additive models developed with the integrated nested Laplace approximation (with stochastic partial differential equation). We found that the occurrence of the Japanese beetle was negatively related to the percentage of broadleaf forests and pastures, while it was positively related to sparse and dense human settlements as well as intensive crops. Moreover, the occurrence of the Japanese beetle increased in relation to the percentage of rice fields until a peak at around 50%. The Japanese beetle was likely to occur in 32.49% of our study area, corresponding to 16,000.02 km^2, mainly located in the Po plain, low hills, and mountain valleys. We stress that the Japanese beetle is a high-risk invasive species in human-dominated landscapes. Thus, we strongly recommend that local administrations quickly enact pest management in order to reduce further spread.

Keywords: GAM; GLM; iNaturalist; INLA; invasive species; pest; species distribution models; SPDE

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1. Introduction

The globalization of trade and travel has facilitated the spread of invasive species throughout the world [1]. Despite the great effort of public administrations, invasive pests are a threat that can affect global biodiversity [2] and lead to huge economic damage [3]. Thus, invasive alien species are one of the top five drivers of environmental change with the largest relative global impact [4]. Many invasive species change ecosystem functioning and the delivery of ecosystem services by altering nutrient and contaminant cycling, hydrology, habitat structure, and disturbance regimes [5].

Moreover, the management and control of invasive pests are not easy tasks, as their consequences on biodiversity and ecosystems raise numerous issues [6–8]. This is particularly true in Europe, which, as a long-time center of trade, has historically seen the introduction and subsequent establishment of thousands of invasive species in several agricultural landscapes throughout the continent; among these is the Po plain in Italy [1]. In this area, a new destructive invasive species, the Japanese beetle *Popillia japonica* (Newman 1841; Coleoptera: Scarabaeidae: Rutelinae [9]; referred to as Pj hereafter) was observed for the first time in 2014 [10]. Because its first discovery was close to the Malpensa Airport, Pj probably arrived in Italy via cargo aircraft [11].

Given its highly polyphagous invasive behavior [12] and high dispersal abilities [13], the species has been designated as a high-priority candidate in the new phytosanitary legislation of the European Union [14,15], and it is listed in Annex I Part A/1 of Council Directive 2000/29/EC4. The year 2014 marked the year of the invasion of Pj on the European continent, and since then, governments have activated management actions to contain the pest and prevent its spread. However, since 2014, the species has progressively colonized new areas in Italy, and to date, its occurrence is still limited to the Piedmont and Lombardy regions, which occupy about 0.6% of European suitable territories [16]. Recently developed Species Distribution Models (SDMs) predict that by 2050, on the basis of climate and land use change, the species will rapidly expand its distribution range to occupy between 45 and 50% of all European suitable territories [16]. On a global scale, the main factor driving the spread of Pj is the increase in annual temperature [16,17], resulting in an increase in areas with the minimum number of degree days needed to complete the development from a larva to an adult [18,19].

However, what happens on a local scale? Which parameters influence the expansion of Pj in areas where the mean annual temperature is relatively homogeneous? Soil moisture has been recognized as a key parameter to limit the potential spread of Pj [12,20]. However, it seems improbable that a single parameter could be so critical in the expansion of a species, especially in cases of adaptable species, such as Pj. Furthermore, it is hard to believe that in the past 100 years (since Pj was first introduced to the USA [17]), the species did not accidentally reach Europe until 2014. Instead, it is more likely that it arrived several times but never found suitable conditions for colonization. Is it possible that an area with a high human population, such as the Po plain (one of the most urbanized areas in Europe [21]), is suitable for the expansion of Pj? What are the parameters that favor its dramatic expansion in northern Italy? We aimed to identify these factors and areas at high risk of invasion to prevent further spread in these human-dominated landscapes and throughout the rest of Europe.

Species distribution models are useful tools for predicting the spread of invasive species [16,22–25], combining species occurrences with spatial predictors. Recently, the increase in spatial data on species occurrence stored on online platforms, combined with innovative modeling approaches, has provided researchers with essential information to develop sound strategies for species conservation [26].

