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Research Article

A hitchhiker's guide to Europe: mapping human-mediated spread of the invasive Japanese beetle

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Abstract

Early detection of hitchhiking pests requires the identification of strategic introduction points via transport. We propose a framework for achieving this in Europe using the Japanese beetle (*Popillia japonica*) as a case study. Human-mediated spread has been responsible for its introduction into several continents over the last century, including a recent introduction in continental Europe, where it is now listed as a priority pest. Furthermore, recent interceptions far from the infested area confirm the risk of unintentional transport within continental Europe. Here, we analysed how three modes of transport - air, rail and road - connect the infested area to the rest of Europe. We ranked all European regions from most to least reachable from the infested area. We identified border regions and distant major cities that are readily reachable and observed differences between modes. We propose a composite reachability index combining the three transport modes, which provides a valuable tool for designing a continental surveillance strategy and prioritising highly reachable regions, as demonstrated by recent interceptions.

Key words: Biological invasion, hitchhiking pest, likelihood of introduction, pest risk assessment, *Popillia japonica*, surveillance, transport network

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Introduction

The increasing global movement of goods and people provides countless opportunities for species to move around the world outside of their natural range, increasing the rate of biological invasion (Hulme 2009; Blackburn et al. 2011). Insects in particular can hitchhike on a variety of modes of transport, including planes, ships, trains and trucks (Saccaggi et al. 2016; Turner et al. 2021). Hitchhiking, which is part of unintentional human-mediated transport, facilitates the introduction of insects into new regions and, where conditions are suitable, their subsequent establishment (Early et al. 2016; Rosace et al. 2023). Predicting the risk of introduction of invasive insect pests through transport is therefore crucial for developing effective surveillance strategies (Essl et al. 2011).

Risk assessments of Invasive Alien Species (IAS) are becoming increasingly quantitative, particularly with the advent of environmental distribution models used to estimate suitability and hence establishment risk (Venette 2015). However, IAS introduction risk analyses are still often qualitative and expert-based, especially when considering human-mediated transport rather than active spread (accounted for by diffusion models) (Hulme 2009). Human-mediated introduction can occur by transport of traded goods and hitchhiking on cargo, on passengers or in vehicles. To be relevant to surveillance strategies for hitchhiking invasive insects, the analysis of risk of introduction should include directional (from infested regions to other regions) and weighted (volume measure) transport data, especially passenger travel (Hulme 2021). Most studies that use directional and weighted data focus on the trade of specific commodities that are pathways of entry for IAS (Piel et al. 2008; Yemshanov et al. 2012; Meurisse et al. 2019; Jamieson et al. 2022). Few studies include passenger movement data, and these studies usually focus on a specific region (Perry and Vice 2009; Szyniszewska et al. 2016) and rarely extend at a continental scale (Frem et al. 2020). As there is no framework for predicting the risk of hitchhiker IAS spreading across Europe through anthropogenic dispersal, we propose a method using directional and weighted transport data, including passenger movements, on a continental scale and at the finest possible spatial resolution. We use the Japanese beetle as a case study.

The Japanese beetle (*Popillia japonica*) is a prime example of a hitchhiker pest. Native to Japan, it was accidentally introduced into the United States of America at the beginning of the last century, causing a major invasion that still persists today (Frank 2016). From there, it was introduced to the Azores archipelago in the 1970s, and more recently to continental Europe. After its first detection in Italy in 2014, the beetle has spread to an area of more than 16,500 km^2 covering parts of northern Italy and southern Switzerland (Gotta et al. 2023). Due to its potential impact on the environment, food safety and economic balances, it has been listed as a priority pest by EU authorities (Commission Delegated Regulation (EU) 2019). Furthermore, several interceptions of the beetle far from the infested area have raised concerns about possible introductions to other parts of Europe. Although the source of the beetle's introduction into Europe has been phylogenetically reconstructed (Strangi et al. 2023), its potential spread in Europe and the risk of introduction through human movement have not been investigated.

In this paper, we present a novel approach to map the potential human-mediated spread of the beetle from the infested area to the rest of Europe. We considered three transport networks - air, rail and road - that are relevant to the beetle's pathways of entry from the infested area. We examined how reachability, i.e. the likelihood of introduction from the infested area, varied according to mode of transport. Finally, we combined transport modes to identify the most likely points of introduction and used interception sites to assess our reachability map.

Materials and methods

Data processing and analyses were performed using R version 4.2.1 (R Core Team 2021).

