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RAPID COMMUNICATION

Tracking the invasion of the alien fruit pest *Drosophila suzukii* in Europe

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Abstract Biological invasions are a leading threat to native wildlife, human health and food production worldwide. Understanding the invasion history helps identifying introduction pathways and organizing integrated management strategies especially aimed at avoiding multiple reintroductions. We coupled a recently developed spatial analysis (Geographic profiling) with trade flows quantification to identify the most likely spreading centre of a recent invader of Europe, the spotted wing drosophila, *Drosophila suzukii*. This polyphagous vinegar fly recently colonized western countries, where it is heavily threatening fruit production causing severe economic losses. Characterized by a rapid spread and a huge impact, the invasion of this pest has a few precedents and it is becoming a model in invasion biology and pest management. Thanks to our spatial approach based on data presence of *D. suzukii* in European countries in the very first years of it spread, we update the current knowledge of a first spread in Spain and Italy, suggesting on the contrary that the South of France may be the most likely spreading centre of *D. suzukii* in Europe. Estimates of propagule pressure (fresh host fruits importation) support this finding as imports from contaminated South East Asian countries are higher in France than in Spain or Italy. Our study provides a first step in the comprehension of invasion history of this pest species and emphasizes geographic profiling as an efficient technique to track down invaders colonization patterns.

Keywords Biological invasion · Spotted wing drosophila · Fruit fly · Invasive species · Geographic profiling

Key message

The alien invasive pest, *Drosophila suzukii*, recently colonized Europe, where it is causing severe economic losses.

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Understanding its invasion history may help organizing integrated management strategies and avoiding multiple reintroductions. By coupling spatial analysis with trade flows quantification, we identified the most likely spreading centre and update the current knowledge of a first spread in Spain and Italy, suggesting that the South of France may rather be the most likely spreading centre of *D. suzukii* in Europe.

Introduction

Biological invasions cause severe ecological and economic impacts across the globe. Invasive alien species (IAS) are in particular one of the leading threats to native wildlife, human health and food safety/production, with associated economic impacts estimated in hundreds of US$ billion each year worldwide (Pimentel et al. 2005; Pyšek and Richardson 2010). A first key step in the comprehension and management of biological invasions is to understand the pathways and vectors of introduction, the spreading origin/s and the spatio-temporal dynamics of colonization. In particular, the identification of those invaded areas that were colonized first or more likely allowed the first successful establishment of the IAS is needed to both prevent recurrent introductions of the same or other IAS and to identify possible idiosyncratic features that facilitated the invasion.

Since the last few years, a new IAS is dramatically threatening agriculture in Western countries. The vinegar fly *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) (also known as Spotted Wing Drosophila, hereafter SWD) is a highly polyphagous invasive pest which mainly infests thin-skinned fruits such as soft and stone fruits, cherries and apricots (reviewed in Cini et al. 2012). Thanks to its serrated ovipositor, SWD lays eggs in healthy, unwounded fruits (Sasaki and Sato 1995) and larval feeding and development on fruit flesh make fruits unmarketable (Rota-Stabelli et al. 2013). The impact of SWD on fruit production is therefore enormous, exacerbated by the high number of generations per year (10–15), the high fecundity of females (up to 600 eggs, 400 eggs on average) (life cycle details in Kanzawa 1939; Mitsui et al. 2006; Walsh et al. 2011) and by the possible secondary damages caused by other insects, fungi and bacteria after SWD attack (Goodhue et al. 2011; Walsh et al. 2011). With yield losses ranging from 30–40 to 100 % depending on the crop and the area, economic losses of fruit production are severe and estimated to cost more than 500 millions dollars every year only in the USA (Bolda et al. 2010). A recent study estimated that only in the Trento Province, Italy, the 400-ha soft fruit production areas faced losses of around 500,000 EUR in 2010 and 3 millions EUR in 2011 (De Ros et al. 2012). Consequently, many different management techniques (such as chemical control, e.g. Yee and Alston 2012, or biological control, e.g. Chabert et al. 2012; Rossi Stacconi et al. 2013) are under investigation.

