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Spread modelling: a suitable tool to explore the role of human-mediated dispersal in the range expansion of the yellow-legged hornet in Europe

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ABSTRACT

Invasive species can spread locally on their own and can be introduced at long distance by humans. Here, we show how a spread model can be used to explore the role of humans in the range expansion of the invasive yellow-legged hornet, *Vespa velutina nigrithorax*, in Europe with a special focus on some islands. In 2017, the hornet distribution in France, southern Belgium, south-eastern Germany and northern Spain could largely be explained by the insect's own dispersal while the occurrence in Portugal, Italy, the Netherlands and Great Britain likely results from human-mediated dispersal. However, in the following years, it could spread to Portugal, Italy and Great Britain also by its own means. The yellow-legged hornet has likely reached the Channel Islands by its own flight but it could hardly reach the Mediterranean islands. Hence, the infestation in Majorca likely results from an accidental introduction. When simulating human-mediated dispersal in the Mediterranean islands, the hornet density would remain relatively low anyhow. Assessing the means of dispersal is important in terms of pest management as the target is either to reduce the spread rate and the population density, or to reduce the risk of entry.

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1. Introduction

There are more and more biological invasions documented throughout the world and they are mainly driven by international trade (Pyšek et al. 2010) and/or climate warming (Walther et al. 2009). The number of biological invasions is unlikely to drop since there is no sign of alien species saturation so far (Seebens et al. 2017). Alien species have large economic impacts (Bradshaw et al. 2016) and increasing pressures on biodiversity (Butchart et al. 2010). Furthermore, in Europe, the spread rate of alien insect species is significantly higher for species detected after 1990 than before, thus showing the potential effects of political changes on the freedom of trade (e.g., the collapse of the Iron Curtain and European Union facilitating the trade within European countries) (Roques et al. 2016). The rapid spread of several plant pests has been observed during the last few years. For instance, the western conifer-seed bug, *Leptoglossus occidentalis*, was first detected in Europe (Italy) in 1999 and it is now present in 26 European countries (CABI 2017a). The box tree moth, *Cydalima perspectalis*, was detected in Europe (Germany) in 2007 and it is now present in 20 European countries (CABI 2017b). These rapid spreads question the role of humans in the dispersal of pests at long distance.

Several pathways explaining the invasion of alien species have been highlighted (Hulme 2009), such as live plant imports for the introduction of plant pests (Liebhold et al. 2012) or transportation of wood products for the introduction of forest pests (Yemshanov et al. 2012). Although accidental transportation of species are generally associated with a closely linked commodity, they can also be transported with another commodity neither providing a habitat nor a resource to the species. In this case, the alien species is simply a hitchhiker. Identifying the introduction pathway is thus a very complex task.

If human-mediated dispersal can explain the dispersal of a species from one continent to another, it can also explain long distance jumps observed within the invaded range. For instance, the horse-chestnut leaf miner, *Cameraria ohridella*, is known to disperse over long distance in Europe with the transport of infested leaves by car traffic (Gilbert et al. 2004). The pine wood nematode, *Bursaphelenchus xylophilus*, is known to disperse at long distance in China with the transport of infested wood material (Robinet et al. 2009). The emerald ash borer, *Agrilus planipennis*, is known to disperse at long distance in the US with the transport of fire wood (Muirhead et al. 2006).

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Identifying the pest pathway and disentangling the role of human mediated dispersal from active dispersal is challenging at both large and fine spatial scales. Several tools are available with large variation in their effectiveness. For instance, interception data are largely biased and cannot be used to assess the invasion likelihood with the transportation of a given commodity because inspection usually targets a set of quarantine pests and commodities only (Eschen et al. 2015). Sentinel trees can be used to estimate the likelihood of transporting a pest with a living plant grown in a given area (Roques et al. 2015). Genetic analyses can be done to track the origin of the individuals among continents (Boissin et al. 2012; Lombaert et al. 2010) but also at finer scales (Robinet et al. 2012). However when species can disperse very fast on their own and when there is low genetic variability, the populations are generally not differentiated and thus genetic analyses are poorly informative.