2022 European infested area

We first assessed the extent of the European infested area, taking into account both the municipalities where the presence of the beetle was confirmed and the neighbouring municipalities included in the buffer zone, according to 2022 official reports (Poggi et al. 2022a). This area will be considered as the origin for human-mediated spread of the Japanese beetle in Europe. The 2022 infested area covers approximately 16,500 km^2, spanning over five regions and more than 1900 municipalities

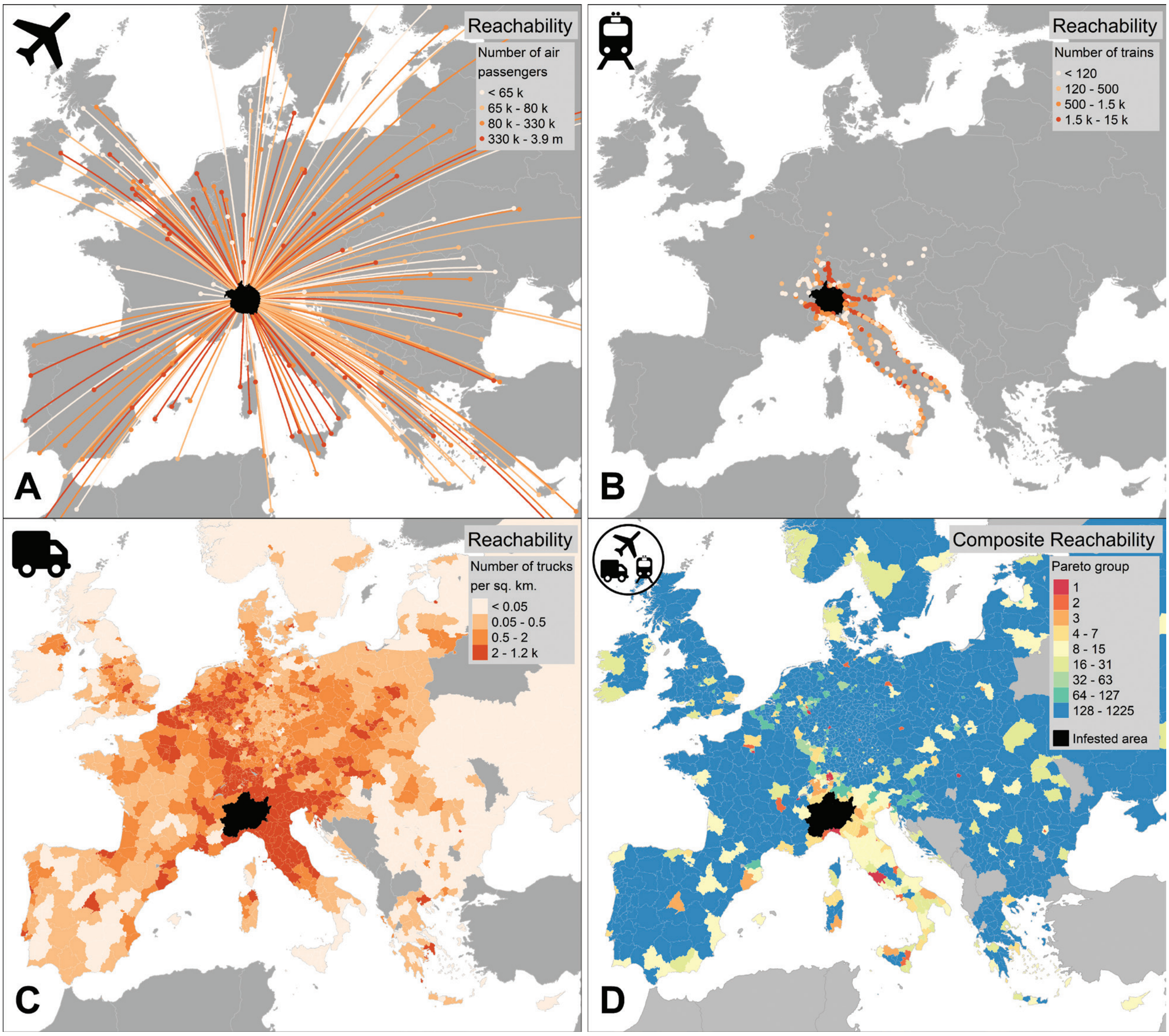

Figure 1. Reachability of Europe for *Popillia japonica* from the infested area (in black), by air, rail, road transport, and a combination of modes (composite index). Quantile-classified reachability maps showing: **A** the number of passengers arriving at airports **B** the number of trains arriving at stations, and **C** the number of trucks per square kilometre reaching NUTS 3 regions, departing from the infested area. Darker colours correspond to higher reachability **D** composite reachability map, i.e. risk of introduction for NUTS 3 regions ordered by Pareto fronts from most to least reachable. Warmer colours correspond to higher reachability.

in northern Italy and southern Switzerland (in black on Fig. 1). Six interceptions of *Popillia japonica*, i.e. captures of an isolated adult without establishment of a population, were made in Europe since 2018, far away from the infested area: one in the Netherlands (Amsterdam, EPPO 2019), one in Germany (Freiburg, EPPO 2022a), two in Italy (Udine, Bassi et al. (2022) & Cagliari, EPPO (2022b)) and two in Switzerland (Basel, NPPO of Switzerland (2021) & Zurich, EPPO (2023)).