As eradication and containment do not seem feasible, in order to keep SWD populations at a manageable level it is crucial to avoid recurrent introductions and re-infestations (Cini et al. 2012). Despite research efforts, SWD invasion dynamics in Western countries still remain unknown. SWD is endemic to South East Asia, where it is present in several temperate countries from Japan to Pakistan (Kanzawa 1936; Cini et al. 2012). After the first detection in Western countries in 2008 (simultaneous reports in California, Spain, and Italy), SWD rapidly colonized a large part of the USA and Canada as well as most countries of Europe (Walsh et al. 2011; Cini et al. 2012), and has been recently discovered in South America (Deprá et al. 2014). In Europe, SWD was found for the first time in Spain (Rasquera Province, Calabria et al. 2012) and in Italy in 2008 (Tuscany, Raspi et al. 2011). In 2009, it was detected in the South of France (Calabria et al. 2012), while first catches from the Eastern Mediterranean area were reported in 2010 in Slovenia (Seljak 2011) and Croatia (Masten Milek et al. 2011). In 2011, SWD was reported also in Switzerland (Baroffio and Fisher 2011), Austria (Lethmayer 2011), Germany (Vogt et al. 2012) and Belgium (Mortelmans et al. 2012). By 2012, the fly was spread in most Europe (e.g. The Netherland, NPPO 2012; United Kingdom EPPO 2012; Hungary, Kiss et al. 2013), and it is likely that few countries will remain SWD free (Cini et al. 2012; Rota-Stabelli et al. 2013).

The first known damage to commercial small fruits in Europe was found in Italy, Trento Province, during 2009 (Grassi et al. 2009). Characterized by a high dispersal rate, a wide host range (more than 30 species have reported as hosts, Cini et al. 2012), an ecological pre-adaption to temperate climates and a deep impact, the invasion of this pest has a few precedents (Rota-Stabelli et al. 2013; Ometto et al. 2013), and SWD is quickly becoming a model for research on invasion biology and pest management (Dreves 2011; Cini et al. 2012).

In this paper, we took a first step towards the understanding of SWD invasion in Europe using a spatial analysis technique (Geographic profiling, hereafter GP) to understand the possible spreading centre/s of SWD in European countries.

GP is an analytic tool which at identifying the geometrical origin of linked events, for instance crimes by a serial killer in criminology or spreading populations of an alien species. GP uses coordinates on a map of linked events (e.g. homicides in criminology or locations where an IAS has been reported, in invasion biology) to create a probability surface to superimpose on the original map to produce the so-called geoprofile (Rossmo 2000). Such geoprofiles, based only on presence data, do not provide the exact origin of the events, but produces decreasing probability density, thus rather prioritizing geographical areas (Rossmo 2000). GP was applied in biology to the targeting of an infectious disease (Le Comber et al. 2011), animal foraging (Le Comber et al. 2006) and the prediction of nest locations of bumble bees (Suzuki-Ohno et al. 2010). Recently, GP was used to identify the source population(s) of invasive species using the known positions of their current populations (Stevenson et al. 2012; Papini et al. 2013). The identification of the invasion sources can be useful to target control methods, which are more efficient and cost effective than untargeted intervention (Le Comber and Stevenson 2012).

The likelihood of IAS invasion depends on many interacting factors, with propagule pressure (a composite measure of the number of individuals released into an area to which they are not native, also known as "introduction effort", Lockwood et al. 2005) being one of the key ones (Lockwood et al. 2005). The magnitude of merchandise imports has been shown to be one of the major factors increasing propagule pressure and thus the risk of an area to be invaded (Levine and D'Antonio 2003, Lockwood et al. 2005; Westphal et al. 2008). In the case of SWD, the most likely pathway of introduction is considered to be the trade of fresh fruits, with first individuals arriving unnoticed as eggs or larvae in fruits sea-traded from South East Asia (Rota-Stabelli et al. 2013), so that post harvest sanitation protocol is under development (Follett et al. 2014). In order to corroborate the results given by our spatial approach through the GP technique, we estimated the propagule pressure of SWD in European countries by considering the annual import of fresh fruits of known SWD hosts from South East Asia in the years before SWD invasion.