To date, much of the Pj occurrence data available for Europe refer exclusively to the northern Italian regions of Piedmont and Lombardy; therefore, on the basis of these available data and the land cover characteristics of both regions, we developed spatial models to (1) identify landscape factors related to the pest species distribution and (2) assess the potential spread, identifying areas of potential invasion. In this study, we combined Pj occurrences collected by citizen scientists during the years 2014–2021 in the Po plain (Italy) and 'observer-oriented' pseudo-absences (occurrences of species other than the target species collected by the same observers of the target species [26]) with accurate and recently developed land-cover layers in the INLA (Integrated Nested Laplace Approximation [27]), a Bayesian framework that also accounts for spatial dependencies in species locations through the Stochastic Partial Differential Equations. Specifically, we developed an ensemble approach that averages linear and smoothing approaches (hereafter GLM-INLA and GAM-INLA, respectively).

2. Materials and Methods

2.1. Study Area

We investigated the distribution of Pj in an area of the Po Valley between the regions of Lombardy and Piedmont in Italy, encompassing a total of 12 and 8 provinces, respectively (Figure 1). This area is located between two major mountain ranges, the Western–

Central Alps and the Northern Apennines, and it is crossed from west to east by the Po River. The study area is characterized by cold and foggy winters and hot and humid summers typical of the temperate, sub-continental climate, with a mean minimum temperature of −1 to −2 °C and a mean maximum temperature of 25–28 °C [28]. Rainfall is distributed throughout the year, with peaks in the spring and autumn (the average total annual rainfall ranges between 700 and 1200 mm). The high water availability from spring precipitation, the runoff from the surrounding mountain ranges [29], and the highly developed irrigation infrastructure have made the Po Valley one of the most intensively cultivated areas in Europe [30]. Piedmont and Lombardy account for 37% and 53% of irrigated land with respect to arable land, respectively, and for 35% of the country's agricultural production, mostly represented by rice (90% of the country's rice production), followed by maize, wheat, sugar beet, fruit, and horticultural products [31,32]. The Po Valley is also the most densely populated and urbanized area of the country [33]. As a consequence, 81% of the plain shows low to medium-low levels of landscape diversity [34]. Natural areas are residual and mostly located close to pre-alpine hills or along the main tributaries of the Po River [35], where many invasive tree species also occur (e.g., the black locust *Robinia pseudoacacia* [36]).