Popillia japonica's pathways of entry and spread

Popillia japonica's pathways of entry and spread include national and international trade in commodities such as plant products, soil, fruits; and hitchhiking on cargo, on passengers (including in their baggage, Early et al. 2016) and in the vehicle itself (aircraft, train, car, truck, ship, EFSA Panel on Plant Health (PLH) et al.

2018; Poggi et al. 2022b). Here, we study hitchhiking by targeting three modes of transport that are relevant for the case study and for which comprehensive databases were readily available. Firstly, we assessed the air traffic via flights from the infested area to the rest of Europe. We focused on passenger air travel, since it has already been recognized as a major mode of introduction of IAS (e.g., 73% of interceptions at the US ports of entry between 1984 and 2000 occurred at international airports (Early et al. 2016)). Secondly, we considered terrestrial transport by assessing both road and rail traffic from the infested area to the rest of Europe (Hulme 2021). Private cars have been excluded due to lack of data, while maritime transport has been excluded from this analysis as there is no seaport in the area currently infested.

Data sources

Air transport

We used the Eurostat detailed air passenger transport by reporting country and routes (available at https://ec.europa.eu/eurostat/databrowser/explore/all/transp?lang=en&subtheme=avia&display=list&sort=category&extractionId=AVIA_PAR) and the World Bank - Global airports database (available at https://datacatalog.worldbank.org/search/dataset/0038117), which are complementary. From Eurostat, we extracted the number of air passengers between the main airports within the infested area of Italy and Switzerland, and their destinations in Europe (routes data, https://doi.org/10.2908/AVIA_PAR_IT and https://doi.org/10.2908/AVIA_PAR_CH). World Bank data provides the number of passengers on connecting flights between airports worldwide for 2019.

Rail transport

Data related to rail transport were retrieved from the EuroGlobalMap 2022 dataset (EGM 2022.2 © EuroGeographics, available at https://www.mapsforeurope.org/datasets/euro-global-map) and the Deutsche Bahn Transport Rest API V5 database. The EuroGlobalMap 2022 dataset includes locations of railway stations in Europe. Based on these locations, we have extracted data on train travel between railway stations in Europe, by querying the Deutsche Bahn Transport Rest API V5. Deutsche Bahn Transport Rest API is an open database that returns real-time data on most long-distance and regional traffic, as well as international trains, in Central Europe. This database has previously been used to display European train journeys, showing how far one can travel from any station in Europe in less than 8 hours (https://www.chronotrains.com/). Queries to Deutsche Bahn Transport Rest API V5 were made using the httr2 package 0.2.2 (Wickham 2022).

Road transport

Data related to road transport were retrieved from a recently published dataset on European road freight traffic (Speth et al. 2022). These data describe the flows of trucks (both in tonnes and number of trucks) between 1675 regions in Europe at NUTS 3 spatial resolution during 2019.

Reachability analysis

Our introduction risk assessment framework is based on three main steps. First, for each transport mode, we identify all source locations within the infested area (e.g. airports or railway stations). Then, we measure the intensity of connections to all possible destinations elsewhere in Europe. Finally, reachability by all modes of transport is combined using a Pareto optimality method to rank regions according to their risk of introduction. The following sections describe this framework in more detail.

Air transport

We selected the airports located in the infested area and all the European airports reachable from these airports from the Eurostat and World Bank databases. For each reachable European airport, we summed the total number of passengers on flights departing from airports within the infested area. For the World Bank database, these data were available for 2019, and for Eurostat, we extracted data during the beetle emergence period, from May to August, for years 2010 to 2019. Some major reachable airports were missing from the Eurostat database and were present in the World Bank database. We predicted Eurostat missing data using the World Bank data as there was a strong correlation in the total number of passengers at reachable airports shared between the two databases ($R=0.95$, $p<0.001$, Pearson correlation). On a subset of the data made of airports found in both World Bank and Eurostat databases, we fitted a Generalized Additive Model (GAM) with a Poisson distribution. We used World Bank number of passengers as the only explanatory variable to predict Eurostat number of passengers using the gam function of mgcv package 1.8–42 (Wood 2011) (k = 4, family = “poisson”). This model explained 84.6% of deviance found in the data with an adjusted R-squared of 0.89. We applied this model to predict the number of passengers where data was missing from the Eurostat database. The obtained value, accounting for the cumulated number of passengers arriving at any European airport from all airports located within the infested area, was used as a proxy for the risk of introduction by air.

