

Bulletin of Entomological Research

cambridge.org/ber

Research Paper

Cite this article: Lessio F, Lioy S, Colombo M, Alma A (2025) Factors affecting the impact of Popillia japonica Newman, 1841 (Coleoptera: Scarabaeidae) on grapevine in Northwestern Italy. Bulletin of Entomological Research 115, 175-183. https://doi.org/10.1017/ S0007485325000021

Received: 1 August 2024 Revised: 8 January 2025 Accepted: 9 January 2025

First published online: 07 February 2025

Keywords:

defoliation; landscape ecology; larvae; Scarabaeidae; spatial analysis

Corresponding author: Alberto Alma; Email: alberto.alma@unito.it

Factors affecting the impact of *Popillia* japonica Newman, 1841 (Coleoptera: Scarabaeidae) on grapevine in Northwestern Italy

Federico Lessio¹, Simone Lioy¹, Michele Colombo² and Alberto Alma³



¹Regione Piemonte, Direzione Agricoltura e Cibo-Settore Fitosanitario e Servizi Tecnico-Scientifici, Torino, Italy; ²Studio Associato RisorsaTerra, Biella, Italy and ³DISAFA, Entomology Unit, University of Torino, Grugliasco, Italy

Abstract

The relationships between the Japanese beetle (JB) Popillia japonica Newman, 1841 and the grapevine agroecosystem were investigated in Piedmont in 2020 and 2021, to assess the impact of the species and its distribution within vineyards in relation to the proximity of environmental risk factors. Grubs were sampled by soil coring in the inter-rows of vineyards, whereas both adult beetles and defoliation were counted directly on grapevine plants. The presence of spatial autocorrelation was assessed and the influence of environmental variables (distance from woodlands, meadows and the margin of the vineyard, soil parameters, year of sampling, and year of first detection of the JB) was evaluated through generalized linear mixed models. Beetles and defoliation were more clustered at the edges of vineyards, whereas grubs were localized in few hot spots, generally close to meadows. Spatial autocorrelation was weaker for grubs with respect to adults and defoliation. Grub density depended on distance from meadows, and partially on soil features. Adults abundance was influenced by the proximity to meadows, woodlands, and their presence was clustered at the margin of vineyards. The JBs seem to rely on grapevine mainly as a food source rather than a reproductive site, preferring meadows for egg-laying: therefore, pest management in vineyards should be more focused on adult beetles rather than larvae in the vineyard inter-rows.

Introduction

The Japanese beetle (JB), Popillia japonica Newman (Coleoptera: Scarabaeidae), is a devastating pest introduced into the US during the 20th century (Potter and Held, 2002), and it has been recorded for the first time in Europe in 2014, in Northwestern (NW) Italy (Gotta et al., 2023). The pest status in Italy is defined as 'Present, only in some parts of the Member State concerned, under containment, being settled in restricted areas within the regions of Piedmont, Lombardy, Emilia-Romagna, and Aosta Valley (EPPO, 2024). Larvae (white grubs) develop into the soil feeding on roots of weeds and (mainly) grasses, being harmful to meadows, lawns, sport courses, and others, whereas adult beetles feed on more than 300 plant species, causing intense defoliation (Potter and Held, 2002). Adults are capable of spreading by active flight, covering average distances of 2-3 km in 24 h, albeit some specimens may fly up to 10 km (Lessio et al., 2022). As a result of this capability, the annual increase of JB-infested area by active flight is about 10 km (Mondino et al., 2022). On the other hand, passive transport may involve both grubs hidden in the soil, and adult beetles as hitchers. To limit the spread of P. japonica, phytosanitary measures have been put in place, both by National and Regional Plan Protection Organizations and by the European Union, including sprays and prevention actions in nursery stocks.

Among host plant species, grapevine (Vitis vinifera L.) is one of the most affected (Fleming, 1972). Grapevine also undergoes official detection surveys in pest-free areas, as a sort of sentinel-plant (EFSA (European Food Safety Authority), 2023). The defoliation by JBs affects both the quality parameters of grapevine at harvest (Ebbenga et al., 2022; Selli et al., 2023) and the cold-hardiness of buds (Hammons et al., 2010). Although the impact of the JB on the vineyard agro-ecosystem is well documented in the New World, little is known about what happens in Italy given the substantial differences with respect to American grapevine growing areas. In fact, the vineyards of the JB-infested areas of NW Italy are generally quite small in size, and surrounded by different kind of crops and/or natural environments, which might act as a reservoir (source) of incoming adult beetles. On the other hand, these vineyards have generally a

© The Author(s), 2025. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.