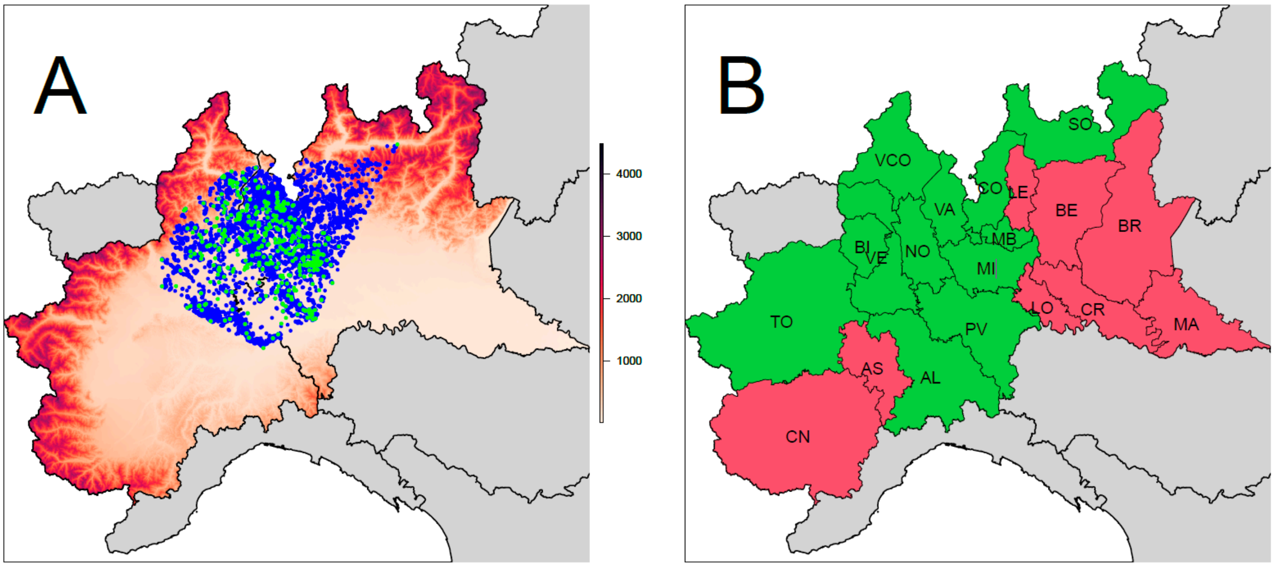

Figure 1. Study area. (**A**) Light/dark red indicates low/high elevation (m a.s.l.), and borders of the Italian regions are shown in black. Japanese beetle locations are green; observer-oriented pseudo-absences (i.e., locations of species other than target species collected by the observers of the target species) are blue. (**B**) Green and red polygons indicate provinces with and without the occurrence of our target species, respectively. In Lombardy: BE, Bergamo; BR, Brescia; CO, Como; CR, Cremona; LE, Lecco; LO, Lodi; MA, Mantua; MB, Monza-Brianza; MI, Milan; PV, Pavia; SO, Sondrio; VA, Varese. In Piedmont: AL, Alessandria; AS, Asti; BI, Biella; CN, Cuneo; NO, Novara; TO, Turin; VCO, Verbania Cusio Ossola; VE, Vercelli.

2.2. Study Species and Data

Our species dataset consisted of all occurrences of Pj collected in our study area by citizen scientists and stored on the iNaturalist platform (www.inaturalist.org (accessed on 22 April 2022) [37]). iNaturalist is an open-access platform for citizen scientists based on the concept of mapping and sharing observations of biodiversity around the world; it allows species occurrences to be downloaded using specific queries (i.e., taxon, place, user/observer, date, etc.). Thus, we downloaded only Pj locations (with geographic coordinates) collected in the years 2014–2021 between June and August, as this range of months corresponds to the activity biological period of our target species [19].

Considering the same monthly range and years, we collected all the locations of all the species from the iNaturalist platform, including both plants and animals (but excluding Pj), collected by the observers of Pj to derive 'observer-oriented' (oo) pseudo-absences [16,26]. Specifically, we used the functions 'get_inat_obs' and 'get_inat_obs_user' in the R package 'rinat' [38] to download the Pj locations and the locations of all the species (excluding Pj) collected by the observers of Pj, respectively. However, to avoid introducing false pseudo-absences, where our target species had not yet colonized the area, we considered only the oo-pseudo-absences occurring inside the minimum convex polygons (MCPs, derived using the function 'mcp' in the R package 'adehabitatHR' [39]) estimated around our target species' locations. We selected a total of 10,000 oo-pseudo-absences to develop SDMs [40].

2.3. Predictor Variables

We initially took into account a total of 11 predictors (two topographic, seven land-cover, and two anthropogenic variables) that may represent the habitat characteristics of Pj (Table 1).

Table 1. Predictor variables considered and their relative VIF (Variance Inflation Factor). Predictors with VIF > 3 were not considered in further analysis. Altitude in in meter above sea level (m a.s.l).

Variable	**Unit**	**VIF**
Altitude	m a.s.l.	>3
Slope	°	>3
Bare areas	%	>3
Deciduous forests	%	1.283
Coniferous forests	%	>3
Grasslands	%	1.126
Shrublands	%	>3
Intensive crops	%	1.302
Rice fields	%	1.101
Dense human settlements	%	1.039
Sparse human settlements	%	1.103

The topographic variables were derived from a digital elevation model (DEM) with a spatial resolution of 20 m (http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/dem20/view (accessed on 22 April 2022) [41]), and the land cover features were derived from CORINE Land Cover 2018 (CLC2018), which was 4th-level detailed for Italy (https://groupware.sinanet.isprambiente.it/uso-copertura-e-consumo-di-suolo/library/copertura-del-suolo/corine-land-cover/corine-land-cover-2018-iv-livello (accessed on 22 April 2022) [42]). The two anthropogenic variables were also derived from CLC2018. All these predictors were resampled at a spatial resolution of 100 m.

