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Predicting the invasion risk of *Bactrocera dorsalis* in Italy under climate and land cover change

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***Bactrocera dorsalis*, the oriental fruit fly (OFF), is a highly polyphagous and multivoltine invasive insect threatening over 600 fruit crop species globally. Originating in Asia, OFF has spread to Africa, Europe, and the United States. This study assessed the current and future potential distribution of OFF in Italy, a likely entry point for its invasion into Europe. Climate and land cover changes projected for 2070 and 2100 were considered. Potential connectivity corridors were identified, and habitat suitability was evaluated within orchards and vineyards. Ecological Niche Models (ENMs) and connectivity analyses revealed a dramatic increase in suitable habitats for OFF under future scenarios. The potential distribution is projected to expand on average by over 1600% under mild conditions and over 7000% under severe conditions, up to 2100. Key environmental factors include mean temperature of the driest quarter, isothermality, precipitation during the driest months, and proximity to forests, urban areas, and roads. Our findings suggest a significant rise in OFF suitability within agricultural areas, particularly vineyards and orchards, posing increased risks to these sectors. Effective management strategies – possibly supported by ecological modelling such as this study – should focus on mass trapping, habitat management, and public awareness to mitigate and contain this pest's spread. These predictions are based on the working assumption that *B. dorsalis* is locally acclimatized in inland Campania, southern Italy. Although definitive evidence of establishment is still pending, repeated detections in the same area over four consecutive years support the use of Italian records in risk modelling as an early warning strategy.**

Keywords Invasive alien species, Agricultural pest, Invasion risk, Ecological niche models, Connectivity corridors, Global change.

Bactrocera dorsalis (Hendel) (Diptera: Tephritidae), also known as the oriental fruit fly (hereafter OFF), is an exceptionally polyphagous and multivoltine insect, which poses a substantial threat to more than 600 fruit crop species[1–3]. Due to its high invasive potential, the species was included in the priority list of relevant quarantine pests under Commission Delegated Regulation (EU) 2019/1702, for which annual surveys are required.

OFF host range include key commercial fruits such as mango, peach, orange, apple, apricot, fig, and guava, as well as wild and ornamental plants[4–7]. In Italy, recent field surveys confirmed active infestations primarily in *Citrus* spp., but OFF has also been associated with other cultivated fruits such as persimmon and peach[5]. This pest thrives in warm, humid environments, particularly in anthropized areas with mixed orchards, urban gardens, and road-adjacent habitat types[4,5]. The species is multivoltine, with overlapping generations throughout the warm season, and it can disperse actively over several kilometres[4,6,7].

Bactrocera dorsalis is a member of the oriental fruit fly (*B. dorsalis*) species complex, which was initially believed to be widely distributed across Asia. However, further studies narrowed down its native geographical distribution to continental Asian nations situated north of the Malay Peninsula[8–10]. Some introduced populations of *B. dorsalis* have also successfully established on the Hawaiian Islands[11,12]. The global invasive process of the *B. dorsalis* complex is ongoing and progressive, particularly speeding up since 2003, when the species invaded Sub-Saharan Africa from the coastal regions of Kenya[4,13,14]. These populations were originally attributed to *Bactrocera invadens* Drew, Tsuruta & White[15], though subsequent studies led to its reclassification as *B. dorsalis*[16–19]. After the invasion of a significant portion of the African continent, sporadic catches were documented in Europe,

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primarily within market areas or close to airports (EPPO, 2019/227[20]). Moreover, several specimens of *B. dorsalis* have been detected in the continental United States over time[21]. These findings have different explanations, as suggested by several studies, sparking a 40–years–long debate on this topic. Some authors believe that the captured individuals are the result of frequent and continuous reintroductions, while other authors propose that these specimens originate from a low-density population yet currently established in the United States[22–24]. Different and substantial tests have been presented to support both theories, and it is possible that both might be in operation simultaneously. Nevertheless, further evidence is needed to definitively corroborate or refute either hypothesis[21].

Captures of *B. dorsalis* in traps placed in open fields in Italy began in 2018[25]. This first evidence triggered strict surveillance efforts especially in Italy, which were followed by gradually increasing captures across various European nations[20,26–28]. These efforts did not provide evidence of continuous infestations or overwintering populations. Therefore, all captures from 2018 to 2019 were classified as incursions[28]. In addition, the onset of the Covid-19 pandemic during the biennium of 2020–2022 resulted in an interruption of captures, despite the high number of traps that were originally set[29]. In 2022, the number of commercial exchanges and passenger mobility returned to pre-pandemic levels[30], leading to an increased frequency of fruit fly detections in Italy and France[5,31].

Following the initial detection of an invasive species, the demarcation of the infested region was one of the key measures that should be defined[23,32–34]. The promptness of both detection and subsequent demarcation has a substantial impact on the success of eradication activities[33]. Demarcation is an important stage in determining the best method for eradicating or, at the very least, limiting invasive species[32]. Among the several actions outlined in the action plans, one crucial component is the establishment of a buffer zone that requires additional efforts in monitoring activity, particularly through increased deployment of traps and intensified visual inspections. At the same time, it is critical to exploit collected data to determine the most likely routes of distribution as well as to identify potentially suitable locations where invasive species could readily acclimatize. Interception and fast demarcation of the infested region can greatly improve the precision of containment and risk mitigation measures, particularly along potential invasion routes. Furthermore, this method allows for the most effective use of limited resources (such as traps and controls) to regulate an invasive process[35].

Given OFF remarkable dispersal ability and capacity to exploit diverse environments, early detection and rapid response are pivotal to prevent establishment and minimize impacts. Effective management strategies rely on accurate knowledge of potential distribution and spread pathways. Currently, available control options in Europe focus mainly on monitoring, sanitation measures, and attract-and-kill techniques. Moreover, European agricultural policies are increasingly oriented towards reducing the use of synthetic products, further highlighting the need to explore sustainable and environmentally sound alternatives. Although some parasitoid species have demonstrated high efficacy in integrated pest management programs elsewhere, the introduction of new biological control agents in Europe remains highly constrained by stringent regulatory frameworks and the requirement for comprehensive risk assessments. These limitations currently hinder the practical application of classical biological control against invasive fruit flies[36–38].

As for the prediction of *B. dorsalis* geographic distribution in non-native areas, several studies recognized its high invasion risk[12,39,40]. For instance, early modelling efforts made use of the semi-mechanistic CLIMEX model trained considering the seasonal phenology of the pest[12]. Other approaches relying on correlative models (e.g. GARP and Maxent) were also implemented using established occurrence records originating from Africa and Asia[41]. The outcomes of these projections indicate that *B. dorsalis* tends to flourish under conditions of elevated heat and humidity, making it particularly adapted to equatorial climates. The CLIMEX approach proposed by Stephens et al.[12] was further refined by accounting for the potential influence of irrigation on *B. dorsalis* distribution, in combination with seasonal phenology parameters (i.e., temperature, moisture, cold, dry, and heat stress), to generate a distribution risk map[39]. Mostly, all these modelling efforts highlight OFF potential ability to overwinter in climatic circumstances like those occurring in temperate European countries[42,43]. In consideration of that, additional recent evidence emphasized *B. dorsalis* as a serious threat, due to its potential to form viable populations in numerous southern European locations[4], likely leading to its establishment in Europe.