The yellow-legged hornet, *Vespa velutina nigrithorax*, is one of these fast spreading invaders. Native to Asia, it was first discovered in Europe (France) in 2005 (Haxaire et al. 2006; Monceau et al. 2014). Niche models predict that a large part of Europe is suitable for the species establishment and this suitable area could further expand with climate warming (Barbet-Massin et al. 2013, 2018; Villemant et al. 2011a). The yellow-legged hornet is now present in a large part of France and it is also spreading in Spain, Portugal, Italy, Germany, Belgium and Great Britain (Figure 1). A young queen was also recently detected in Switzerland (JRC 2017). The occurrence of satellite colonies far from the species main distribution in France observed in 2009 may suggest human-mediated dispersal within France (Darrouzet 2010). However, a study based on spread simulations concluded that these satellite colonies do not necessarily result from accidental transport by human activities (Robinet et al. 2017). The estimated spread rate of the yellow-legged hornet in France was 78 km/year and this high spread rate is consistent with data collected in flight mill experiments (Sauvard et al. 2018). Since the hornet invasion in Europe likely results from the introduction of very few or a single multi-mated female with the import of bonsai pots (Arca et al. 2015), French colonies can produce early diploid males as a result of inbreeding (Darrouzet et al. 2015) linked to a genetic bottleneck (Arca et al. 2015). Consequently, the genetic variability would probably be too low in Europe to use genetic markers in order to disentangle human-mediated dispersal from active dispersal within this area. We thus use the spread model previously developed for France to test various hypotheses regarding the means of dispersal to different places in Europe.

In this study, we determine the potential spread of the yellow-legged hornet with and without

Figure 1. Observed spread (in red) of the yellow-legged hornet in Europe (in September 2017; derived from the map provided by Q. Rome, MNHN-INPN, http://frelonasiatique.mnhn.fr) and the islands considered in this study. The Channel Islands (Jersey and Guernsey) and Majorca were colonized by the hornet whereas Corsica, Sardinia and Sicilia were not colonized. The black dot in France indicates the location of first record of the yellow-legged hornet in Europe.
Source: reproduced by the authors from the map provided by Q. Rome, MNHN-INPN, http://frelonasiatique.mnhn.fr

human-mediated dispersal at the European scale and at local scales. Since several islands have been colonized (Great Britain, Majorca and the Channels Islands; Figure 1), spread modelling was used to determine whether the invasion of yellow-legged hornet on these islands is likely due to human activity or due to the hornet own dispersal. On the other hand, several islands seem still free from the hornet (e.g., Corsica, Sardinia, and Sicilia), and we explored whether they could be colonized either by natural spread or by human activities. The objective of this paper is to illustrate how spread modelling can help to clarify the role of human-mediated dispersal, and accordingly, give directions about possible pest management.

2. Study species

The yellow-legged hornet completes its biological life-cycle within one year. During winter, founder queens hibernate in various types of habitats. In spring, they emerge, disperse and build a primary nest, sometimes nearby buildings and man-made structures, to lay their first eggs. Then, as the colony grows, workers emerge and the colony builds sometimes a secondary nest, which is a permanent and much larger nest, generally hung at the top of trees (Franklin et al. 2017). The yellow-legged hornets build relatively large nests, around 60–80 cm in diameter and 60–100 cm in length (Darrouzet 2013; Rome et al. 2015). Adults mainly feed on sweet liquids and proteinaceous juice produced by the larvae and they catch a large range of insect species, and notably domestic honeybees, to feed their larvae (Villemant et al. 2011b). Various materials including plants and water are used by workers to build the nest. Hornet predation of domestic honeybees, *Apis mellifera*, and local entomofauna, together with potential allergic reactions caused by the hornet's sting, are clearly the main concerns related to the invasion of this species in Europe (Monceau et al. 2014).