Table 1. Main features of the investigated vineyards/sites

Site	Municipality	°N	°E	VAR	Size (m²)	TXT	ORG	PM	YR
1	Mezzomerico	45.622622	8.599135	1	2200	1	3	1	2017
2	Mezzomerico	45.628730	8.594090	1	4300	1	3	1	2017
3	Suno	45.628568	8.578782	1	3100	2	3	1	2017
4	Suno	45.636942	8.579113	1	11100	1	3	1	2017
5	Suno	45.630437	8.578034	1	1460	2	3	1	2017
6	Mezzomerico	45.610722	8.594451	1	2900	1	3	1	2017
7	Fontaneto	45.665117	8.506813	1	2200	3	2	1	2019
8	Fontaneto	45.665981	8.506102	1	2900	3	1	1	2019
9	Cavaglio d'Agogna	45.601363	8.477669	1	5300	1	3	1	2019
10	Ghemme	45.612793	8.421697	1	2000	1	3	1	2019
11	Briona	45.543760	8.504262	2	5000	1	3	2	2019
12	Briona	45.546277	8.501218	2	17200	1	3	2	2019

VAR, vine variety (1: Nebbiolo; 2: Croatina); TXT, soil texture (1: silty-loam; 2: loam; 3: sandy-loam); ORG, organic matter amount (1: low; 2: average; 3: high); PM, pest management (1: IPM conventional; 2: organic); YR, year of first JB detection.

grass cover in the inter-rows, which may promote the settlement of *P. japonica* directly inside the vineyard by egg-laying. Within this frame, the present research was aimed to determine if vineyards are suitable for JBs to lay eggs. Moreover, the environmental risk factors that may promote the presence of JB (distance from woodlands and meadows, distance from the edge of the vineyard, soil structure) were evaluated to understand their effects on the presence and distribution of the pest within vineyards.

Materials and methods

Study area

The present research has been conducted during 2020 and 2021 in grapevine growing areas of Piedmont, NW Italy, within the JB-infested area. Twelve vineyards were investigated: details are given in table 1. All the vineyards had a grass-cover in the interrows, and were trained with the 'Guyot' pruning system. Vineyards were sprayed with insecticides, within the frame of the mandatory pest management against Flavescence dorée and its main vector, Scaphoideus titanus Ball, 1932 (Hemiptera: Cicadellidae). Active substances used in conventional Integrated Pest Management (IPM) vineyards included acetamiprid, etofenprox, flupyradifurone, and pyrethroids such as lambda-cialothrin, deltamethrin, and tau-fluvalinate; whereas in organic vineyards, only natural pyrethrum was used. Sprays were made twice: at the end of June and after the middle of July in conventional vineyards, and at the middle and end of June in organic ones. Moreover, in organic vineyards adult JBs were removed by hand 2–3 times per season.

Sampling

In each vineyard, an experimental plot was selected, consisting of 10 rows having approximately 60 plants each, distributed on eight inter-poles (approx plot size: 100 m^2). Within the plot, transects consisting in six grapevine plants were defined; each transect was repeated four times on five different grapevine rows (total transects per vineyard, N=20), with the exception of Site 1 which was too small and therefore had five transects on four different rows.

A group of six plants between two transects was not sampled, as well as a whole row between two sampling rows.

Grubs were monitored once a year, during April–May. Soil cores (size 10 × 10 cm, depth 20 cm) were collected using a shovel. Twenty cores per vineyard were made close to each transect, four on five different alternate inter-rows, with a 10 m distance one from another. Soil turfs were extracted and accurately inspected: grubs were preserved under 70% vol. ethanol inside plastic vials, and brought to the laboratory facility of the University of Turin in Grugliasco (TO). In the lab, the setae raster on the last abdominal segment of grubs was observed under a stereomicroscope (20× magnification) to distinguish larvae of *P. japonica* from those belonging to other species of Scarabaeidae (Balachowsky, 1962; Fleming, 1972).

For each vineyard, soil samples were analyzed in order to measure physical and chemical parameters, with a particular focus on granulometry and amount of organic matter. Analyses were performed by the Agrochemical Laboratory of the Regional Plant Protection Service of Piedmont. Results are provided in Supplementary material S1.

Adult beetles were sampled three times (June 24, July 1, July 16), and five times (June 22 and 29, July 5 and 15, August 6 and 18) in 2020 and 2021, respectively. In each vineyard, visual inspections were made on single transects. An operator moved along the transect, counting the number of either single beetles or clusters of beetles on leaves and shoots. A cluster was defined as two or more beetles feeding and/or mating on the same leaf. At the same times, the degree of defoliation on each transect was evaluated by observing two grapevine shoots bearing at least five leaves. Four defoliation classes were defined: class 1 (0–25% defoliation); class 2 (25–50%); class 3 (50–75%); class 4 (75–100%).