Therefore, all the assessments of OFF potential distribution in Europe have relied on data collected from populations in native regions or from populations that have invaded other territories but not in Europe[4,39]. Moreover, considering the different species and populations ascribed to the *B. dorsalis* complex, each with likely distinct biological traits and environmental preferences, it is imperative to evaluate the potential distribution and spread pathways of this species in European countries. Furthermore, since climate and land cover alterations are known to affect invasion risk patterns[44,45], it is of crucial importance to assess if and how these global change drivers might have a boosting or detrimental effect on *B. dorsalis* invasibility, both in terms of potential suitable habitat and connectivity corridors. Since Italy is expected to act as a primary bridgehead for OFF populations to potentially invade Europe[46], we considered this country as an experimental ground where to set out an Ecological Niche Modelling (ENMs) effort, in combination with landscape connectivity analysis, to predict current and future species distribution and spread potentialities. Therefore, a study encompassing the following objectives is proposed:

(1) Assessing *B. dorsalis* current and future potential distribution in Italy under climate and land cover change scenarios as forecasted for 2070 and 2100, identifying which environmental factors are most strongly involved in shaping species distribution;
(2) Generating potential current and future connectivity corridors for OFF in Italy, as to identify which portions of predicted suitable patches are likely reachable by the species due to natural spread;

(3) Quantifying the impact of future climate and land cover change on OFF distribution and connectivity by calculating range net change, percentage of connected suitable habitat, number of connectivity corridors per patch and length of connectivity corridors;
(4) Quantifying current and future OFF habitat suitability within reachable orchards and vineyards in Italy, as to assess potential impacts on agricultural productions.

Results

Ecological niche models

Both global and regional ENMs achieved good–to–excellent predictive performances, as defined by Swets[47]. Under spatial block cross–validation, mean AUC (Area Under the Curve of the Receiver Operating Characteristic) values were 0.835 (SD = 0.122) and 0.987 (SD = 0.013) respectively. Values of mean Continuous Boyce Index (CBI) were 0.99 (SD = 0.002) for global ENMs and 0.878 (SD = 0.124) for regional ENMs. When tested against independent plots, AUC and CBI values confirmed excellent predictive performances. They scored 0.989 and 0.960, respectively. Regional ENM variable importance indicated mean temperature of the driest quarter, precipitation of the driest month, and isothermality as the three most important climatic variables, while distance from forests, urban areas, and roads emerged as the three most important land cover variables (Fig. 1). In particular, OFF most suitable habitat is characterized by hot and rainy forested areas close to roads and urban zones of the study area (Fig. 1 and see Fig. 6 in "Methods" section).

Climate and land cover change effect on *B. dorsalis* invasion risk.

Suitable areas for *B. dorsalis* predicted for the current time are mostly restricted to small areas in the Campania region, with some potentially suitable enclaves found toward the Southern–Adriatic side of the Italian Peninsula (Fig. 2).

Regional ENM projections on future climate and land cover scenarios indicate a dramatic increase in the potentially suitable areas for the species by 2070, and even more so by 2100. Specifically, *B. dorsalis* is predicted to expand its mean potential distribution by more than 1600% under the mild scenario in both 2070 and 2100, whereas this increase exceeds 5000% under the severe scenario in 2070 and reaches up to 7000% in 2100, with significant differences between the scenarios (Fig. 3a; see also Figs. S1 and S2).

As for connectivity analysis, the current time predictions showed most of the suitable patches being reachable via the same corridor groups under all the binarization threshold combinations, though the potential connectivity is mainly oriented toward South–East (Figs. 4a and 5a; see also Supplementary Figs. S3–S6).

Under the mild climate and land cover change scenarios, several corridors were predicted to link suitable patches along most of the Southern–Tyrrhenian side of Italy by 2070, where most combinations of binarization thresholds and GCMs coherently individuated easily reachable patches. According to this scenario, some corridors link patches toward the Northernmost areas of the Apennine chains (Fig. 4b). Under the severe climate and land cover change scenarios, OFF is predicted to find potential connectivity corridors along the entire Tyrrhenian side of Italy, linking most of the suitable patches located from the coast to the Apennine chain (Fig. 4c). This trend applies also to 2100 predictions, albeit showing an overall greater magnitude (Fig. 5b and c). In particular, some combinations of binarization thresholds and GCMs even predict corridors reaching the Northernmost regions of Italy up to the Alps (i.e., Piedmont, Valle d'Aosta, and Veneto regions; Fig. 5c).

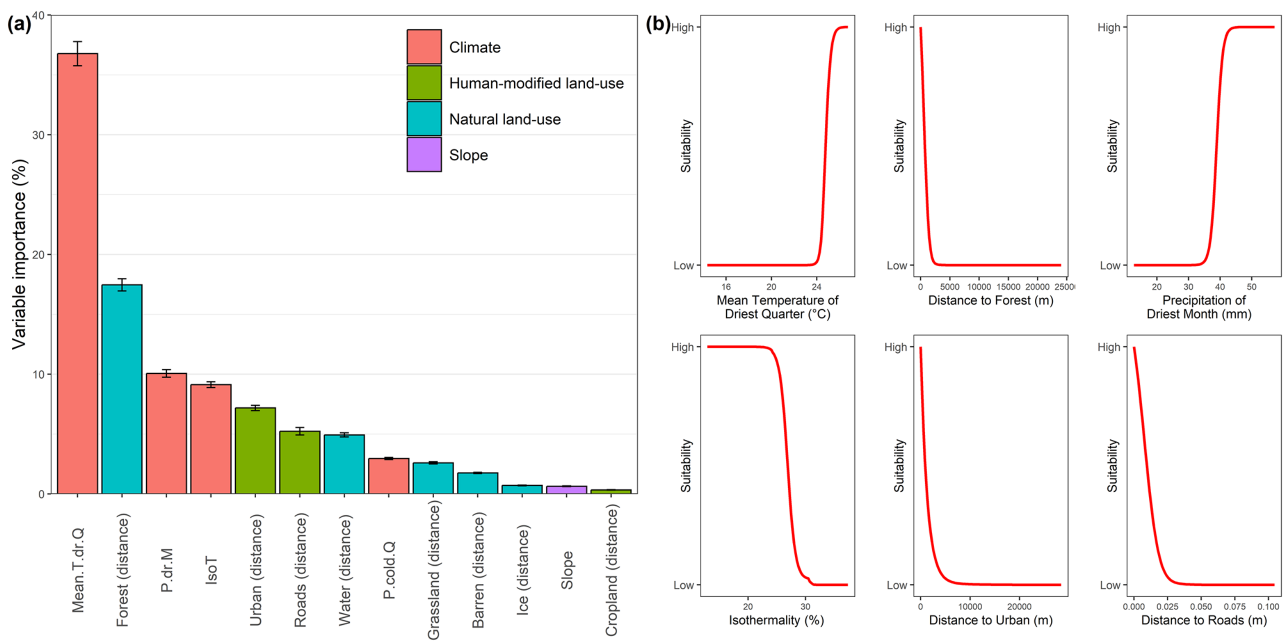

Fig. 1. Variables importance (**a**) and response curves (**b**) as generated by regional ENMs.