Thus, we calculated the Variance Inflation Factor [43] considering all values of the predictors in the whole study area to prevent multicollinearity among predictors from negatively affecting the SDMs. We used the function 'vifstep' in the R package 'usdm' [44] to carry out a stepwise selection analysis in which variables were removed until the highest VIF value was < 3 [43].

2.4. Data Analysis

To estimate the relationship between the occurrence of Pj and the predictors considered, we regressed the presence and oo-pseudo-absence locations with predictor variables through the recently developed method of Integrated Nested Laplace Approximation (INLA) [27]. INLA offers a highly flexible modeling environment that can also incorporate spatial random effects into binomial models and is effective in producing SDM-type spatial predictions [45]. Specifically, in this study, we developed a binomial model in INLA that considered Pj presence/oo-pseudo-absence as the response variable and uncorrelated predictor variables as fixed effects, and we also took into account the spatial dependency among species locations through the Stochastic Partial Differential Equation (SPDE) approach of [46], which is based on computations using a Gaussian Markov Random Field representation of the Gaussian Field [47].

Instead of fitting INLA considering only the linear relationship between Pj occurrence and predictor variables (similar to a generalized linear model, GLM), we allowed INLA to include smoothing parameters to account for the non-linear relationship of the predictors with the response variable (similar to a generalized additive model, GAM). Thus, we combined INLA models including linear predictors (GLM-INLA, hereafter) and non-linear predictors (GAM-INLA, hereafter) into an ensemble prediction (wEP), weighted by the True Skill Statistic (TSS, see below).

By using a random subsample of 90% of the locations to calibrate the models and the remnant 10% to evaluate them [48], we carried out 10-fold cross-validation to test the prediction accuracy of our model. Specifically, we considered two widely used indices to evaluate model performance: (i) the area under the receiver operating characteristic curve (AUC) and (ii) the TSS. The AUC ranges between 0 and 1 (worse than a random model and best discriminating model, respectively), while the TSS ranges between −1 and 1 (higher values indicate good predictive accuracy, while 0 indicates random prediction).

Thus, we converted the resulting continuous maps of current and future distribution into binary ones, considering the threshold values estimated by maximizing the TSS [49,50]. Values higher and lower than these thresholds represented sites where Pj was likely to occur and not likely to occur, respectively.

3. Results

From the data available in iNaturalist between June and September of the years 2014–2021, we collected a total of 468 occurrences of Pj distributed in a total of 12 provinces between Piedmont and Lombardy (Figure 1). These Pj occurrences were uploaded by a total of 260 observers, who also collected a total of 86,170 non-target species occurrences (Figure 1). Thus, to develop SDMs, our dataset consisted of 445 cells (at a 100×100 m^2 resolution) in which Pj occurred and another 10,000 cells (at a 100×100 m^2 resolution) in which the same observers of our target species collected occurrences of species other than our target species within the MCPs identified considering Pj occurrences (Figure 1).

We found five predictors with VIF values of >3 (multi-correlated; Table 1), and thus we considered the remaining six predictors in the further analyses.

Considering these reaming predictors, we found that Pj was negatively related to the percentage of broadleaf forests and pastures, while it was positively related to sparse and dense human settlements as well as intensive crops (Figure 2). The occurrence of Pj slightly increased in relation to the percentage of rice fields until a peak at around 50% (Figure 2).