Data analyses

Georeferenced data of grubs, adults, and defoliation were analyzed by means of QGIS Software (version 3.22.6). Interpolation maps were produced using the Inverse Distance Weighting (IDW) method (Bartier and Keller, 1996), applying a distance coefficient of d=2.

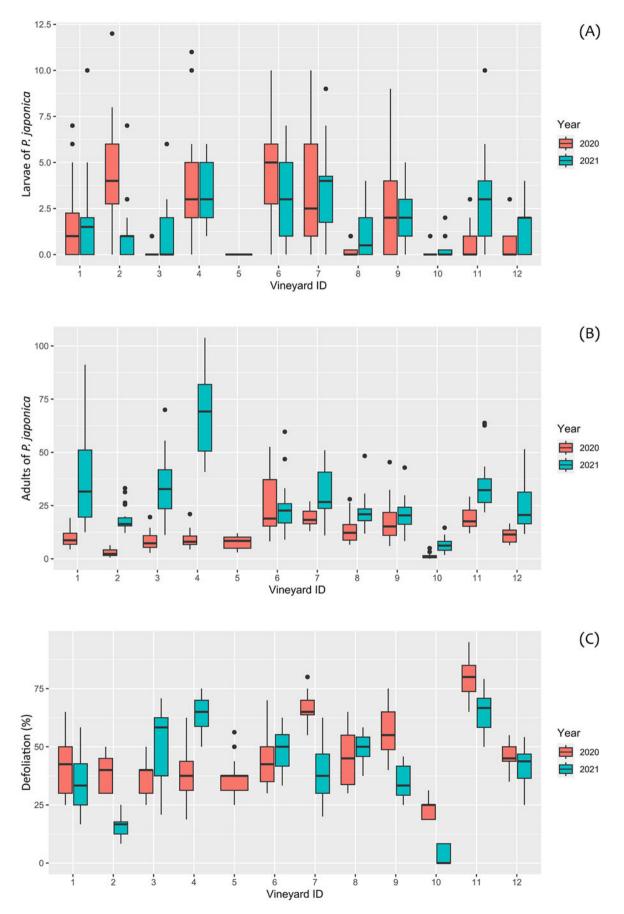


Figure 1. Sampling data of JB in the investigated vineyards: (A) larvae; (B) adults; (C) defoliation. Horizontal line: median values; box: interquartile range (25–75%); whiskers: minimum and maximum scores without outliers; dots: outliers.

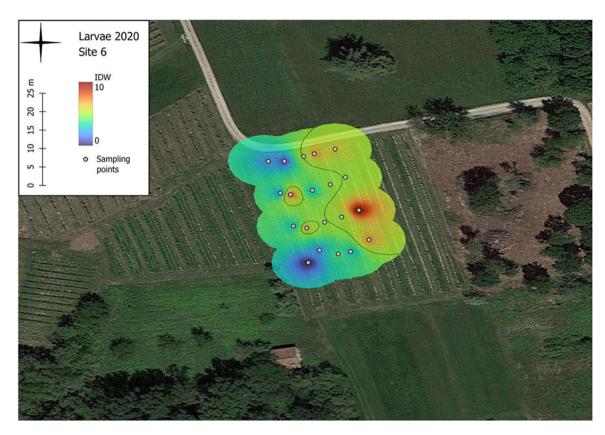


Figure 2. Interpolation map obtained by Inverse Distance Weighting (IDW) of Japanese beetles larvae in site 6 for year 2020. The maps of the other sites and years are provided in the Supplementary Material.

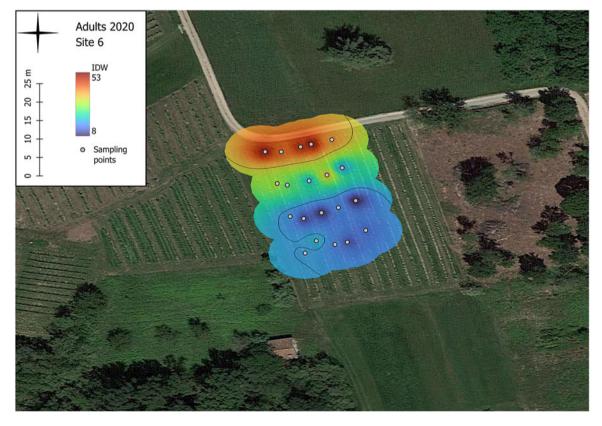


Figure 3. Interpolation map obtained by Inverse Distance Weighting (IDW) of Japanese beetles adults in site 6 for year 2020. The maps of the other sites and years are provided in the Supplementary Material.