Rail transport

We identified the spatial coordinates of all railway stations located within the European infested area from EuroGlobalMap 2022. We fed these coordinates to the “GET /stops/nearby” query to extract the railway stations identifier from the Deutsche Bahn Transport Rest API V5, hence locating the closest railway station within a 500-meter radius from given coordinates. We retrieved the trip identification number (tripID) for all trains departing from these stations during the adults’ emergence period, between 2022-05-01 and 2022-08-31, using the “GET /stops/:id/departures” query. For each tripID, we retrieved all railway stations where the train stopped on its trip using the “GET /trips/:id” query. The final database contains all tripID with corresponding information on the stations of departure and destination, as well as the train stops (station id, name and coordinates, as well as the time of arrival and departure).

We mapped the resulting railway stations, excluding those that were already within the infested area. We computed the cumulated number of trains reaching these stations by counting the number of unique trip ids at these stations. The obtained value, accounting for the total number of trains arriving at European railway stations from stations in the infested area during the chosen period, was used as a proxy for the risk of introduction by rail.

Road transport

Road transport sources were identified as the NUTS 3 regions (ID_origin_region in the database from Speth et al. 2022) which were either completely or partially covered by the infested area. For each destination region (ID_destination_region), we cumulated the number of trucks (Traffic_flow_trucks_2019) departing from the NUTS 3 located within the infested area. Finally, for each destination region, we weighted the total number of trucks arriving from the infested area by the area of the destination region (in km^2) in order to account for the variable NUTS 3 sizes and to avoid underestimating the importance of smaller regions. The obtained value, the total number of trucks per square kilometre reaching NUTS 3 regions from the infested area, was used as a proxy for the risk of introduction by road.

Combining air, rail and road transport - composite reachability

We combined reachability by air, rail and road transport using a Pareto front ranking method (Roocks 2016). This method is based on a well-known multi-objective optimization algorithm, where all feasible solutions of a given problem are characterized by a vector describing their score with respect to different objectives. A solution is said to be non-dominated (or Pareto optimal) if it cannot be improved in any of the objectives without degrading at least one of the other objectives. The set of all non-dominated solutions (that may include one or multiple feasible solutions) is called the Pareto front.

Our method iteratively searches for the Pareto front that maximises the risk of introduction for the three modes of transport combined (no priority is given to any of the transport modes, which are therefore considered to be equally risky). The set of feasible solutions consists of all non-infested NUTS 3 regions of Europe, each one characterized by a three-dimensional vector reporting its reachability index for the three modes of transport. For air and train transport modes, we aggregated the number of passengers reaching an airport and the number of trains reaching a station across all airports and railway stations located within each NUTS 3 region in order to assign a unique reachability value for these two modes of transport.

All NUTS 3 belonging to the first Pareto front that maximize the reachability are labelled as 1 and then removed from the dataset. A new Pareto front is then identified, whose solutions are labelled as 2 and removed afterwards. This process continues until all NUTS 3 have been labelled and assigned a composite reachability index value from 1 to 1225, with 1 being the most reachable and 1225 being the least reachable when air, rail and road transport from the infested area are combined. The Pareto front analysis was performed using the psel function of rPref package 1.4.0 (Roocks 2016).

Results

Among the 1675 European NUTS3 regions, twenty were considered infested in 2022 because they contained at least one infested municipality. Within this infested area, there are 6 airports and 540 railway stations. Outside of that area, a total of 160 airports (from 30 different countries), 422 railway stations (located in 5 different countries), and 1446 NUTS 3 regions (from 33 countries) can be reached by planes, trains, and trucks, respectively. Reachability from the infested area varies between modes of transport (Fig. 1A–C). With the exception of a few distant major European cities, the rail transport network mainly connects areas adjacent to the infested area (7 NUTS 3 in Germany, 6 in Austria and 4 in France), most of Italy (65 NUTS 3 out of 107) and Switzerland (13 NUTS 3 out of 26). The road freight network is both local, with Switzerland, northern and central Italy highly reachable from the infested area; and international, with many major European cities also highly reachable. Finally, the air transport network is mostly international, with direct access to all major cities in Europe. Our analysis shows that of all NUTS 3 regions directly reachable by at least one transport mode from the infested area, 10% and 7% are reachable by air and rail respectively. On the other hand, almost all of these regions (99.8%) are reachable by road freight.