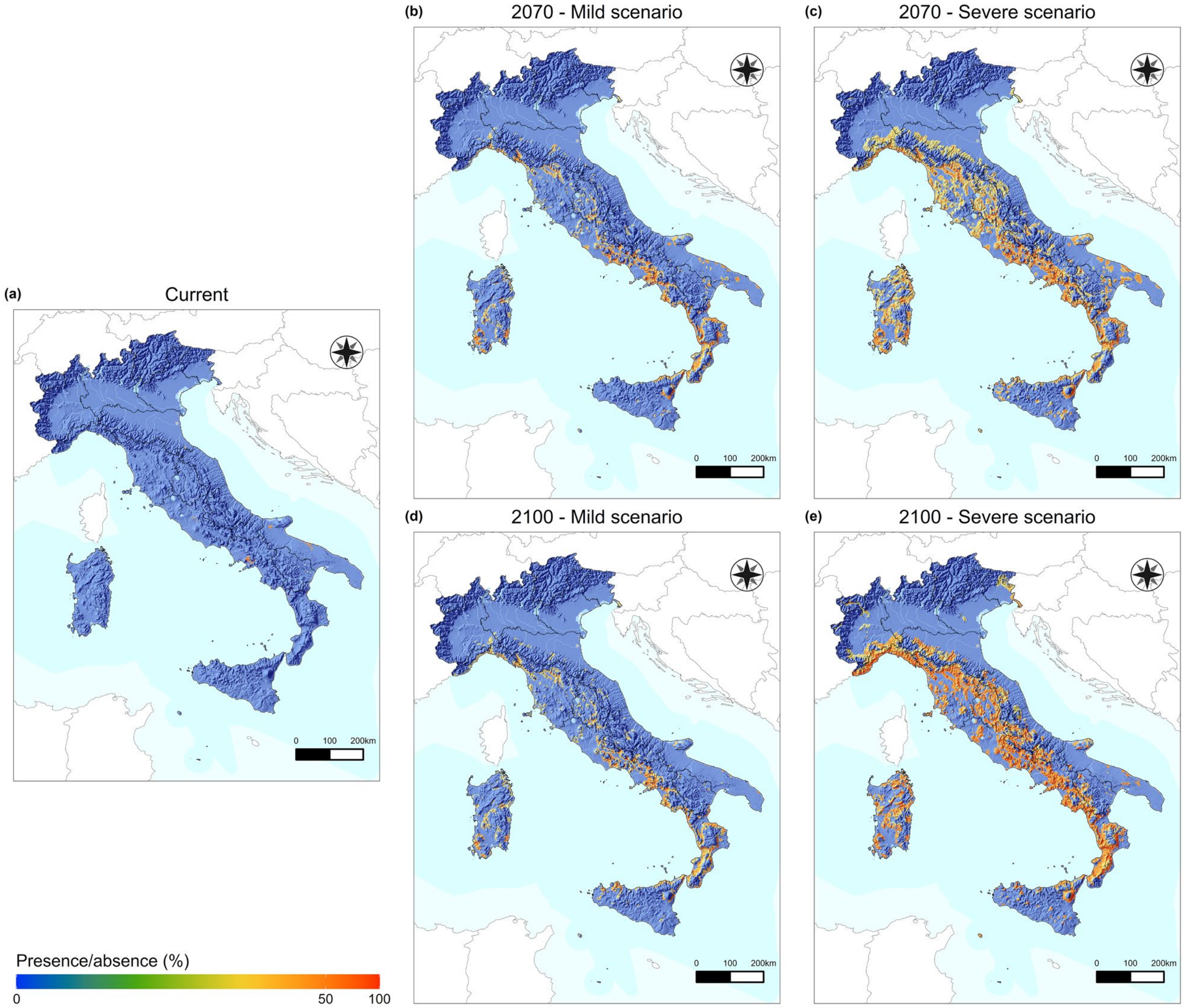

Fig. 2. Overlay of the *B. dorsalis* binary distribution maps generated by regional ENMs for the current time (**a**), 2070 (**b**, **c**) and 2100 (**d**, **e**). Panels labelled with "(**b**)" and "(**d**)" report predictions under the mild climate and land cover change scenario, while the "(**c**)" and "(**e**)" panels refer to predictions under the severe one. Red (blue) colours indicate pixels of predicted presence by a high (low) percentage of binarization threshold and global circulation model combinations and are depicted with a logarithmic colour ramp.

Climate and land cover change are predicted to dramatically increase potential connectivity corridors for *B. dorsalis* in Italy. Specifically, the percentage of patches reachable via connectivity corridors increased from approximately 70% under current conditions to about 87% and 92% under the mild and severe scenarios, respectively, according to projections for 2070. These figures reach up to ca. 95% and ca. 97%, for 2100 predictions (Fig. 3b). Similarly, the number of corridors per patch increased from ca. 2 on average, under the current time predictions, to ca. 25 under the mild scenario and ca. 18 under the severe one in 2070. This statistic showed marginally lower values for 2100 predictions, with ca. 16 under the mild scenario and ca. 15 under the severe one (Fig. 3c). As for the corridor length, we found an increase from ca. 200 km on average, under the current time, to ca. 600 km and ca. 800 km in 2070, under the mild and severe scenarios, respectively. Similar statistic values were detected for 2100 as well (Fig. 3d).

Lastly, as for *B. dorsalis* suitability values within reachable orchards and vineyards, we found an apparent increase from a baseline value of ca. 0.10 for the current time to values between ca. 0.45 and 0.58, depending on time step and scenario (Supplementary Fig. S7).

Discussion

The present study highlighted the potentially dramatic invasion risk posed by the first detected population of *B. dorsalis* in Italy. If the forecasted risk appeared low under current time predictions, future climate and land cover change scenarios – especially the most severe ones – will likely provide an enormous amount of potentially suitable and reachable habitat patches, exposing almost the entire Italian Peninsula to its spread. The high habitat

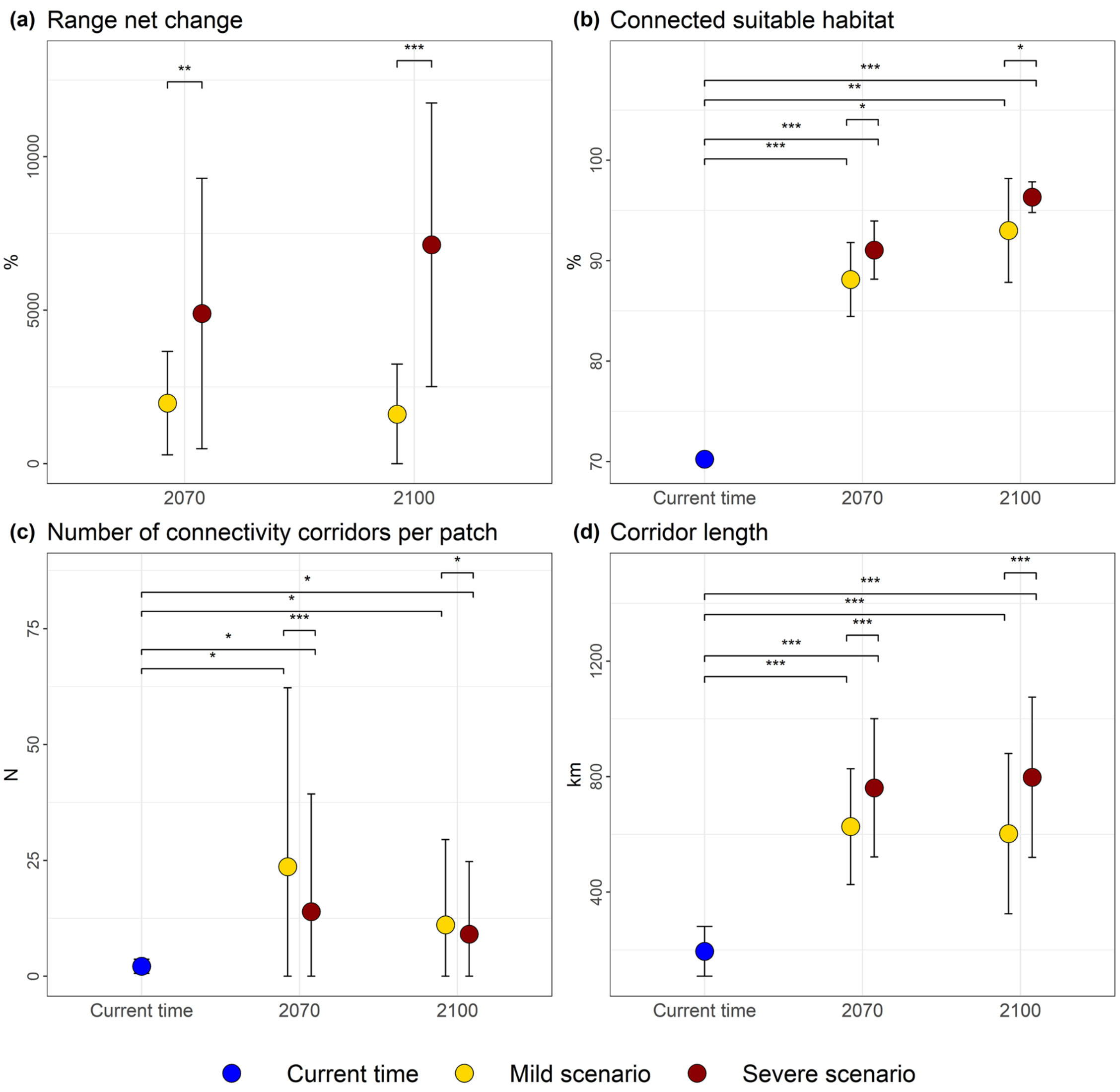

Fig. 3. Statistics calculated on *B. dorsalis* binary distribution maps generated by regional ENMs and connectivity analysis. Panel "(**a**)" depicts the range net change values calculated on binary distribution maps. The plots in the other panels summarize the percentage of connected suitable habitat (**b**), the number of connectivity corridors per patch (**c**) and the connectivity corridor length (**d**), as calculated under the "nearly linear" suitability–to–resistance transformation (see text). Each plot reports the mean value for each statistic, along with the standard deviation representing the variation across the five global circulation models and the four binarization thresholds. Differences in mean statistic values were tested via permutational ANOVA, depicting statistical significance using the following notation: "ns" – not significant; "*" – $p < 0.05$; "**" – $p < 0.01$; "***" – $p < 0.001$.

suitability predicted for the species within vineyards and orchards appears particularly concerning, regardless of the tested scenarios.