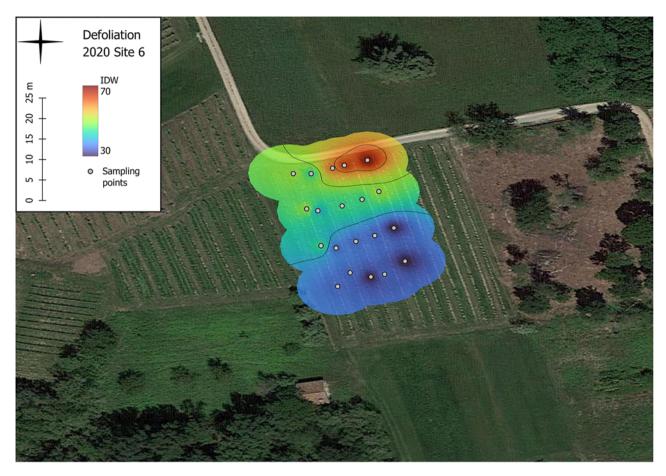


Figure 4. Interpolation map obtained by Inverse Distance Weighting (IDW) of Japanese beetles defoliation in site 6 for year 2020. The maps of the other sites and years are provided in the Supplementary Material.

Statistical analyses were performed with R software (version 4.2.3). A correlation analysis was made between the following data: larvae vs adults, larvae vs defoliation, and adults vs defoliation, considering the single transect as the sampling unit (N=460), whereas for both adults and defoliation the mean value of different sampling dates per transect was used. Normality of data was assessed via the Shapiro–Wilk test: as the test failed for all of the data, we applied the Spearman correlation test with a Bonferroni correction for multiple comparisons.

The spatial autocorrelation of each of the three variables at the vineyard level was calculated with the Moran's *I* index and tested against the null hypothesis of no correlation (Dormann *et al.*, 2007; Gittleman and Kot, 1990). If the observed values of *I* are significantly greater than the expected values, then data show a positive autocorrelation, meaning that similar values, either high or low, are spatially clustered.

Data on adults and grubs were further modeled with generalized linear mixed models (GLMMs) with the Template Model Builder approach (Brooks *et al.*, 2017). The model on adults was fitted to a Gamma distribution of the error and a log link function, with an autoregressive order-1 structured variance-covariance matrix (ar1) for taking into account the spatial autocorrelation of the data. Data of grubs presented weaker spatial autocorrelation; therefore, they were fitted to a zero-inflated model with a Poisson distribution of the error and a log link function without considering spatial autocorrelation. The following predictive variables were considered:

- Distance from woodlands, as a continuous variable.
- Distance from wet (irrigated) meadows, as a categorical variable: A < 20 m; B: 20-40 m; C: 40-60 m; D > 60 m (category A was used as a reference).
- Distance from the edge of the vineyard, as a continuous variable.
- Year of first detection of *P. japonica* in the municipality (2017 or 2019), Year of monitoring (2020 or 2021) and the interaction between the two variables.
- Soil texture and carbon amount (just for the model on grubs) as a categorical variable: A: sandy-loam, low amount; B: sandy-loam, average amount; C: loam, average amount; D: silty-loam, high amount (category D was used as a reference).

The following variables were included as random effects into the GLMMs: (1) sampling site (vineyard) in which the sampling was conducted (for both models); pest management strategy: organic or integrated (just for the model on adults). All the models used for the analyses were selected based on Akaike information criterion after controlling for model diagnostics.

Results

Larvae of *P. japonica* were found in all of the monitored vineyards, except for Vineyard 5 in 2020. Besides, this vineyard was roughed in 2021, so no data are available for the second year. On the whole, 428 and 437 grubs were identified as belonging to *P. japonica*

Table 2. *P*-values of Moran's *I* index calculated for adults, larvae, and defoliation caused by Japanese beetles in the investigated vineyards; when *P* < 0.05, data are spatially self-correlated