Materials and methods

Distribution data

Presence data of SWD across Europe were obtained from published data ($n = 61$ reports; Calabria et al. 2012; Raspi et al. 2011; Weydert et al. 2012; Griffo et al. 2012; Pansa et al. 2011; Suss and Costanzi 2011; Boselli et al. 2012) and from authors' surveys (monitoring of SWD presence with baited traps in North Spain, North Italy, Slovenia and Croazia; $n = 30$ reports) and mapped on the European map (data are available in Table S1 and Fig. S1 of the Supplementary materials). We included in the database either presence reports published in scientific literature than those in grey literature (after having checked the reliability of the reports, all coming from recognized experts). This allowed us to include many more data than those present in ISI papers, thus providing a more complete dataset.

In order to homogenize the heterogeneous presence data, reports occurring at a distance smaller than 30 km were pooled together. As GP is particularly suggested for analyses at the early stage of the invasion process (Stevenson et al. 2012), we focused on SWD presence data in the first three years since the first reports (2008–2010).

The model and parameters choice

We used the model for Geoprofiling analysis described by Rossmo (2000) and modified according to Papini et al. (2013). The analysis is based on a model with two functions: a distance decay function, so built to make the probability of the event (spreading of an alien species, or a crime in the first analyses) tending to drop with increasing distance from the events origin due simply to energy costs of the dispersal mechanisms; and a buffer zone, within which the events probability increases with distance (Rossmo 2000), meaning that spreading cannot occur too close to the starting point, either because for some reasons the invader does not stop too close to the starting point or/and for geometric reasons (Stevenson et al. 2012), since area increases with distance squared and hence optimal locations for the setting of a propagule will increase with distance from the origin. As suggested by Stevenson et al. (2012), it may be possible to use general, taxon- or habitat-specific values for the model parameters in cases where data on a certain species are lacking. The parameters of the model were chosen according to Stevenson et al. (2012) and Papini et al. (2013) and adapted the parameters to our different map scale. Since we do not have any information about the possible real values of the buffer zone radius (B) in this or related species, and since it depends on many factors (dispersal ability, habitat heterogeneity, etc.), we selected from Stevenson et al. (2012) the values obtained for the most similar species (insects, B values: 0.38–0.42). The B value, rescaled to our map, was evaluated to be $B = 2$. In order to evaluate the influence of the B value on the GP results, we performed the analysis with several values of B (ranging from $B = 0.5$ to $B = 16$), which spanned across the values found for other terrestrial flying insects (Stevenson et al. 2012, adapted to the different map scale).

Our programs were written in Python 2.6.4 (http://www.python.org/) and are available at www.unifi.it/caryologia/PapiniPrograms.html. The maps were downloaded from Open Street Map (http://www.openstreetmap.org and is available in the Supplementary materials, Fig. S1).

Propagule pressure estimation

Propagule pressure was estimated as the amount (tons) of import of potentially infested fresh fruits in the 5 years (2003–2007) before SWD invasion. Fresh fruit Import data (tons for each fruit category for each EU country) were obtained by TradeMap (International Trade Center, www.trademap.org). We selected imports of the following host fresh fruits, which are known to be attacked by SWD (reviewed in Cini et al. 2012) (Harmonized System classification, hereafter HSC): fresh apricots, cherries, peaches, nectarines, plums & sloes (*Prunus* sp, HSC category 0809); fresh strawberries (*Fragaria* sp.), raspberries, blackberries, mulberries, loganberries, currants and gooseberries, cranberries (*Rubus* and *Vaccinium* sp., but excluding kiwi, durians, persimmon and others non-host species) (HSC category 0810); fresh grapes (*Vitis vinifera*) (HSC category 080610). We filtered the data retaining only the imports from South East Asian countries in which SWD is reported (from Cini et al. 2012).