Our forecasts indicate a low suitability within the Italian territory in the short term, in contrast to previous studies that highlighted a high invasion risk in this area[4]. This reduced risk under current conditions reflects the climatic limitations still present across much of the Italian territory. In particular, suboptimal values of isothermality and limited rainfall during the dry season hinder the establishment and survival of the species. However, the modelling framework explicitly incorporates future climate and land cover change projections, which predict an increase in average temperatures and change in precipitation patterns that are more favourable to the species. These changes result in a substantial expansion of suitable and reachable areas for *B. dorsalis* under both future scenarios. This outcome aligns with broader climate change projections for Italy, which foresee increased temperatures and altered precipitation regimes that could progressively favour the establishment of tropical and subtropical species. In this context, our results emphasize that both ongoing and future climatic trends may act as key drivers enabling the persistence and spread of *B. dorsalis*, even in areas that are currently suboptimal. Indeed, these predictions were based on data from the period 1990–2007, which may have hampered

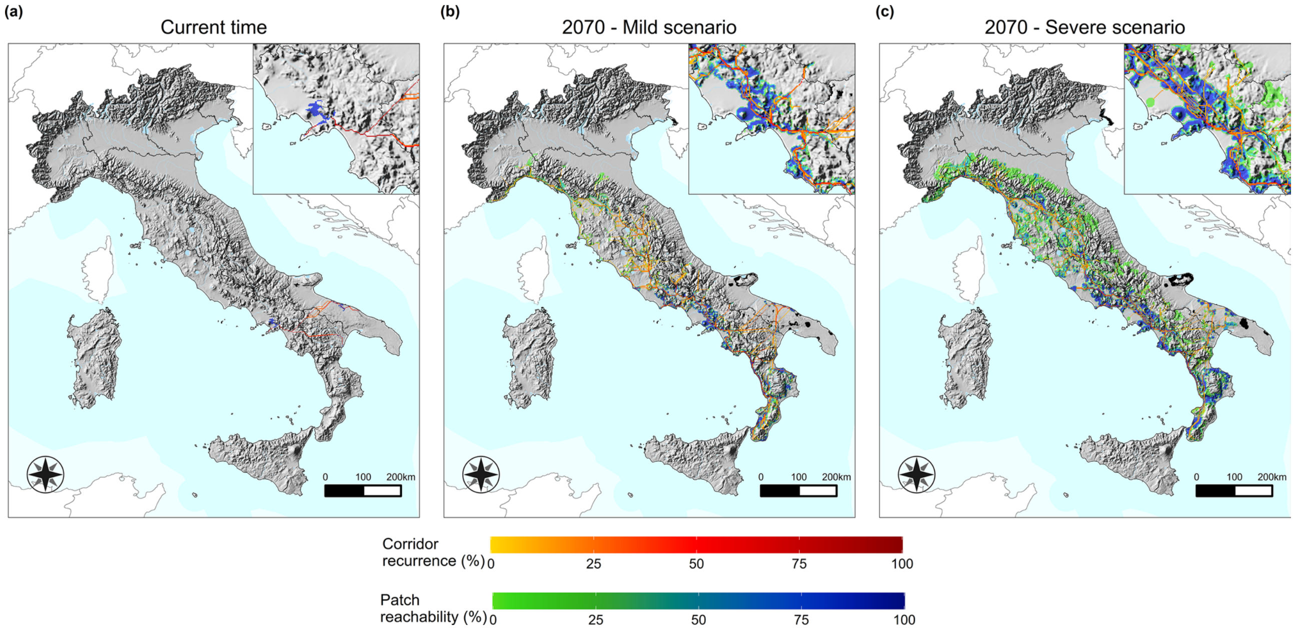

Fig. 4. Connectivity corridors and degree of patch reachability for *B. dorsalis* as derived by Circuitscape analysis considering the "nearly linear" suitability–to–resistance transformation (see text), for the current time (**a**) and 2070 under the mild (**b**) and severe (**c**) climate and land cover change scenarios. Red (yellow) colours indicate corridors that resulted among the most important ones (i.e., those passing through mean conductance values above the third quartile of the conductance values of the entire network) in a high (low) percentage of binarization thresholds and global circulation models combinations. Similarly, blue (green) colours refer to patches that are reached by the most important corridors in a high (low) percentage of binarization thresholds and global circulation models combinations. Patches in black were not reached by any important corridor. Insets in the upper right corners depict a zoom on the Campania Region, where most OFF detections occur.

model reliability due to quite outdated occurrence and environmental information. In any case, all the most recent modelling efforts are coherent in projecting an increase in habitat suitability over the coming years (e.g., Ullah et al.[48]), as similarly shown by our results for Italy. This pattern aligns with the tropical origin of *B. dorsalis* and supports the findings of Ullah et al.[48], who highlighted the importance of the average temperature during the warmest season. According to ENM predictions, habitat suitability in the Italian territory is influenced by climate, particularly when the average temperature during the dry season reaches at least 24 °C. Habitat suitability is further favoured by temperature values steadily within the larval development range (i.e., between 9.7 and 31.3 °C[49]). In addition, such specific environmental tolerance could explain the initial infestation findings in Campania, within an area sheltered between two mountains, i.e., Mount Vesuvius and Mount Sant'Angelo, protected from strong winds and with limited air movement (see Fig. 6 in "Methods" section).

Our results indicated that areas close to forests play a crucial role in determining OFF habitat suitability. Specifically, areas with active infestations and high catch rates are situated close to the Crocelle Natural Park. This area is characterized by a humid forested area with mixed assemblages of both thermophilous and mesophilous plants, including trees such as *Quercus ilex*, *Castanea sativa*, and *Fagus sylvatica*. Although these species are not commonly reported among the primary hosts of *B. dorsalis*, the park provides favourable microclimatic conditions, such as high humidity generated through evapotranspiration[50], which appear suitable for the ecological requirements of the species. In addition, the species is highly polyphagous and can develop on more than 600 plant species[6]. This wide range of usable hosts may compensate for the absence of preferred fruits and support the persistence of populations even in areas where suitable fruit species are limited. In addition, proximity to forests can also act as a buffer against high temperatures[50–52], which could easily exceed the temperature range considered most favourable for the species (20–30 °C[53]). In fact, while maximum temperatures recorded during summer in the infested zone are markedly higher than 30 °C (Authors pers. comm.), OFF survival mostly depends on exposure duration and habitat heterogeneity. Forest proximity may improve survival chances by providing shaded and humid microhabitats, which mitigate thermal stress[54]. This interpretation is consistent with the findings of Hoskins et al.[55], who highlighted that vegetation structure and the availability of moist refuges within heterogeneous landscapes play a key role in enhancing fruit fly survival under high-temperature conditions.

Rainfall during the driest months emerges as a third important variable, with low humidity adversely impacting OFF habitat suitability. This finding aligns with results from other studies[39,49], which emphasize the importance of irrigation in supporting OFF survival in dry climates. According to Hoskins et al.[55], moisture availability, including that from irrigated or vegetated areas, is essential to counteract desiccation stress. The relatively small amount of rainfall in the infested zone during the dry summer period seems to further support the importance of proximity to the forest for OFF survival.