3. Description of the spread model for the yellow-legged hornet

The spread model already developed combines a reaction-diffusion model to describe the hornet spread, a long-distance dispersal stochastic model to describe human-mediated dispersal, and the effects of control measures. The spread is then simulated on an area considered as favourable for the species survival (elevation below 791.5 m). Each model component is briefly described hereafter but more details are given by Robinet et al. (2017).

3.1. Reaction-diffusion model

The reaction-diffusion model is based on the Fisher equation:

$$\frac{\partial N}{\partial t} = D\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) + rN\left(1 - \frac{N}{K}\right) \qquad (1)$$

where N is nest density (km^{-2}) which depends on time t and spatial location (x,y), D is the diffusion coefficient ($D = 984\ \text{km}^2\ \text{year}^{-1}$), K is carrying capacity (0.06 nest.km^{-2}), and r is growth rate (year^{-1}) which depends on climatic conditions. From Robinet et al. (2017), r is linearly correlated with a growth index GI as follows:

$$r = -1.29593 + 0.09502 \times GI \qquad (2)$$

This growth index describes the growth potential of a population during favorable conditions (GI, varying from 0 to 100). Growth index values were extracted from a CLIMEX model previously developed for the yellow-legged hornet (Ibáñez-Justicia and Loomans 2011) and applied to Europe based on CliMond high resolution climate database (Kriticos et al. 2012).

3.2. Human-mediated dispersal model

We choose at random whether there is a human-mediated dispersal event each year based on a yearly probability of observing such event, *Pldd*. Then, if there is a human-mediated dispersal event, the destination location is chosen at random where human population density is above a given threshold ($H = 125$ inhabitants.km^{-2}).

3.3. Control measures

To faithfully describe the population dynamics, it is necessary to take into account the effects of control measures (e.g. nest removal and destruction) as they can profoundly impact the population density. The intensity of control measures, $C(h)$, is given by:

$$C(h) = \frac{\alpha h}{\frac{1}{2\rho} + h} \qquad (3)$$

where h is the human population density, ρ is the proportion of a given area that one person can observe ($\rho = 7.85\ 10^{-5}$ for a cell of 10 km $\times$10 km), and α is the maximal control intensity if all nests were detected ($\alpha = 0.3$ meaning that 30% of detected nests are supposed to be destroyed). The nest density at each time step is then multiplied by

$$(1 - C(h)).$$

4. Simulations of the spread of the yellow-legged hornet in Europe and in the islands

4.1. Input variables

The growth rate, human population density and elevation were projected at the scale of Europe (Figure 2). The growth rate was relatively low in mountainous areas such as the Alps but also in central Spain compared to other parts in Europe.

4.2. Model simulations

We explored the potential spread of the yellow-legged hornet with and without human-mediated dispersal at different scales, focusing on Europe and, at smaller scales, on a set of European islands (Channel Islands, Majorca, Corsica, Sardinia and Sicilia). We simulated the spread from 2004 (with 2 nests at the initial infested location; 44.42721°N, 0.58317°E) to 2017 for comparisons with observations, and to 2030 to make projections in the future. When simulating spread with human-mediated dispersal, the probability to accidentally move the yellow-legged hornet every year was set to $Pldd = 1$ (i.e., each year, the yellow-legged hornet is accidentally introduced elsewhere). Since the model with the human-mediated component is stochastic, we ran 100 replicate simulations and calculated the average spread. The R scripts used to do these simulations are available at: https://zenodo.org/record/1193663.

4.3. Spread at European scale

The spread model was applied to Europe on a grid resolution of 20 km × 20 km. We have notably focused on the potential spread in Great Britain (an island already colonized by the hornet) and on Spain, where the observed spread is currently relatively limited.