Interestingly, the distribution of planes, trains and trucks that reach NUTS 3 regions in Europe is far from uniform, with very few NUTS 3 concentrating most of the traffic from the infested area. Indeed, the 1% of NUTS 3 most reachable by rail (14 NUTS 3) account for over 60% of all trains leaving the infested area. Similarly, the top 1% of NUTS 3 reachable by air account for 52% of all flights, and the same is true for road freight, with the top 1% of NUTS 3 reachable by trucks accounting for 46% of all trucks leaving the infested area.

The composite reachability index, which combines air, rail and road transport, ranks NUTS 3 regions into ordered groups, from most to least reachable (Fig. 1D). The five groups of most reachable regions contain 62 NUTS 3 (from 16 different countries), of which 13 are reachable by all three modes of transport. Furthermore, these 62 NUTS 3 account for 70%, 72%, and 47% of the total number of planes, trains and trucks leaving the infested area, respectively.

The distribution of composite reachability by number of NUTS 3 per country is shown in Fig. 2: Italy (IT), Germany (DE), United Kingdom (UK), France (FR), Switzerland (CH), and Spain (ES) contribute with both a high number of reachable NUTS 3 and their relative importance in terms of the composite reachability index. On the other hand, eastern countries like Hungary (HU), Romania (RO) and the Czech Republic (CZ) have fewer, but highly reachable NUTS 3. The large number of small NUTS 3 regions in Germany explains the over-representation of this country in Fig. 2.

Finally, reachability correlates negatively with distance from the infested area for train, trucks and the composite index (Kendall correlation of -0.25***, -0.44*** and -0.32***, respectively), which means that more distant destinations are less reachable than closer destinations (Fig. 3). On the contrary, reachability by flight correlates positively with distance (Kendall correlation of 0.11***). Interestingly, reachability is anisotropic, meaning that it does not distribute uniformly in all direction (see the circular bar plots within the four panels of Fig. 3).

Discussion

In this study, we have mapped the risk of introduction of the Japanese beetle in continental Europe by air, rail and road transport from the infested area as defined in 2022. We found that reachability of regions varies by mode, and detected topological features of transport networks, ranging from a local and national predominance (rail and road transport) to an almost exclusively international dimension (air transport)