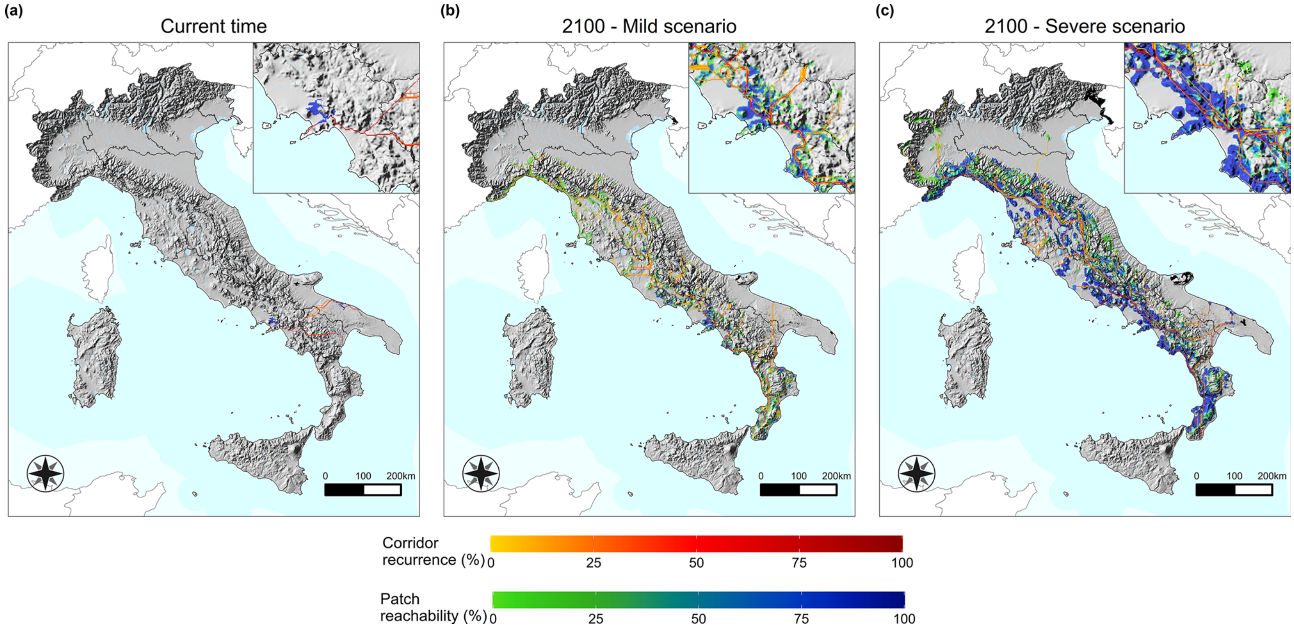

Fig. 5. Connectivity corridors and degree of patch reachability for *B. dorsalis* as derived by Circuitscape analysis considering the "nearly linear" suitability–to–resistance transformation (see text), for the current time (**a**) and 2100 under the mild (**b**) and severe (**c**) climate and land cover change scenarios. Red (yellow) colours indicate corridors that resulted among the most important ones (i.e., those passing through mean conductance values above the third quartile of the conductance values of the entire network) in a high (low) percentage of binarization thresholds and global circulation models combinations. Similarly, blue (green) colours refer to patches that are reached by the most important corridors in a high (low) percentage of binarization thresholds and global circulation models combinations. Patches in black were not reached by any important corridor. Insets in the upper right corners depict a zoom on the Campania Region, where most OFF detections occur.

As for isothermality (i.e., the ratio between diurnal to annual thermal range), our models highlighted OFF to prefer mid–to–low values. This means the species prefers areas with small diurnal temperature ranges along with moderate annual thermal variation. This pattern seems coherent with the well-known thermal preferences of *B. dorsalis*, both in terms of longevity and egg laying capability. In fact, Choi et al.[56] proved that female OFF exhibited the highest longevity at ca. 19 °C, which steeply reduces above 30 °C. Similarly, female reproductive performance (i.e., number of laid eggs) peaks between 20 °C and 30 °C, while it basically stops below 15 °C and above 35 °C[56]. Similar outcomes were provided also by Dongmo et al.[53]. In any case, the thermal preferences identified in our results may serve as a proxy for the temperature requirements–and, consequently, the geographic distribution–of *B. dorsalis* host plants, which strongly influence the seasonal population dynamics of this species complex[57].

Although with a lower magnitude, distance from urban centres is inversely correlated to OFF habitat suitability. Urban areas offer warmer and more stable temperatures compared to rural orchards[58]. Furthermore, neglected urban gardens often harboured uncontrolled host plants, providing undisturbed environments for OFF development[59]. Arguably, repeated introduction of infested fruit imports into luggage by people arriving from OFF native areas (like e.g., Bangladesh, whence about 13% of the population of Palma Campania originates[60]), might also play a role in making urban areas particularly prone to OFF spread. At the same time, irrigation practices in rural orchards can compensate for low summer rainfall and create favourable microclimatic conditions for OFF development, enhancing the suitability of these areas despite their greater distance from urban centres. Lastly, proximity to roads showed a moderately important, inverse relationship with OFF habitat suitability, recalling the well-known role played by road networks as a major pathway easing both plant and animal alien species spread[61–63].

According to the spatially explicit predictions generated by our models, Southern Italy appears more prone to the expansion of *B. dorsalis*. Considering this, the low invasion risk predicted for Emilia-Romagna (Northern Italy) can be interpreted as evidence that the adult specimens trapped in this region during 2022–2023[26,27,64] may not pose a significant threat. This hypothesis is partially supported by the revocation of the delimited zone in Imola[64], following the absence of captures for over a year. By 2100, climate and land cover alterations are predicted to make several new areas across most of Italy suitable and reachable by OFF. These changes also highlight the increasing importance of orchards and vineyards as invasion hotspots. Furthermore, the apparent role of urban areas (including private gardens), roads, and semi–natural elements such as orchards and vineyards in shaping OFF habitat suitability also contributes to the expansion of potential connectivity corridors, as projected for 2070 and 2100. These landscape features may act as steppingstones, facilitating movement across the landscape. Specifically, on private gardens, Ullah et al.[48] highlighted a clear co-occurrence between suitable areas for citrus cultivation and *B. dorsalis* development. The frequent presence of private gardens and orchards with citrus plants throughout the infested zones in Campania (Authors, pers. comm.) may highlight the significant vulnerability