SWD is a generalist species with a certain host choice flexibility (Cini et al. 2012; Burrack et al. 2013). We thus opted for including all potential hosts that may act as vectors of SWD. However, different fruits have different potential as SWD host and could thus have different potential as SWD sources of introduction. We thus also estimate a weighted propagule pressure by multiplying the amount of tons imported for each host category for the mean Host Potential Index of each category (hereafter HPI, calculated by averaging for each fruit class the host potential index data of each host fruit available in Bellamy et al. 2013), which assumes higher values for most preferred and suitable hosts.

Our approach to estimate propagule pressure mainly depends on three parameters: the time frame, the countries considered as potential sources of SWD infections and the host species. In order to evaluate the robustness of our approach, we perform the analysis also by varying these parameters as follows: time frame, 2 years (2006–2007) and 7 years (2001–2007); source countries, including only countries which reported SWD presence (according to Cini et al. 2012) or including also South East Asian countries with no official SWD reports but neighbouring to infested countries; host species, preferred host range (described above) or host range enlarged also to less-preferred hosts (i.e. including figs, which in Spain have been found to host SWD each year since 2008, unpublished data, A. Escudero Colomar personal observation). All datasets were highly positively correlated with the main analysis one (see Supplementary materials, Table S2) resulting in highly similar results which are not reported here.

Results

GP identified an area of about 400 km^2 in the South of France as the 95 % most likely spreading centre of SWD in Europe (Fig. 1a). Varying the B value did not vary much the result about the area of highest probability of centre of spread, but varied the dimension of such area (Fig. 2). The area with $B = 2$ is localized around Avignon (Fig. 1a). Our data are robust, as the centre of the area remains the same also when changing the parameters (Fig. 2), while only the extension of the area around the possible spreading centre increases, as predicted, with the increase of the buffer zone.

Fresh fruit imports data highlight that France has higher estimated SWD propagule pressure compared to Spain and Italy, the two other countries that reported SWD for first. France imported more potentially SWD infested fruits in the 5 years before SWD first reports than Spain and Italy (Fig. 3). In particular, France imported about 10 and 3 times more potentially infested fresh fruits than, respectively, Italy and Spain. France imported in particular more apricots, cherries, etc. (class 0809, about 20 and 15 times more than Italy and Spain), more berries than Spain (class 0810, about 3 time more) and more grapes (class 080610) than Italy. On the contrary, France imported a few less grapes than Spain (about 20 % less) and a few less berries than Italy (about 14 % less). When considering all the hosts together, weighed by their different potential as SWD hosts (Bellamy et al. 2013), France has a greater estimated SWD propagule pressure than Spain and Italy, about 10 and 4 times higher, respectively (Fig. 3). Importations were by far higher in many other European countries, such as Finland, UK, Denmark and Germany, compared to the three focal countries (France, Spain and Italy) (Table S3, Supplementary materials), with up to two order of magnitude of difference in the total weighted propagule pressure of UK compared to France. This difference disappears when removing grapes from the analysis (France is the fourth countries in weighted propagule pressure) and completely reveres if considering only HSC 0809 (apricots etc.), for which France is the European country with the highest propagule pressure.

Discussion

Our GP spatial analyses, based on the best current knowledge about SWD presence in Europe, identified an area of about 400 km^2 in the South of France, around Avignon, as the most likely spreading centre of SWD in Europe. This result is corroborated by the estimation of propagule pressure. In the years preceding first SWD reports, France had an estimated propagule pressure from 4