	2020			2021			
Site	Adults	Larvae	Defoliation	Adults	Larvae	Defoliation	
1	< 0.001	0.11	< 0.001	< 0.001	0.51	< 0.001	
2	< 0.001	0.18	< 0.05	< 0.001	< 0.05	0.73	
3	< 0.001	< 0.001	< 0.001	< 0.001	< 0.05	< 0.001	
4	< 0.001	0.72	< 0.001	< 0.001	0.20	< 0.001	
5	0.33	NR	0.44	NR	NR	NR	
6	< 0.001	0.26	< 0.001	< 0.001	0.56	< 0.001	
7	0.06	0.07	< 0.001	< 0.01	0.07	< 0.05	
8	< 0.05	0.60	< 0.05	< 0.001	0.23	< 0.01	
9	< 0.001	< 0.05	< 0.001	< 0.001	0.65	< 0.001	
10	< 0.05	0.67	0.18	< 0.001	0.42	< 0.05	
11	0.52	0.79	<0.01	< 0.001	0.92	< 0.001	
12	< 0.01	0.48	< 0.05	< 0.001	0.80	< 0.001	

in 2020 and 2021, respectively. Grubs of other species accounted for 5.0% and 8.3% of the total in the two years, and included *Amphimallon* spp., *Mimela junii* Duftschmid 1805, *Melolontha melolontha* Linnaeus, 1758, and *Aplidia transversa* (Fabricius, 1801). The maximum numbers of grubs per core (median values) were recorded in Vineyards 6 and 7 in 2020 and 2021, respectively (fig. 1A).

Adult beetles peaked at the beginning of July, being the mean number of clusters per transect equal to 29.9 and 65.6 in 2020 and 2021, respectively. In the same dates, the maximum defoliation was also recorded. The minimum number of both adult clusters and defoliation (median values) was recorded in Vineyard 10 in both years. On the other hand, adult clusters were maximum in Vineyard 6 in 2020 and in Vineyard 4 in 2021 (fig. 1B). Finally, the maximum defoliation was recorded in Vineyard 11 in both years (fig. 1C).

On the whole, interpolation maps showed that grubs were localized in few hot spots, generally closer to meadows (if any). This aspect was much more evident with respect to adult beetles, always clustering along edges bordering with meadows or (secondarily) woodlands. Finally, the spatial distribution of defoliation was similar to that of adult beetles. Examples of interpolated maps for grubs, adults and defoliation are reported in figs. 2–4, whereas maps of all vineyards are shown in Figures S2 and S3.

The observed data were not normally distributed (Shapiro–Wilk normality test, adult beetles: W=0.83, P<0.001; larvae: W=0.80 P<0.001; defoliation: W=0.99, P<0.05); therefore, a Spearman correlation test was performed. All variables resulted correlated to each other (adults vs. defoliation, $\rho=0.55$, P<0.001; adults vs. larvae, $\rho=0.31, P<0.001$; defoliation vs. larvae, $\rho=0.20, P<0.001$).

Spatial autocorrelation of adult beetles, calculated with the Moran's I index at a significance level of 95% (P < 0.05), was detected in 20 vineyards out of 23, representing 87% of the total. Overall, the same value was observed for defoliation. Concerning larvae, only four vineyards out of 22 (17%) showed autocorrelation. Data are presented in table 2.

The best GLMM for adult beetles was obtained using the following explanatory variables: distance from woodlands; distance

Table 3. Results of GLMM of adult beetles

Model variables	Estimate	SD	Z	Р
Intercept	2.97	0.26	11.39	< 0.001
Distance from woodlands	-0.009	0.002	-3.57	< 0.001
Distance from meadows-B (20–40 m)	-0.42	0.12	-3.67	<0.001
Distance from meadows-C (40–60 m)	-0.54	0.14	-3.98	<0.001
Distance from meadows-D (>60 m)	-0.12	0.36	-0.34	0.73
Distance from vineyard edge	-0.014	0.003	-4.12	<0.001
Sampling year (2021)	1.24	0.06	21.51	< 0.001
Detection year (2019)	0.15	0.35	0.44	0.66
Sampling year (2021) : Detection year (2019)	-0.64	0.08	-8.37	<0.001

References for categorical variables: Distance from meadows A (< 20 m); sampling year (2020); detection year (2017). SD: standard deviation. Random effects: sampling site (variance = 0.27; SD = 0.52); pest management strategy (Variance < 0.001; SD < 0.001).

from meadows; distance from the edge of the vineyard; year of first infestation and year of sampling. A correction for spatial auto-correlation was necessary, and a gamma-distribution was applied. Results of the model are presented in table 3 and fig. 5. Significant differences were detected with respect to all of the explanatory variables except for year of detection. Among random factors, pest management was significant resulting in higher levels of beetles in organic vineyards.