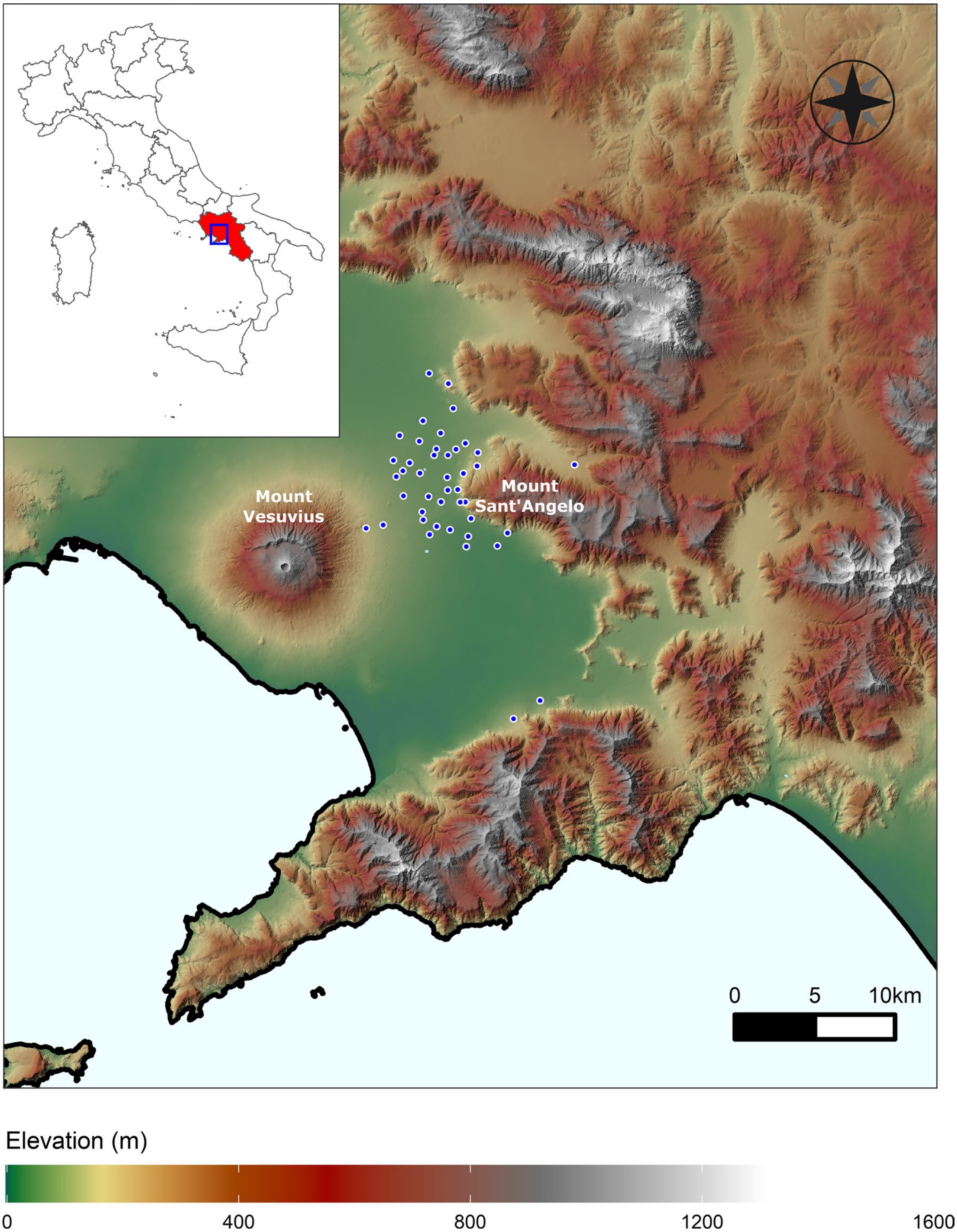

Fig. 6. Study area and occurrence records (blue dots) used to calibrate regional ENMs. The background elevation map was derived from https://srtm.csi.cgiar.org/)

of these areas to OFF spread and establishment. Irrespective of specific host preferences, the high polyphagy of the species – combined with its ability to readily complete its life cycle on crop fruits such as tomatoes and peppers[4] – suggests that greenhouse cultivations of these crops may serve as reservoirs or overwintering sites for OFF. However, it is important to note that farm management could also represent a relevant factor in affecting OFF presence (e.g., pesticide use). Nevertheless, the extreme fragmentation of properties (i.e., orchards typically smaller than 1 ha), their predominantly family–run nature, and the considerable variability in crop management practices across the region, make this factor difficult to assess or utilize effectively. Based on current conditions, eradication does not appear to be a realistic objective. The species showed a more than one hundredfold increase in trap captures within less than two months from the first detection, which proves its spread speed and the difficulty of any eradication campaign[5]. A final necessary consideration is that there is ample evidence and numerous studies demonstrating the ability of fruit flies to acclimate and develop tolerance to extreme weather. These physiological and genetic adaptation capabilities enable tephritid fruit flies to expand their geographic range[65–67]. Among these species, *B. dorsalis* likely possesses the greatest genetic potential for adaptation due to the high number of genes encoding heat shock proteins (*Hsps*)[68]. However, including such a variable in ENMs is hardly feasible. It is important to note that the OFF population in Italy, subjected to intense selection pressures during winter, may develop or be selected for overwintering capability. Recent genomic studies further support the high adaptive potential of *B. dorsalis*[68]. reported expansions in gene families involved in stress response, including heat shock proteins and MAPK signalling components. These molecular features contribute to the ecological plasticity of the species and may facilitate selection for increased cold tolerance in temperate regions. As the population size grows, the likelihood of such adaptations increases. Nonetheless, the sharp decline in captures during the years 2023–2024 suggests that this trend could be not ongoing as of now.

The absence of true diapause in *Bactrocera dorsalis* may limit its ability to survive cold seasons in temperate regions. This factor was not explicitly incorporated into our ecological niche modelling approach, which relies on species occurrence data and environmental correlations. However, recent studies have reported that some *Bactrocera* species, including *B. dorsalis*, may undergo temporary reproductive arrest under unfavourable environmental conditions. This mechanism differs from physiological diapause in that it does not involve a complete shutdown of metabolic activity, yet it may still contribute to the species' persistence during cold periods[69]. Such a reversible arrest, distinct from true diapause, may enable survival during times of low temperature or limited host availability, even in the absence of active reproduction.

In keeping with this, field monitoring conducted in Italy from 2022 to 2025 revealed that, although captures ceased entirely for approximately five to six months during winter, the species reappeared each year within the same confined area. These patterns suggest that *B. dorsalis* could persist locally through overwintering in a non-reproductive state or at low, undetectable densities. Such dynamics are not captured by correlative ENM approaches, which do not incorporate physiological constraints. However, this biological background reinforces the interpretation of our projections as conservative, and supports the view that establishment remains conditional on climatic and ecological thresholds.

OFF spread could also be facilitated by human intervention. The human–assisted movement of infested host plant materials and soil could serve as an additional means of long–range dispersal. Eggs and larvae may be present inside infested fruits, while puparia could be found in the soil. Before restrictions were implemented on handling the infested zone, a documented case of infested fruit movement led to the arrival and detection of infested fruits 7.67 km away[28]. However, starting in early 2023, restrictions were introduced in Italy on the handling of fruit, soil, and potted plants according to the official Regional Government Resolution of Campania (DGR n. 714 of 20/12/2022)[70]. As a result, this diffusion mode has currently become unlikely. Nevertheless, given the potential for further spread, the risk persists and could play a decisive yet unpredictable role in the invasive process in Italy in the coming years.

We utilized spatially explicit predictions yielded by ENMs to rearrange the trap distribution in the Campania region in 2023. Several traps were strategically placed along potential connectivity corridors throughout the region (see insets in Figs. 4 and 5). Accordingly, ENM results could profitably be used to guide the implementation of national monitoring plans by the phytosanitary services, as to allow a better trap positioning along with a more efficient resource allocation. This could ensure an effective monitoring implementation, also preventing the current infestation in Italy to act as a bridgehead for further infestations in other European countries. The management of new invasive processes of *B. dorsalis* has already been addressed by several researchers, with well–defined guidelines for trapping in surveillance areas and established criteria for its management[14,71–74].

It is also important to mention that, starting from 2023, the enforcement of strict regulations on fruit movement, supported by a formal agreement with the Italian Forestry Corps of the Carabinieri, has substantially reduced the likelihood of human-assisted spread. For this reason, the invasion path described in this study is expected to represent the natural dispersal pattern of the species. Due to the current ban on the movement of fresh fruit outside the infested zone, which is rigorously enforced, the risk of *B. dorsalis* reaching the islands of Sicily or Sardinia via human-mediated pathways is considered low. Consequently, these islands were excluded from the connectivity analysis, which was restricted to modelling natural dispersal through suitable and connected habitats.