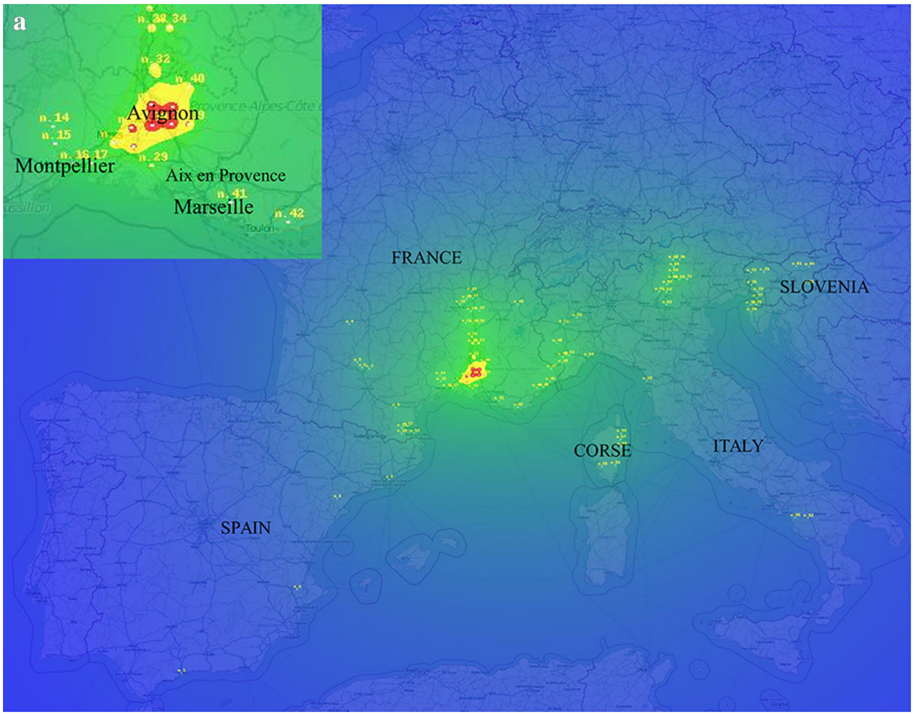

Fig. 1 Sites of occurrence of *Drosophila suzukii* in Europe (presence reports for the years 2008, 2009 and 2010, pooled) and most probable spreading centre calculated with Geoprofiling. Warmer *colours* represent areas with higher probability of being the spreading centre. *Red colour* pixels correspond to the area with the 5 % highest probability, *yellow colour pixels* to areas with probability >5 and <10 %, *green pixels* are further 5 %, while varying tones of *blue* indicate lower probability pixels (intense blue those with minimum probability). *White squares* with numbers (visible in the higher magnification picture and enlarging the main picture) correspond to known presence of the fly. Buffer zone radius (B) was set equal to 2. 1*a*—Higher magnification of Fig. 1 corresponds to the surroundings of Avignon. (Color figure online)