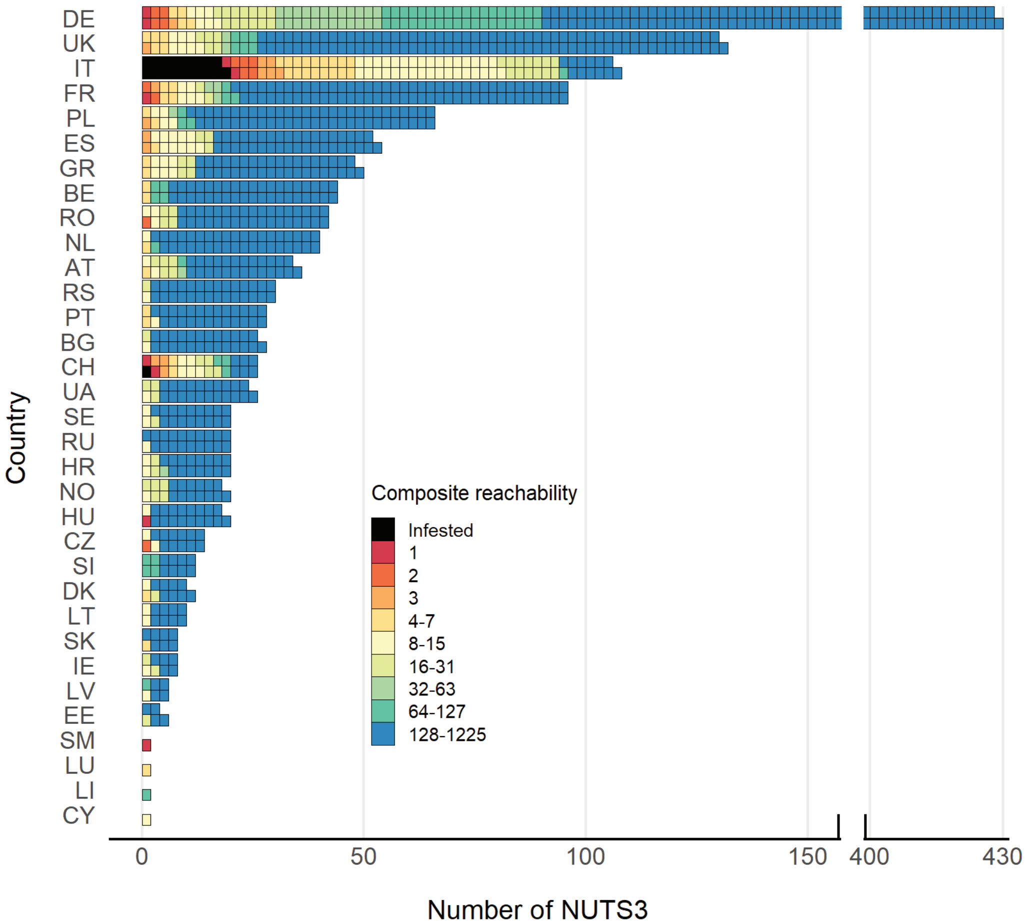

Figure 2. Distribution of reachable NUTS 3 regions per country when combining air, rail and road transport (composite reachability). Warmer colours correspond to higher reachability. Countries are shown using alpha-2 country ISO codes as described in the ISO 3166 international standard.

(Banks et al. 2015; Tatem 2017). The proposed composite reachability index, which combines the three transport modes, highlights a few scattered highly-reachable major cities across Europe, as well as a cluster of high reachability comprising many regions of Italy, Germany, Switzerland and France surrounding the infested area.

As this is the first analysis of the risk of Japanese beetle spread through human-mediated transport across continental Europe, our identification of likely introduction points cannot be compared with previous results. Nevertheless, the BeNeLux countries and northern Italy have also been identified as presenting a high risk of IAS introduction into Europe by a previous study that examined risk as a function of climate, soil, water, and anthropogenic factors (Schneider et al. 2021). Our results highlight transport network characteristics that have also been observed in previous studies, such as the international nature of air transport and the predominantly regional and national nature of rail and road freight transport (Hulme 2021). In addition, we have identified a disproportionate distribution of connections between the infested area and a small number of distinguished NUTS 3: indeed, for each of the three modes of transport, the 1% of the most reachable NUTS 3 accounts for more than 45% of the total outbound flow from the infested area. This demonstrates an assortative type of mixing (Newman 2003), a property of complex networks where nodes (here NUTS 3 regions) that are in some sense similar tend to be more connected. In our case, the infested area encompasses a major European hub (MXP-Milan