The current management of the new invasive process of *B. dorsalis* worldwide often relies primarily on Male Annihilation Technique (MAT) and Bait Attractant Technique (BAT). These techniques involve the simultaneous use of high-density bait stations containing either a male lure (methyl-eugenol) (ME) combined with an insecticide, or a food-based bait combined with an insecticide[75–77]. The density of bait stations should not exceed 110 per km^2 to avoid a reduction in effectiveness[78]. However, this approach is particularly challenging in Italy and Europe due to the adverse effects of ME on human health. The Scientific Committee on Food of the European Commission classified ME as both genotoxic and carcinogenic, as it induced liver and gastric tumours in rodents even at low doses (≥ 37 mg/kg body weight/day). Moderate systemic toxicity, including liver damage, was observed from 30 mg/kg body weight/day. No safe threshold for human exposure was established, and restrictions on its use were recommended[79] Moreover, significant limitations apply to the use of insecticides in urban areas, which further complicates this approach in European urban settings and especially in Italy, where the infestation occurs primarily in urban and suburban zones. In addition, the ecological impact of trapping strategies varies according to the type of trap employed. Protein-based baits are specifically formulated to attract tephritid fruit flies and generally involve a limited risk for other insect communities. However, the level of trap selectivity remains an essential consideration. Preliminary findings from a comparative study currently in progress suggest that McPhail traps are highly selective, capturing almost all fruit-infesting tephritid species recorded in Italy but *Rhagoletis cerasi*, and result in minimal incidental catches. In contrast, yellow sticky traps, while effective against all tephritids, also capture a wide variety of non-target insects, including hymenopterans and other beneficial groups. Although this issue is outside the main scope of the present study, these differences should be carefully evaluated when planning monitoring or control activities, particularly in urban areas or environments with high ecological value. Therefore, the use of male annihilation would ensure the best results while maintaining the lowest cost within other operational and regulatory considerations. This implies that the optimal strategy within the current framework of European legislation essentially involves the following measures to control this invasive species:

(1) Regulating the movement of host fruit beyond the infested zone. In fact, fruit movement by humans has been identified as the primary threat to rapid and extensive spread of the pest, given the exceptional OFF diffusion capabilities[4,80]. However, this measure entails significant management costs both socially (as it may disrupt entire economies reliant on fruit production) and in terms of public controls (requiring extensive monitoring to ensure compliance with the ban on handling).
(2) The use of traps baited with methyl–eugenol, torula–yeast, or protein baits is essential for mass capturing of the pest. Therefore, it is crucial to have a thorough understanding of the territory and identify ecological corridors exploited by the species for spreading. This knowledge enables the strategic placement of these costly traps in the most suitable areas for effective pest control.
(3) Collection and destruction of infested fruits that have fallen to the ground. The species predominantly overwinters as puparium stage in areas with a climate similar to Italy, primarily within the soil but also, to a lesser extent, in infested fallen fruits[81]. Implementing this measure is relatively straightforward in agricultural environments and is a fundamental aspect of proper crop management. However, it becomes challenging in urban settings, where isolated plants in fenced gardens necessitate a whole different approach. Therefore, if the climatic conditions allow establishment, containment acts only as a measurement able to slow down the spread of the pest. However, it is important to note that most countries with climates suitable for fruit flies have either implemented quarantine restrictions on fruit imports or mandatory phytosanitary treatments for all imported fruits[82]. Hence, containment of the species emerges as the only viable solution, albeit with substantial costs.
(4) Treatments with insecticides. If chemical treatments were applied promptly in conjunction with the start of OFF flights, and if they were applied with suitable precautions, they could make fruits marketable by lowering the risk of human–mediated spread to an acceptable level. However, this approach entails very high direct and indirect economic costs.

Our results should be interpreted considering three main caveats. First, the use of Italian occurrence data in this modelling effort is based on the assumption that the population detected in inland Campania has acclimatized to local environmental conditions. Although definitive evidence of successful overwintering is not yet available, *B. dorsalis* has been consistently recorded in the same limited area over four consecutive years (2022–2025), with evidence of local reproduction in multiple years[5]. This persistence, in the absence of additional detections across the region despite repeated monitoring, supports the hypothesis of a localized and potentially adapting population. A similar uncertainty has long characterized the situation in California, where repeated detections of *B. dorsalis* since the 1960s have raised debate about whether the species persists at low densities or is periodically reintroduced[83,84]. In this context, delaying the implementation of surveillance and containment strategies until irrefutable proof of establishment becomes available would be both scientifically and operationally unwise. The precautionary approach adopted in this study is consistent with previous modelling efforts that explored invasion dynamics under conditions of uncertain establishment. Recent findings on climate-associated shifts in allele frequency in *Ceratitis capitata* suggest that tephritid fruit flies may exhibit rapid genetic responses to environmental pressures during the early stages of invasion[85]. The modelling framework presented here aims to anticipate areas at risk and to support the implementation of effective monitoring systems, even when establishment evidence is limited or ambiguous.

Second, while human-mediated transport remains an important pathway for long-distance dispersal, the connectivity analysis conducted in this study focused exclusively on the potential for natural spread through suitable and connected habitats. This approach allowed us to identify ecological corridors that could facilitate range expansion following accidental introduction events, and to support risk-based allocation of surveillance resources.

Third, in this study, suitability is inferred from landscape–level environmental variables rather than from direct measurements of internal habitat characteristics such as fruit species composition or resource availability. Accordingly, any potential habitat characteristic represented at a finer spatial resolution than the one we used (e.g., hedgerows, forest fragments) are not directly modelled due to scale limitations. Although the modelling approach used in this study is correlative and does not incorporate physiological mechanisms, it is supported by reliable occurrence data and ecologically meaningful environmental predictors. Models based on phenology or physiological thresholds, such as CLIMEX, may offer complementary information when biological parameters are well known. In the absence of complete physiological datasets for the populations detected in Europe, we opted for a correlative approach that provides robust and spatially detailed predictions of habitat suitability under different scenarios. This methodological choice was explicitly made considering the exploratory scope of the study and the absence of validated physiological thresholds for *B. dorsalis* populations recently detected in Europe, as previously discussed.

Conclusions

This study underscores the dramatic invasion risk potentially posed by the first population of *B. dorsalis* in Italy, particularly considering climate and land cover changes forecasted by 2100. While current projections suggest a limited risk, future scenarios indicate a substantial expansion of suitable habitat patches and connectivity corridors, potentially exposing the entire Italian Peninsula to the pest spread, especially considering its high suitability within vineyards and orchards. The overall low risk predicted for current time diverges from previous studies, which reported a higher suitability for *B. dorsalis* in Italy, whereas our results substantially align with projections of increasing suitability over time. Despite different methodologies, all the predictions coherently indicate a steeply increasing trend in suitability, with potentially severe implications for Italian agricultural production.

Given the challenges posed by the current strict regulations on insecticides and fruit movement, effective containment measures must prioritize mass trapping, habitat management, and public awareness. Implementing these measures, alongside international cooperation, and strict phytosanitary regulations, is essential to mitigate the threat of *B. dorsalis* and safeguard agricultural and environmental ecosystems across Europe.

However, it is important to consider that OFF, like many other fruit fly species, exhibits high level of genetic adaptability to thermal stress, potentially enabling the rapid selection of populations better suited to Italian and European climatic conditions.

Methods

Analytical framework

To assess the effect of climate and land cover change on the invasion risk of *B. dorsalis* in Italy, we modelled its potential distribution and connectivity corridors under current environmental conditions and projected changes in range and connectivity under two climate and land cover scenarios for 2070 and 2100. In particular, since the study area (Fig. 6) encompasses just a small fraction of the global range of *B. dorsalis*, ENMs were calibrated using a hierarchical structure, namely from global to regional scales[45,86], as to avoid truncated niche estimations[87,88]. Accordingly, a first group of ENMs was trained considering the global species range and bioclimatic predictors. Then, we calibrated a second set of models, refining global scale projections at the study area level (i.e., Italy; regional ENMs). Connectivity analysis was carried out by deriving input resistance surfaces from current and future suitability maps generated by regional ENMs.

Species occurrence data

Global ENMs were calibrated relying on occurrence data gathered from both native and invasive OFF range[45,89,90]. Occurrences were collected from the "Global Biodiversity Information Facility" (GBIF) database. The accuracy of records derived from GBIF was evaluated by retaining only records provided to at least two decimal places (0.01 decimal degrees, i.e., 1.11 km at the equator) and by filtering out duplicated data and those with unrealistic coordinates.

As for the regional ENMs, occurrence data at local scale were gathered following the methodology outlined in Nugnes et al.[5]. Specifically, traps of different types [i.e., McPhail and yellow sticky traps (Rebel Amarillo and Wing)] were placed in the Campania region from 2018 onwards. McPhail traps were baited with either methyl-eugenol or Torula yeast, while sticky traps were exclusively baited with methyl-eugenol. The number of sampling sites changed over the years, reaching 343 in 2022. Traps were inspected weekly and collected specimens were identified following the methodology described in Nugnes et al.[25].