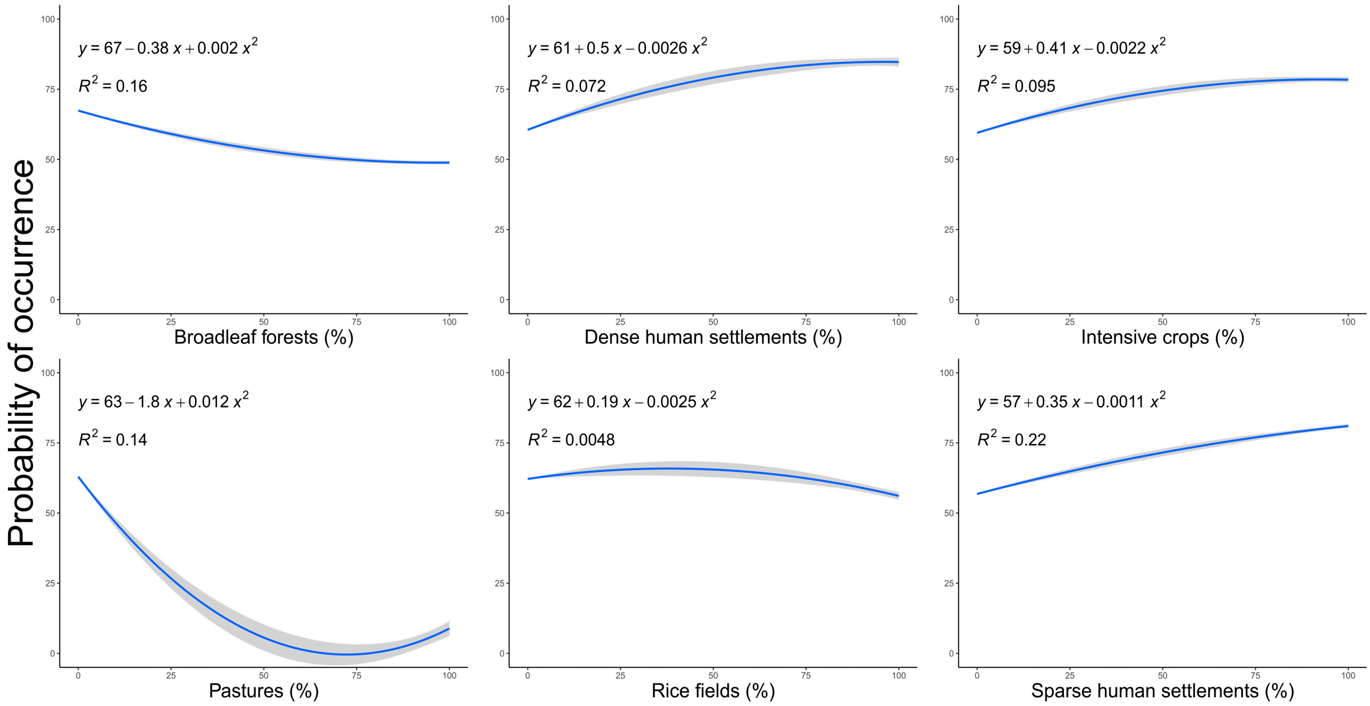

Figure 2. Response curves (in blue) and relative 95% confidence intervals (in gray) of probability of occurrence of the Japanese beetle in relation to predictor variables. Model equation with response variable (y) and explanatory variable (x), as well as coefficient of determination (R^2) are shown.

Ten-fold cross-validations showed high predictive accuracy of both GLM- and GAM- INLA SPDE (AUC: 0.913 ± 0.045 and 0.929 ± 0.052, respectively; TSS: 0.901 ± 0.021 and 0.909 ± 0.039, respectively) as well as those of their wEP (AUC and TSS: 0.919 ± 0.073 and 0.911 ± 0.024, respectively).

Thus, we estimated that 16,000.02 km^2 (32.49%) of our study area was potentially suitable for Pj, mainly located in the Po Valley in Lombardy (Figure 3). The most suitable areas for Pj were located in Lombardy, especially in the provinces of Milan, Monza–Brianza, Lodi, Cremona, and Mantua as well as the lowest part of the provinces of Bergamo and Brescia. Pavia was one of the provinces least affected by the presence of Pj. However, there was a range of high suitability for the species located in a pre-Apennine area parallel to the course of the Po River. This area continues through part of the province of Alessandria in Piedmont. Generally, the distribution of Pj should be relatively limited in Piedmont compared with that in Lombardy. However, we identified large areas of distribution of Pj in the pre-alpine areas of Piedmont, specifically in the provinces of Cuneo, Turin, and Vercelli (Figure 3).