Concerning larvae, the best model was a zero-inflated GLMM with a Poisson distribution, including the following explanatory variables: distance from woodlands; distance from meadows; distance from the margin of the vineyard; year of infestation and year of monitoring; soil features, including both soil texture and organic matter. Results of the model are presented in table 4 and fig. 6. Significant differences were detected with respect to all of

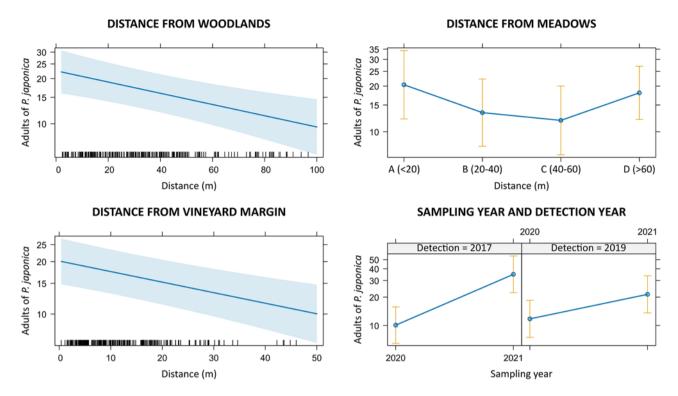


Figure 5. Effects of environmental variables on beetles abundance (GLMM estimates and P-values are reported in table 3).

Table 4. Results of GLMM of larvae

Model variables	Estimate	SD	Z	Р
Intercept	1.90	0.35	5.43	< 0.001
Distance from woodlands	-0.009	0.004	-2.09	< 0.05
Distance from meadows-B (20–40 m)	-0.33	0.15	-2.23	< 0.05
Distance from meadows-C (40–60 m)	-0.59	0.20	-2.95	<0.01
Distance from meadows-D (>60 m)	-1.08	0.48	-2.25	< 0.05
Distance from vineyard edge	0.008	0.006	1.38	0.17
Sampling year (2021)	-0.25	0.10	-2.65	< 0.01
Detection year (2019)	-0.76	0.49	-1.56	0.12
Sampling year (2021): Detection year (2019)	0.58	0.15	3.77	< 0.001
Soil texture and organic amount (A)	-0.59	0.73	-0.82	0.41
Soil texture and organic amount (B)	1.22	0.69	1.76	0.08
Soil texture and organic amount (C)	-2.17	0.63	-3.44	< 0.001

References for categorical variables: Distance from meadows A (<20 m); sampling year (2020); detection year (2017). Soil features, A: sandy-loam, low amount; B: sandy-loam, average amount; C: loam, high amount; D: silty-loam, high amount (category D was used as a reference). SD: standard deviation. Random effects: sampling site (variance = 0.34; SD = 0.58).

the explanatory variables except for the distance from the edge of the vineyards.

Discussion

All of the data recorded for JBs in vineyards (larvae, adults, and defoliation) showed some spatial autocorrelation according to both IDW interpolation maps and Moran I index calculation, in particular data related to adult beetles and defoliation. The spatial dependence observed in adults agrees with the findings of previous researches (Dalthorp et al., 2000; Mondino et al., 2022). Since adults are much more mobile, the mutual influence of their 'hot spots' is more evident and is driven by their well-known olfactory cues (Kowles and Switzer, 2012; Potter and Held, 2002). GLMMs corroborate these findings, demonstrating an aggregation pattern of adults at the edge of the vineyards and in the proximity of both meadows and woodlands, also in agreement with Henden and Guédot (2022). This means that a high number of adults is generally present when vineyards are near meadows or woodlands. Furthermore, adults tend to concentrate their presence at the edges of the vineyards, probably because these sites are located at a lower distance from other environmental suitable areas that may favor the immigration of the pest from outside (Gotta et al., 2023; Lessio et al., 2022). Finally, differences between year of sampling in relation to year of first infestation were significant too for adults, in agreement with Dalthorp et al. (2000), meaning that a higher number of beetles was present during the second year of monitoring.