To prevent any possible effect of sampling bias in occurrence records, we filtered data for both global and regional ENMs by applying the spatial thinning procedure implemented in the "spThin" R package[91]. The procedure relies on a randomization approach to return a dataset including the maximum number of occurrence records separated by a user-defined minimum neighbour distance. A minimum thinning distance of 100 km was set for global ENMs and 2.5 km for regional ENMs for *B. dorsalis*. Different thinning distance values were also tested, and the resulting datasets were nearly identical, indicating that the main data clusters were consistently removed. Overall, 187 training occurrences were retained for global ENMs and 43 for regional ENMs (Fig. 1). The inclusion of records from inland Campania in the regional ENMs is based on the working assumption that the species has acclimatized to local environmental conditions. Although definitive evidence of establishment is not yet available, *B. dorsalis* has been consistently detected in the same limited area over four consecutive years (2022–2025), with confirmed reproduction in multiple years. This assumption provides a precautionary basis for risk modelling and supports the early implementation of surveillance strategies.

Environmental variables

Global ENMs were calibrated considering, as the initial set of environmental predictors, 19 bioclimatic variables from the CHELSA database[92]. Bioclimatic predictors were upscaled at a spatial resolution of ca. 5 km, retaining nine variables for model calibration after checking for multicollinearity (VIF ≤ 5;[93]; Table S1). For regional ENMs training, the 19 CHELSA variables were considered, along with three topographical variables (elevation, slope and roughness[94]), four natural land cover categories (Euclidean distance to barren areas, forests, grasslands, and waterbodies derived from the GeoSOS global database[95]) and five variables referring to human-modified land cover (Euclidean distance to farmlands and urban areas from Chen et al.[95], and distance to roads from OpenStreetMap; https://www.openstreetmap.org). All variables were rasterized at a 1 km spatial resolution and checked for multicollinearity (VIF ≤ 5), retaining 13 final predictors (Table S1).

Ecological niche models

Both global and regional ENMs were trained using an ensemble forecasting approach as provided by the 'biomod2' R package[96]. Specifically, global ENMs were averaged through committee averaging, a procedure that quantifies the percentage of agreement on the species presence among several model predictions[96]. According to Gallien et al.[74], background points generated for regional ENMs training were provided with a varying weight based on committee averaging values derived from global ENMs. Particularly, where the global ENMs showed a high level of agreement with an absence (i.e., a low habitat suitability), a high weight to that absence was attributed (i.e., high probability of being a 'true' absence), and vice versa, calculating the weight through an inverse logistic transformation[86].

Both global and regional ENMs were calibrated considering the following four modelling algorithms: generalized linear models (GLM), generalized additive models (GAM), generalized boosted models (GBM) and random forests (RF). Furthermore, 10.000 background points were placed within all the World Wildlife Fund (WWF) Terrestrial Ecoregions intersecting species occurrences[45,97]. To prevent possible sampling bias still persisting in occurrence data despite the thinning procedure, background points for both global and regional ENMs were geographically placed according to the density of the occurrence data, so that there are more background points where presences are denser[98,99].

Global and regional ENMs predictive accuracy was assessed through a block cross–validation approach[100,101], which implies splitting data into four geographically non-overlapping folds with an equal number of occurrences, referring to each corner of the entire study area. Regional ENMs were also evaluated against 98 independent plots surveyed during 2023. Model accuracy was quantified by calculating the AUC[102] and the CBI[103]. To avoid using poorly trained models, we retained only projections from ENMs achieving an AUC ≥ 0.7. Model averaging was performed by weighting the individual model projections by their AUC values and averaging the result[104].

Regional ENMs were projected to the years 2070 and 2100 under two climate and land cover change scenarios, i.e., SSP1–RCP2.6 (mild) and SSP5–RCP8.5 (severe;[95,105]; specifications on forecasted land cover alterations are provided in Table S2). Since different global circulation models (GCMs) may lead ENMs to predict diverging climate change effects[106], we considered five alternative versions for future climate scenarios, as generated by the GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0 and UKESM1-0-LL global circulation models[107]. To account for the effect of model extrapolation on predictor values outside the calibration range, regional ENMs projections were generated through environmental clamping (i.e., capping covariates at the limit values of the training range[108]). Current and future projections were binarized to generate presence/absence maps according to four thresholding schemes, namely, 'equalize sensitivity and specificity', 'maximize TSS', '10th percentile training presence' and 'minimum training presence'[82], as to account for the effect of using different binarization approaches[109].

Potential connectivity corridors

Potential connectivity corridors for the current time and future scenarios were generated using the Circuitscape software ver. 4.0 (https://circuitscape.org/[110]. This tool applies circuit theory principles to generate multiple random walk pathways on a set of habitat nodes and a resistance surface, quantifying the relative costs of moving through the entire landscape[110]. The software generates a conductance map representing the likelihood of a moving subject choosing to cross a cell with respect to others available to it[110]. Since non–validated expert opinion used to develop resistance maps represents a major source of uncertainty in most landscape resistance modelling approaches[111], resistance maps were generated by applying a transformation function to the suitability maps derived from regional ENMs [44[112,113], . Such function defines an inverse relationship between suitability and resistance values allowing different possible shapes (i.e., from linear to negative exponential[113]). Three alternative suitability transformations were tested according to three function shapes (i.e., nearly linear, moderately, and highly exponential). To individuate habitat nodes, a "one-to-all" setup was adopted. Specifically, a 5 km buffer around *B. dorsalis* occurrences[31] was first calculated, which was set as the source node where the current starts. Then, all the suitable habitat patches extracted from regional ENM binary distribution maps were clustered into groups closer than 5 km to each other, setting each cluster as a target node. Among all the conductance flows generated by Circuitscape, the most important ones were identified by adopting a least-cost path approach, i.e., linking source and target habitat nodes along the pixels with the highest conductance values generated by the software. Connectivity corridors identified this way were subselected according to the conductance values they pass through. Specifically, the corridors were dropped reporting mean conductance values below the third quartile of the conductance values of the entire corridor network linking source and target nodes. All the target habitat patches linked by connectivity corridors as generated for the current time were considered as source nodes – in addition to the 5 km buffer around species occurrences – to calculate connectivity corridors for future scenarios. All the remaining target patches not linked by any of these corridors were considered unreachable.

Climate and land cover change effect on *B. dorsalis* invasion risk

The effect of 2070 and 2100 climate and land cover change on OFF potential distribution in Italy was evaluated by calculating the range net change metric (in terms of gain/loss percentage between the current and the future range) on binary distribution maps generated for threshold and scenario[114]. As for connectivity corridors, the difference between the current time and 2100 was evaluated in three metrics: percentage of connected suitable patches (i.e., with respect of unreachable patches), number of connectivity corridors per patch, and length of connectivity corridors. Possible differences in the four metric values as predicted by mild and severe scenarios in 2070 and 2100 were assessed via permutational ANOVA with a significance level (α) set at 0.05 ("coin" R package[115]).

Lastly, OFF habitat suitability within orchards and vineyards were quantified, as to assess potential damages to agricultural areas of commercial interest. In particular, all orchard and vineyard polygons were identified as mapped by the 10 m land cover product by De Fioravante et al.[116] and falling within suitable and reachable habitat patches as predicted by regional ENMs and connectivity analyses for each time step and scenario. The process involved removing areas that would no longer be classified as agricultural in the future, due to land cover change scenarios. To examine the differences between present and future suitability in orchards and vineyards, both in mild and severe scenarios, a permutational ANOVA was applied with a significance level (α) set at 0.05.

Data availability

All data generated or analysed during this study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

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Author contributions
U.B. and M.D.F. conceived and designed research; U.B. and F.N. carried out the investigation; U.B., F.N., R. A., C.C., M. F. curated the data; U.B., F.N., M.I. and M.D.F. wrote the original draft; U.B., F.N., M.I., R.A., M.D.F., F.M. and C.C. reviewed and edited the manuscript; M.I. and M.D.F: conceptualized the methodology, selected the software, and performed the formal analysis; U.B. and F.N. provided the funds. All authors read and approved the manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

Additional information

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