4.4. Spread at smaller scales

We explored the way the hornet could spread to several islands: the Channel Islands, namely Jersey and Guernsey, and Majorca (islands already colonized by the yellow-legged hornet; Figure 1) and Corsica, Sardinia and Sicilia (islands not yet colonized by the yellow-legged hornet). First, we calculated the likelihood of transporting the hornet to these islands, in a favorable area. For this purpose, we chose at random in Europe the destination location within the favorable area for both, hornet survival (elevation below 791.5 m) and human-mediated dispersal (human population density above 125 inhabitants.km^{-2}). We made 100,000 replicate simulations and calculated the percentage of locations falling in each island. Secondly, the spread model was applied on a grid resolution of 10 km × 10 km on two spatial extents: one grid centered on the Channel Islands and another grid covering the Mediterranean islands (Majorca, Corsica, Sardinia and Sicilia). Since the probability to introduce the yellow-legged hornet in these islands was very low (see results), we had to restrict human-mediated dispersal to each of these islands separately to explore whether once introduced the hornet could establish there and spread.

5. Results of the simulations

5.1. Spread in Europe

Results in 2017. The simulated spread of the yellow-legged hornet across Europe in 2017 was relatively consistent with observations (Figures 1 and 3). The actual spread of the hornet in Europe is likely a

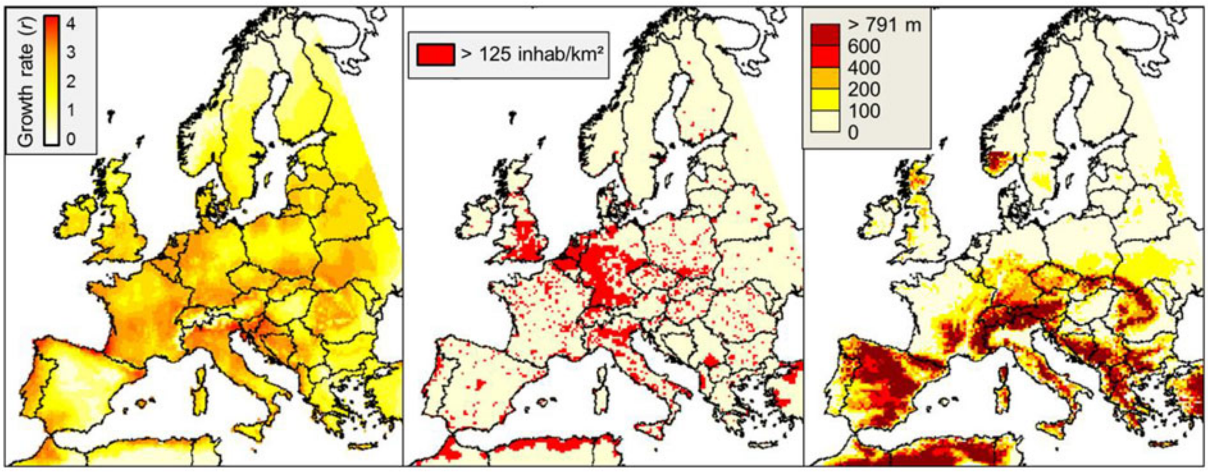

Figure 2. Input variables: predicted growth rates estimated from the Growth Index (CLIMEX model), areas where human population density is above 125 inhabitants/km^2 and areas favourable for the establishment of the yellow-legged hornet (below 791.5 m asl) in Europe.

combination of the insect's own dispersal and human-mediated dispersal because the observed spread is intermediate between the two extreme scenarios (with or without human-mediated dispersal) (Figure 3). It confirms that the spread in France could mainly result from the insect's own dispersal, since nearly all France is predicted to be colonized in the scenario without human-mediated dispersal. It also shows that the species may have spread naturally in southern Belgium and in south-eastern Germany, as well as in northern Spain. However, spread in Portugal, Italy, the Netherlands, and Great Britain likely results from accidental introductions. Surprisingly, the species tends to spread rapidly toward the north-eastern direction and not so much in the southern direction.