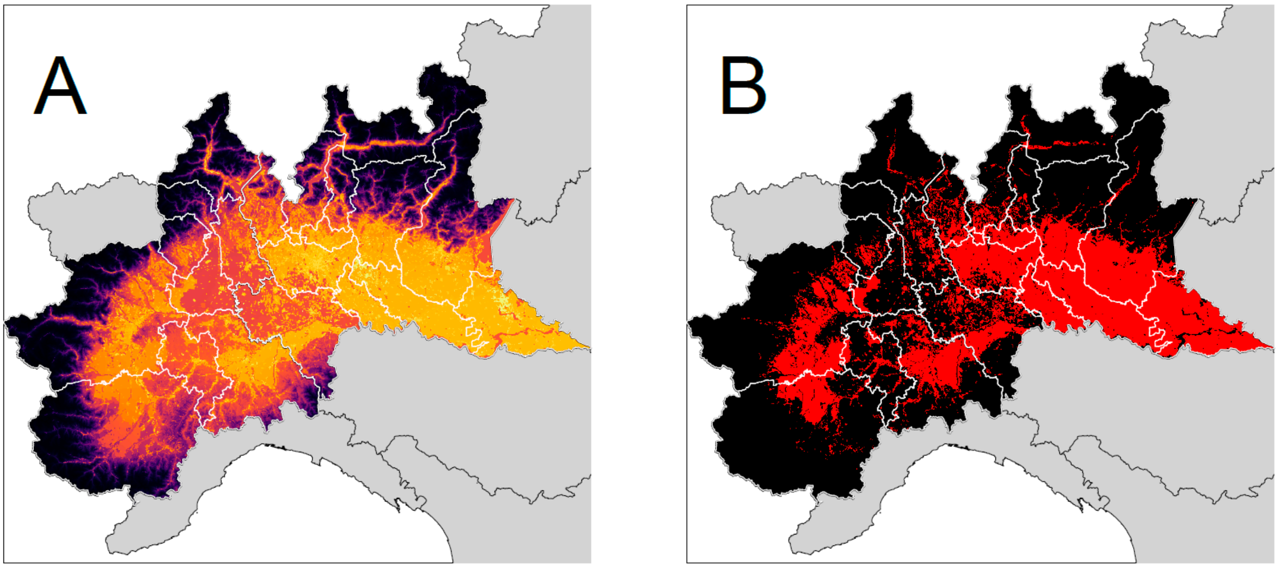

Figure 3. Distribution maps of the Japanese beetle estimated by weighted ensemble prediction of GLM- and GAM-INLA SPDE. (**A**) Yellow–black scale indicates higher–lower occurrence probability values, respectively. (**B**) Areas of predicted species occurrence estimated using a threshold value of 67.28 (threshold values estimated by maximizing TSS): presence indicated by red; absence indicated by black. Borders of the provinces within our study area are indicated by white lines (see Figure 2 for details), while the Italian regions outside our study area are grey, and their borders are indicated by black lines.

4. Discussion

In this study, we investigated the potential distribution of the invasive destructive pest Pj in northern Italy, which is currently the only area in Europe colonized by this species. The great adaptability of Pj and its highly polyphagous behavior make this species widespread, as highlighted by its high estimated probability of occurrence in many different environments.