On the other hand, grubs were spatially related in a smaller number of cases, and in many sites few grubs were found. Since larvae are less mobile, their spatial distribution strongly depends on the pattern of egg-laying by females, that appears correlated primarily to the proximity to meadows and, secondarily, to the proximity to woodlands. Usually, female JBs tend to lay eggs in the proximity of their food source, and only at a second step they move away to find suitable sites (Potter and Held, 2002). This is coherent with the strong clustering of adult beetles that has been observed

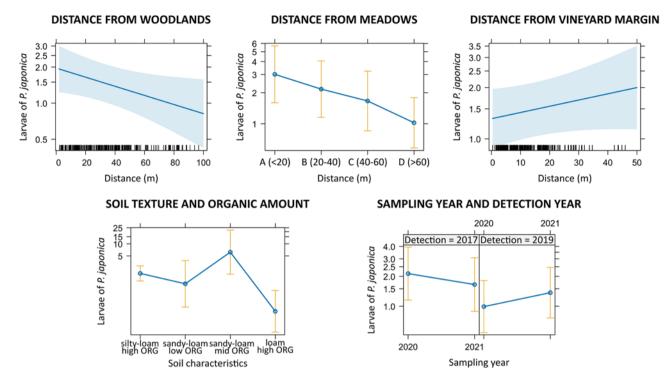


Figure 6. Effects of environmental variables on grubs abundance (GLMM estimates and P-values are reported in table 4).

at the edges of vineyards. However, while adults disperse along grapevine rows when feeding and/or mating, females do not aggregate during egg-laying, resulting in few hot spots of grubs. The physical and chemical characteristics of soil did not result in significant differences in grub density: although this is in contrast with previous researches (Regniere *et al.*, 1981; Simonetto *et al.*, 2022), it is likely that the influence of soil on larval density, while at a landscape scale is very important, in vineyards could be masked by other factors difficult to disentangle, e.g. nematodes (Glazer *et al.*, 2022), suitable plant species (namely grasses) (Fleming, 1972), and pressure caused by agricultural machinery which may result in harsh turfs.

In heterogeneous landscapes, four kinds of sites are recognized concerning their use by JBs, according to Régnière *et al.* (1983): aggregation sites (abundance of preferred hosts for adults, and high densities of grubs), marginal production sites (suitable for oviposition and survival in response to soil moisture), migration alleys (usually unfavorable to oviposition and survival), and feeding sites (islands of plants where adult beetles may aggregate temporarily). Given the variable density of grubs inside vineyards, and that adult beetles are more abundant at the edges, grapevine cultivations within the JB-infested area may be considered as a marginal production site. Therefore, *P. japonica* may be a threat to viticulture especially in areas where aggregation sites are also present.

Conclusions

In conclusion, the JB in NW Italy exploits grapevine cultivation mainly as a food source during the adult stage, whereas other environments are preferred for egg-laying. The feeding activity could lead to severe defoliation which in some cases can exceed 50% of leaves. Adults JB aggregates at the margin of the vineyards, and

their abundance is enhanced by the proximity of suitable environments for the species, such as woodlands and meadows that could be exploited by beetles for feeding and egg-laying, respectively. Therefore, pest management of *P. japonica* in vineyards should be focused mainly on aggregations of adult beetles without considering grubs, which are also much more difficult to target. However, because of the small number of active ingredients authorized on grapevine and effective against JBs (especially in organic viticulture, as partially confirmed by the present research too), and due to restrictions on number of sprays per season with a given active substance, control of *P. japonica* in vine-growing areas should be achieved mainly through an integrated approach at a landscape level (Gotta *et al.*, 2023).

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485325000021.

Acknowledgements. We are grateful to Francesca Avezza, Fabio Mazzetto, and Valeria Colombo for help in field sampling activity, and to all those vine growers who provided suitable sites for this research.

Author contributions. Conceptualization, F.L. and A.A.; methodology, F.L. and S.L.; validation, F.L. and S.L.; formal analysis, S.L.; investigation, F.L. and M.C.; resources, M.C. and A.A.; data curation, F.L. and S.L.; writing—original draft preparation, F.L. and S.L.; writing—review and editing, F.L., S.L. and A.A.; visualization, F.L. and A.A.; supervision, F.L. and A.A.; project administration, A.A. All authors have read and agreed to the published version of the manuscript. The authors declare no conflicts of interest.

References

Balachowsky AS (1962) Entomologie Appliquée a L'agriculture (Tome I. Vol. 1; Coléoptères). Paris, France: Masson et Cie Eds.