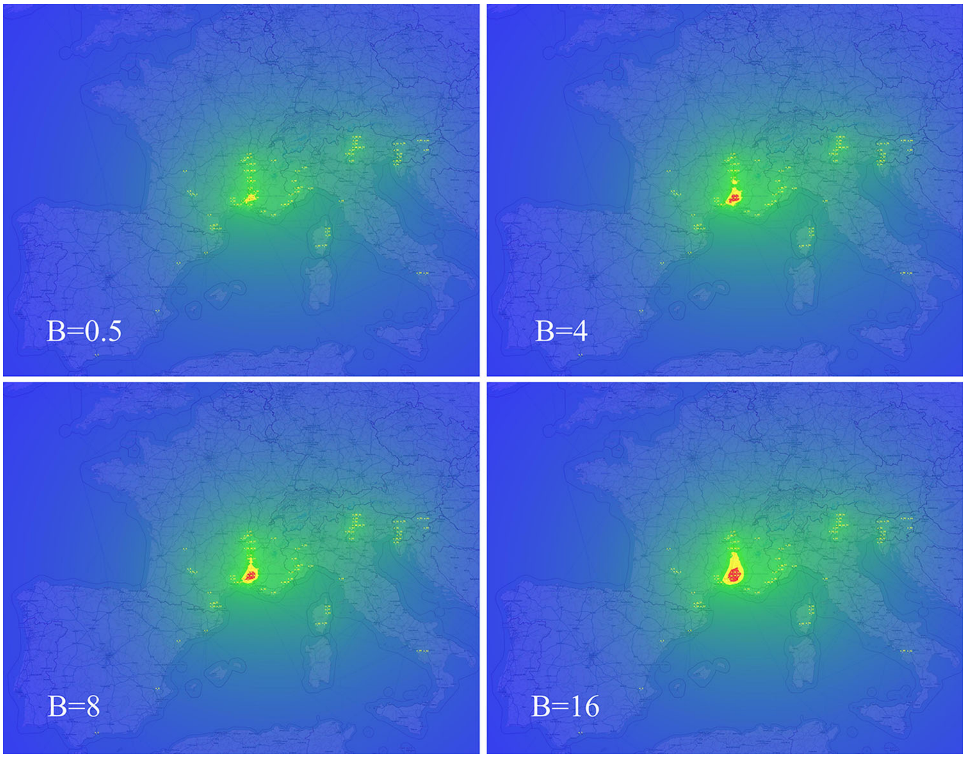

Fig. 2 Sites of occurrence of *Drosophila suzukii* in Europe (data pooled for 2008, 2009 and 2010) and most probable spreading centres under different Geoprofiling B parameter settings. *Colours* of the pixels as in Fig. 1. *Squares* with a number correspond to known presence of the fly. Four cases are shown: $B = 0.5$, $B = 4$, $B = 8$, $B = 16$, starting from *upper left*, clockwise

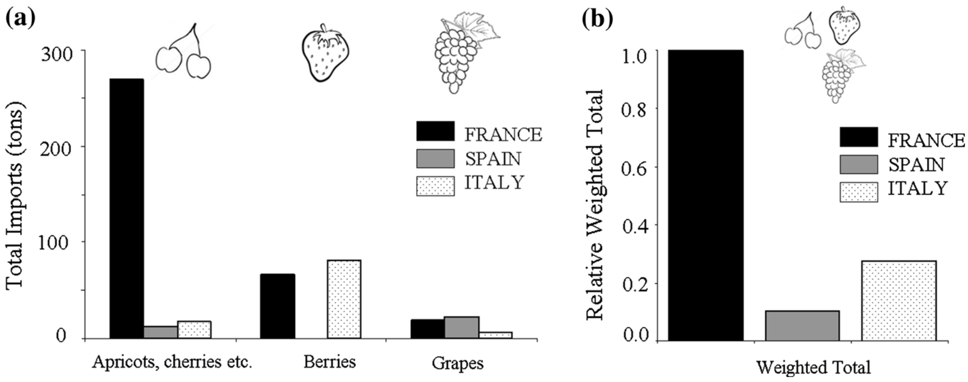

Fig. 3 Estimated SWD Propagule Pressure in France, Italy and Spain in the five years before the first reports (2008), estimated as tons of potentially infested fruit imported. **a** Raw values are presented according to the host species considered (See *text* for details); **b** weighted values (according to Host Potential Index, Bellamy et al. 2013)

to 10 times higher than Italy and Spain, the two other highly infested European countries in which SWD was first reported in 2008.

While France was not the first country to report SWD presence (first reports in Spain and Italy in 2008, Calabria et al. 2012; Raspi et al. 2011), our study thus suggests that SWD was likely present in the South of France before the official first reports (2009), and likely also before the reports from Italy and Spain (2008). According to this hypothesis, the SWD spread in Europe could be reviewed as having started from the South of France before 2008 and then diffused towards Southern and Northern countries in the following years.

Our analysis shows indeed that the putative SWD European spreading centre is located not so far from the important port of Marseille, in line with the suggestions made by other authors about the importance of fruit sea-trade as suggested by the fact that the first records of SWD in the USA and Europe both occurred close to ports (Rota-Stabelli et al. 2013). As Fig. 1 suggests, SWD could have then spread mainly along major trade routes, such as along the directions Marseille-Dijon and Marseille-Nice along the coastline. Indeed, it has been suggested that SWD long-range dispersal could be facilitated by human transportation (Hauser 2011; Calabria et al. 2012). The recent report of isolated SWD presence in a motorway rest area in Hungary interpreted as due to infested fruit that was thrown away at the rest area (Kiss et al. 2013) seems to be an excellent example.