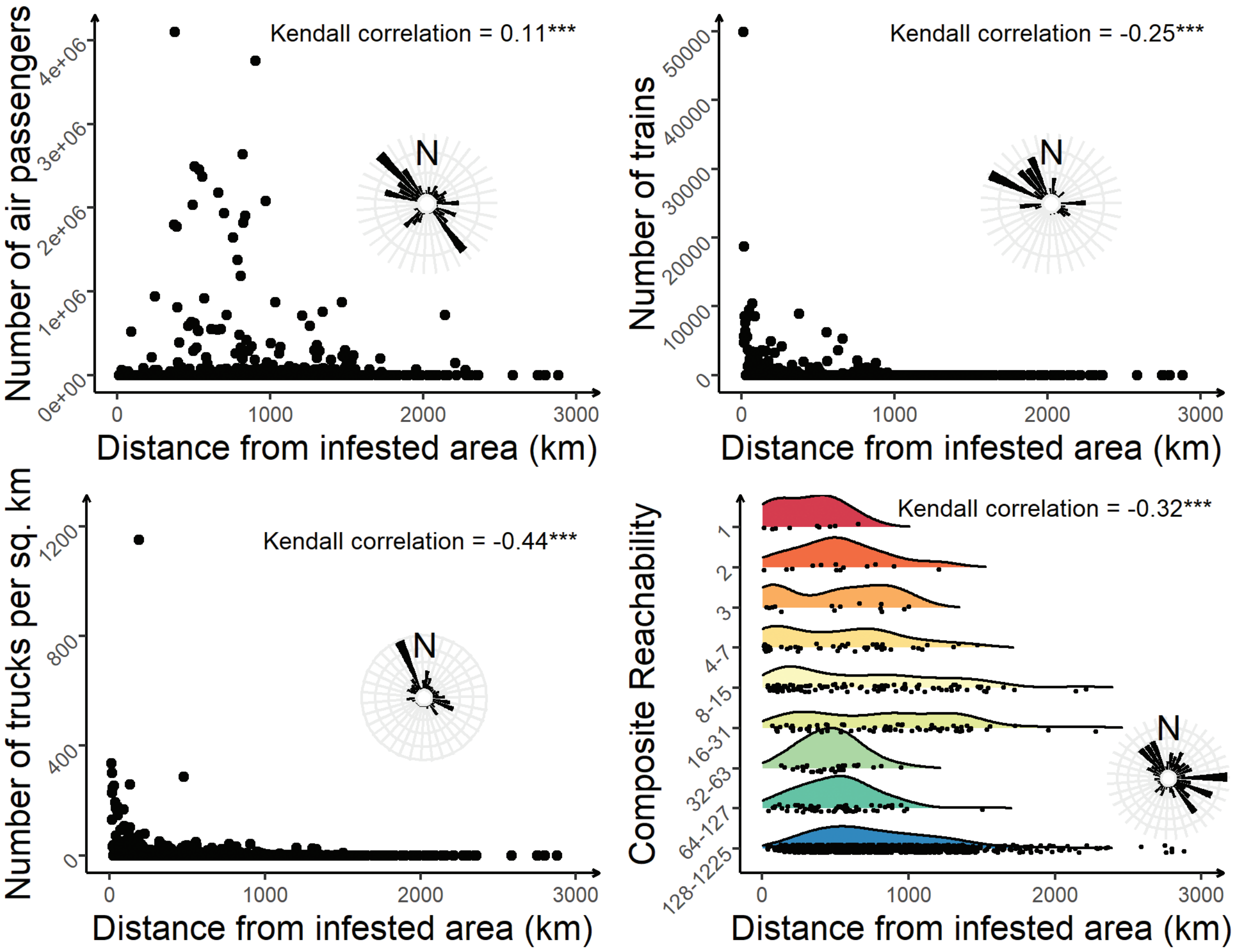

Figure 3. Distribution of air, rail, road and composite reachability of European regions for *Popillia japonica* as a function of distance from the infested area (in km), with the corresponding value of the Kendall correlation test. Within each panel, a circular bar graph shows the main directions in which the four reachability indices spread with respect to the infested area. Air, rail and road reachability are expressed as the number of passengers arriving at airports, the number of trains arriving at stations, and the number of trucks per square kilometre reaching NUTS 3 regions, departing from the infested area, respectively. Composite reachability of NUTS 3 regions is displayed from most reachable (group 1) to least reachable (groups 128-1225).

Malpensa Airport), which is naturally well connected to other hubs on the continent. On the other hand, Figs 1, 2 also show that the infested area is simultaneously connected to scattered, highly reachable hubs and is capillary-linked to surrounding, less reachable regions. This feature is typical of core-periphery graphs, where a subset of nodes in the network (the core) is connected to a few nodes of very high degree, as well as to many peripheric nodes (Pittel et al. 1996; Malliaros et al. 2019).

The highly-reachable hubs identified by combining air, rail and road transport, have already been shown to have particular potential for the spread of IAS (Banks et al. 2015). Interestingly, all Japanese beetle interceptions that have occurred in Europe over the last 5 years have been reported in regions that our analysis identified as highly reachable (Fig. 4), providing preliminary evidence of the robustness of our approach. Furthermore, an outbreak was detected in July 2023 in one of the nine regions we identified as being the most reachable from the infested area (Zurich region, Switzerland). Of all the interceptions known to date, only those in Zurich and Amsterdam could have originated from outside the continental European infested area, as they occurred at or near airports with direct connections to