However, according to our results, urbanization and intensive agriculture are the main drivers of the spread of this species. The effect of human impact on non-native species and the concentration of such species in human-dominated landscapes (human settlements and croplands), especially during the early stages of their introduction, are renowned in the literature [51–53]. Anthropization plays a crucial role in favoring non-native species richness and promoting the establishment of these species, e.g., by creating microclimatic conditions suitable for their settlement and spread [54,55]. *Popillia japonica* finds optimal conditions for its colonization in the human-dominated landscapes of the Po Valley. Thanks to favorable weather conditions and high water availability, the Po Valley is characterized by highly fertile and high-moisture soil [56]. These characteristics have favored the expansion of agriculture in the Po Valley, making it one of the most extensive and productive agricultural areas in Europe [57]. In addition, irrigated soils provide good conditions for the spread of Pj, and soil enrichment due to agricultural practices, such as plowing, fertilization, and irrigation, could have made the soil conditions even more optimal for adult female deposition and grub development [58–60]. Moreover, intensive crops may have favored the expansion of Pj, even indirectly, eliminating its potential predators. Landscape simplification and the recurrent use of chemical fertilizers and pesticides negatively affect the overall biodiversity [61–63] and significantly reduce beneficial insects and predaceous insect guilds [64]. The massive occurrence of PJ in the agricultural landscapes of the Po Valley has led farmers to intensify the use of pesticides and chemical products that have not yet proven to be effective in eradicating Pj [65]. Many insecticides that are widely used in other countries such as the U.S. and are effective against Pj have been restricted or forbidden in Europe since the 2000s

(EU Reg. 1107/2009). Therefore, these pesticides are not available to farmers, landscape managers, or homeowners in European countries.

On the other hand, pheromone-based traps have been widely used in the past few years by farmers in the Po Valley to limit the spread of Pj [66]. However, the excessive use of these devices could paradoxically have contributed to the spread of Pj in our study area. Indeed, the pheromone in the traps attracted more adults than those effectively trapped and thus contributed to the dispersion of Pj and its colonization of new areas [15,65]. Thus, the use of pheromone-based traps in private gardens, sports grounds, and near orchards and nurseries is currently strongly discouraged [15]. However, in urban areas, the use of these devices has increased enormously in the past two years, and they are now available in all gardening and nursery shops and on major online commerce sites. Moreover, the use of traps in cities, where the risk of passive spread of the pest through hitchhiking is high [15], could have greatly favored the spread of the species and its high concentration in urban areas.

5. Conclusions

In this research, we showed that the distribution of the pest species Pj is strongly related to anthropogenic factors, such as human settlements and intensive crops. Thus, given its strong impact on agriculture in the U.S., its recent spread in the Po Valley represents a major economic problem [67]. While the impact of the damage caused by Pj in Italy (as well as in Europe) has not yet been determined, it reaches $450 million annually in the U.S. [68].

Direct human actions, such as the use of pheromone-based traps and hitchhiking, and indirect actions, such as landscape simplification and high pollution rates, contribute to the exponential expansion of Pj, which triggers irreversible damage to biodiversity and natural ecosystems. Urgent management actions and strong synergy between different stakeholders are thus required to find an effective solution to control the spread of Pj without compromising human and natural ecosystem health.

A potential solution is integrated pest management (IPM), which combines the use of natural enemies and cultural techniques to contain the population growth of pest beetles [69]. Several studies have been undertaken in this regard on both a national and an international scale in France and Switzerland (IPM-Popillia projects). Given the high dispersal abilities of adults, current studies are focusing on larval control and eradication through the identification of pathogens, especially fungi and nematodes [70], and pesticide testing [65,71]. Further studies are needed to investigate the role of bacteria and other microorganisms in controlling Pj. These groups are widely recognized as pathogens, parasites, or parasitoids of the infected species [72] but are still poorly studied. For instance, the intracellular bacteria of the genus Wolbachia are the most abundant endosymbionts, infecting many arthropods [73], and their pathogenic effects on Pj should be investigated.

However, to date, satisfactory results for the effective control of Pj have not been achieved, resulting in only moderate control on a large scale [74,75]. On both a national and a European scale, the most effective solution would certainly be to involve the local human population (residents, farmers, and other stakeholders involved) by means of citizen science tools and to combine the abundance and distribution data of both adults and larvae to accurately model chemical and biological factors affecting their survival. Nevertheless, we stress that citizen science online biodiversity platforms are very important tools to detect and, through robust methodological approaches, assess the distribution and spread of invasive species.

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Conflicts of Interest: Not applicable.

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