- Bartier PM and Keller CP (1996) Multivariate interpolation to incorporate thematic surface data using inverse distance weighting (IDW). Computers & Geosciences 22(7), 795–799. https://doi.org/10.1016/0098-3004(96)00021-0
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M and Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9(2), 378–400. https://doi.org/10.32614/RJ-2017-066
- Dalthorp D, Nyrop J and Villani MG (2000) Spatial ecology of the Japanese beetle, *Popillia japonica*. *Entomologia Experimentalis et Applicata* **96**(2), 129–139. https://doi.org/10.1046/j.1570-7458.2000.00688.x
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G ... Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x
- Ebbenga DN, Burkness EC, Clark MD and Hutchison WD (2022) Impact of adult *Popillia japonica* (Coleoptera: Scarabaeidae) foliar feeding injury on fruit yield and quality of a temperate, cold-hardy wine grape, 'Frontenac'. *Frontiers in Insect Science* 2, 12. https://doi.org/10.3389/finsc.2022.887659
- EFSA (European Food Safety Authority) (2023) Pest survey card on Popillia japonica. EFSA supporting publication 2023:EN-7809. Available at https://efsa.europa.eu/plants/planthealth/monitoring/surveillance/popillia-japonica. (Last updated: 27 February 2023).
- **EPPO Global Database-Popillia japonica (POPIJA)** (2024) Available online: https://gd.eppo.int/taxon/POPIJA/distribution/IT (accessed on 31/05/2024)
- **Fleming WE** (1972) *Biology of the Japanese Beetle (No. 1449)*. Washington: US Department of Agriculture.
- Gittleman JL and Kot M (1990) Adaptation: Statistics and a null model for estimating phylogenetic effects. Systematic Zoology 39, 227–241. https://doi. org/10.2307/2992183
- Glazer I, Santoiemma G, Battisti A, De Luca F, Fanelli E, Troccoli A ... Mori N (2022) Invasion of *Popillia japonica* in Lombardy, Italy: Interactions with soil entomopathogenic nematodes and native grubs. *Agricultural and Forest Entomology* **24**(4), 600–608. https://doi.org/10.1111/afe.12524
- Gotta P, Ciampitti M, Cavagna B, Bosio G, Gilioli G, Alma A ... Marianelli L (2023) *Popillia japonica*—Italian outbreak management. *Frontiers in Insect Science* 3(1175138), 1–12. https://doi.org/10.3389/finsc.2023.1175138

- Hammons DL, Kurtural SK and Potter DA (2010) Japanese beetle defoliation reduces primary bud cold hardiness during vineyard establishment. American Journal of Enology and Viticulture 61(1), 130–134. https://doi.org/10.5344/ajev.2010.61.1.130
- Henden J, and Guédot C (2022) Effect of surrounding landscape on Popillia japonica abundance and their spatial pattern within Wisconsin vineyards. Frontiers in Insect Science 2, 41. https://doi.org/10.3389/finsc.2022.961437.
- Kowles KA and Switzer PV (2012) Dynamics of aggregation formation in Japanese beetles, *Popillia japonica. Journal of Insect Behavior* 25, 207–221. https://doi.org/10.1007/s10905-011-9291-7
- Lessio F, Pisa CG, Picciau L, Ciampitti M, Cavagna B and Alma A (2022) An immunomarking method to investigate the flight distance of the Japanese beetle. *Entomologia Generalis* 42(1), 45–56. https://doi.org/10. 1127/entomologia/2021/1117
- Mondino EB, Lessio F, Bianchi A, Ciampitti M, Cavagna B and Alma A (2022) Modelling the spread of *Popillia japonica* Newman (Coleoptera: Scarabaeidae) from a recently infested area. *Entomologia Generalis* **42**(5), 713–721. https://doi.org/10.1127/entomologia/2022/1370
- Potter DA and Held DW (2002) Biology and management of the Japanese beetle. Annual Review of Entomology 47, 175–205. https://doi.org/10.1146/ annurev.ento.47.091201.145153
- Regniere J, Rabb RL and Stinner RE (1981) Popillia japonica: Effect of soil moisture and texture on survival and development of eggs and first instar grubs. Environmental Entomology 10(5), 654–660. https://doi.org/10.1093/ ee/10.5.654
- Régnière J, Rabb RL and Stinner RE (1983) Popillia japonica (Coleoptera: Scarabaeidae): Distribution and movement of adults in heterogeneous environments. The Canadian Entomologist 115(3), 287–294. https://doi.org/10. 4039/Ent115287-3
- Selli S, Perestrelo R, Kelebek H, Sevindik O, Travaglia F, Coïsson JD ... Bordiga M (2023) Impact of Japanese beetles (*Popillia japonica* Newman) on the chemical composition of two grape varieties (Nebbiolo and Erbaluce) grown in Italy. *Food Research International* 165, 112575. https://doi.org/10.1016/j.foodres.2023.112575
- Simonetto A, Sperandio G, Battisti A, Mori N, Ciampitti M, Cavagna B, Bianchi A and Gilioli G (2022) Exploring the main factors influencing habitat preference of *Popillia japonica* in an area of recent introduction. *Ecological Informatics* **70**, 101749. https://doi.org/10.1016/j.ecoinf.2022.101749