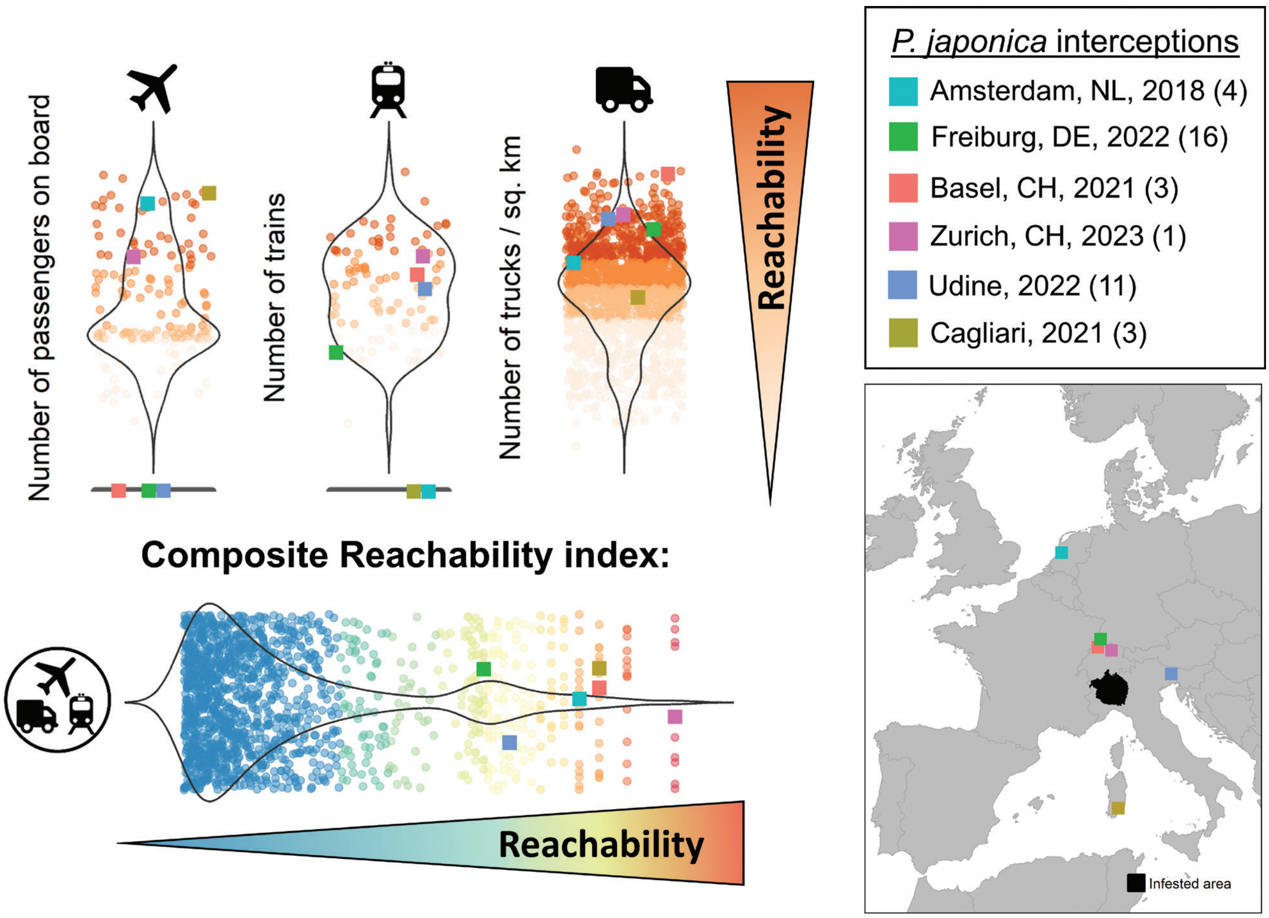

Figure 4. Interceptions of *P. japonica* made in Europe since 2018 and their position in relation to the distribution of reachability indices (air, rail, road, and composite). The number in brackets to the right of the interception site name indicates the group number assigned to the NUTS 3 region by the Pareto ranking method, from most reachable (1) to least reachable (16).

North America and/or Japan. Molecular methods could be used to further assess the most likely origin of these introductions (Strangi et al. 2023).

Although our results appear to be relevant based on interceptions and the published literature on transport networks, this analysis could be improved by considering hitchhiking on air freight, rail freight and private cars (domestic travel). Call detail record (CDR) could be a useful source for domestic travel, which could play an important role in facilitating the spread of the Japanese beetle, especially around the infested area (Tatem 2017).

The proposed framework provides a rapid response tool for decision-makers and phytosanitary services to anticipate the likelihood of hitchhiking pest introduction on a continental scale. Informing risk-based surveillance strategies with likelihood of introduction can significantly reduce surveillance efforts and promote early detection of invasive species (Parnell et al. 2014). As data become available, further improvements may be achieved, for example by targeting commodity movements specifically identified as pest carriers (Fenn-Moltu et al. 2023), or by including other transport modes. Highly reachable regions could also be surveyed for the presence of susceptible host plants or favourable environmental conditions (Tatem et al. 2006; Borner et al. 2023). Our framework highlights the need for local surveillance combined with a transboundary strategy, involving official authorities and stakeholders, and adapted to the scale and means of spread of the pest under surveillance (Radici et al. 2023).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SP, DM, LB. Formal analysis: DM, LB. Funding acquisition: SP. Methodology: SP, DM, LB. Project administration: SP. Supervision: SP, DM. Visualization: DM, LB. Writing - original draft: LB, DM. Writing - review and editing: SP, LB, DM.

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Data availability

The datasets generated during the current study are available in the French Research Government repository, https://doi.org/10.57745/3WUVWJ.

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Supplementary material 1

Reachability of European regions

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Data type: csv

Explanation note: Reachability of European regions by air, rail and road and combining the three modes of transport.

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