We should note that GP identifies the most likely area that could contain the spreading centre of a species, which does not correspond necessarily to the invasion site. As a matter of fact, the first invasion site may be not suitable for spreading (for instance a city for insects feeding on fruit). In this sense, the area around Avignon identified by our GP analysis should be considered as the most likely spreading centre (the site from which SWD spread), but not necessarily also as SWD first invasion area (the first site of SWD arrival). Additionally, biological invasions may derive from more than one first invasion sites (e.g. Ciosi et al. 2008) and spreading may not always occur from the starting point, but also from secondary (and possibly more than one) invasion sites (Papini et al. 2013). Computer simulations (Stevenson et al. 2012) showed GP to better perform than other methods traditionally used to identify the source of an invasion (e.g. spatial mean or kernel density models), especially as the number of sources increased, thus being an optimal method to detect multiple invasion/spreading points (Stevenson et al. 2012). In our case, GP suggested only one area with a high probability of being the spreading centre. We can thus conclude that, given the currently available data, the most parsimonious scenario is the spread of SWD from a unique area (around Avignon, France) to the rest of Europe, with Spain and Italy being the first colonized countries. Future studies should investigate whether the identified area around Avignon also represented the first invasion point.

The reliability of the GP approach depends on the accurateness and coverage of distribution data, and biased sampling may provoke biased results. However, in the case of alien species, it can be very hard to collect precise and standardized data in the very first period after invasion. The GP technique hence provides interesting preliminary results that should be checked and compared to other data, such as population genetic markers. In particular, GP approach allows prioritizing investigations on the source populations, thus identifying areas that should be preferentially included in following researches. For example, our analysis indicates as worthwhile to be investigated with molecular tools the area around Avignon, a region whose importance is not necessary evident from presence data alone. Future approaches, considering both local small scale movements of imported fruits from arrival sites to markets and population genetics (in particular genetic sampling according to the likelihood map produced here) will likely provide more knowledge about this recent invasion.

Fresh fruit imports data highlight that France imported fresher and potentially contaminated fruits than Spain and Italy in the years before SWD report, thus having experienced, likely, a higher propagule pressure. While importations levels differ among countries according to the fruit species, our results clearly show that when considering all the hosts together, weighed by their different potential as SWD hosts, France has a greater estimated SWD propagule pressure than Spain and Italy (Fig. 3).

However, imports are by far higher in many other European countries, such as Finland, UK, Denmark, Germany etc. (Table S3, Supplementary materials). Why didn't SWD invade these countries first? There are two main, non-mutually exclusive explanations which concern propagule pressure and establishment likelihood. First, the countries with the highest propagule pressure actually imported very high quantities of grapes, a less-preferred host of SWD (Bellamy et al. 2013). Indeed, when removing grapes, France becomes the 4th country with the highest estimated propagule pressure (Table S3, Supplementary materials). Secondarily, an IAS should find, after its arrival, a suitable habitat, compete with indigenous species and avoid extinction due to Allee effects (reduced fitness when conspecific density is low, Taylor and Hastings 2005, Drake and Lodge 2006) and chance population fluctuations typical of small introduced populations (Pimm 1989) in order to successfully establish a reproductive population (reviewed in Simberloff 2009). Possible differences in one or more of these aspects (especially in prevention/sanitation measures and habitat suitability) should be thus considered in the future in order to explain SWD invasion pattern in Europe.

In the "era of globalization", increased trade in commodities has resulted in a legacy of biological invasions (Hulme 2009). Our study provides a first step in the comprehension of the pathways of introduction and the invasion history of one of the most recent and most socially dangerous IAS. In addition, results presented herein may give a contribution in understanding ecological factors influencing the current and future distribution of invasive species. Tracking the origin and distribution of invaders are indeed crucial for developing strategies/recommendations to prevent multiple reintroductions of the same species or invasions of new species. This knowledge can improve the decision-making in sanitation, management, and, as a consequence, improve the effectiveness of pest management decisions. As the understanding of invasion patterns strongly depends on the accuracy of the presence/absence data about the pest in the very first years of its arrival (as well showed by the Geoprofiling analysis), the development of effective, standardized and area-wide sampling networks will be a necessary step in the future.

In summary, our results overturn the current opinion that recognizes in Spain and Italy the two first European countries invaded by SWD, and highlight how Geographic profiling, despite some inherent limitations (Papini et al. 2013), can represent an efficient technique to track down invaders colonization patterns, especially when coupled with analyses of international trade.

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