Results in 2030. Due to its own dispersal capability, the yellow-legged hornet could continue to spread by 2030, especially in central Europe but also in Italy and Portugal (Figure 3). The hornet could also spread naturally in Great Britain (likely from northern France or Belgium). Spain would continue to be relatively unfavourable for the species spread. Human-mediated dispersal could considerably enhance the hornet spread within Europe. In particular, Great Britain will likely be colonized by the two different dispersal means: natural dispersal of the hornet and human-mediated dispersal.

5.2. Spread in the islands

Risks of introduction. Following the human-mediated dispersal component of the spread model, the likelihood of introducing the hornet to Sicilia was 0.925%, to Sardinia was 0.206%, to Majorca was 0.095%, to Corsica was 0.032% and to the Channel Islands was 0%. These risks are therefore relatively low. In addition, there is clearly no chance that the yellow-legged hornet is accidentally transported in the Channel Islands because of human activities.

Results in 2017. Spread simulations clearly show that the Channel Islands were colonized because of the yellow-legged hornet own dispersal (Figure 4). Conversely, the Mediterranean islands (Majorca, Corsica, Sardinia and Sicilia) cannot be naturally colonized. It means that Majorca was likely colonized due to an accidental introduction by humans. When simulating human-mediated dispersal in these Mediterranean islands, the hornet could effectively establish in Majorca, in Sardinia and in Sicilia (Figure 5). Only a small area in northern Corsica would be colonized. On the whole, the hornet density in these islands would be relatively low.

Results in 2030. Ongoing simulations do not show important changes in the future in these islands. The hornet density could increase in the Channel Islands whereas it would remain very low in the Mediterranean islands (if introduced).

6. Discussion

Our model globally shows that the yellow-legged hornet could rapidly colonize countries such as Belgium, the Netherlands, Germany as well as central Europe. It is in agreement with previous niche models developed at this geographic scale (Barbet-Massin et al. 2013; Ibáñez-Justicia and Loomans

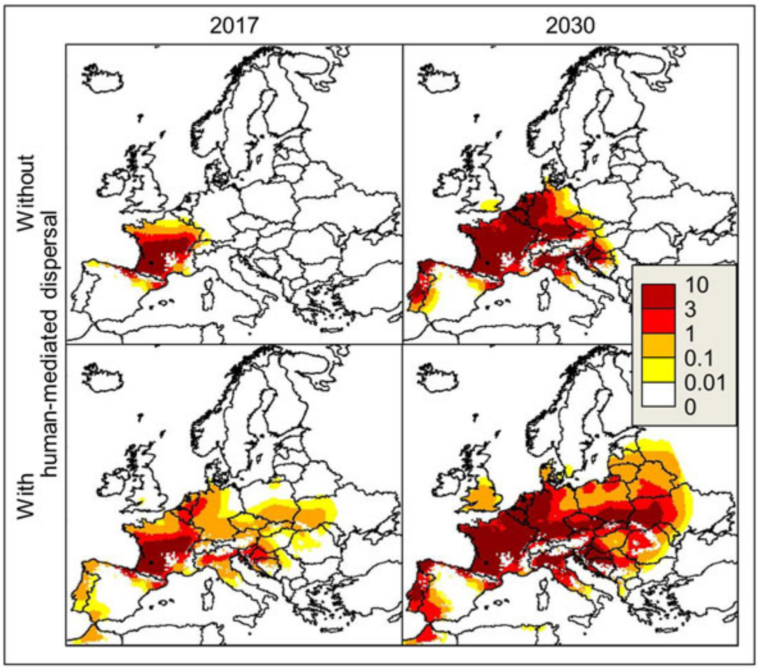

Figure 3. Potential spread of the yellow-legged hornet in Europe in 2017 and 2030, with and without human-mediated dispersal. The gradient colours represent the nest density (i.e., number of nests per 10 km × 10 km).

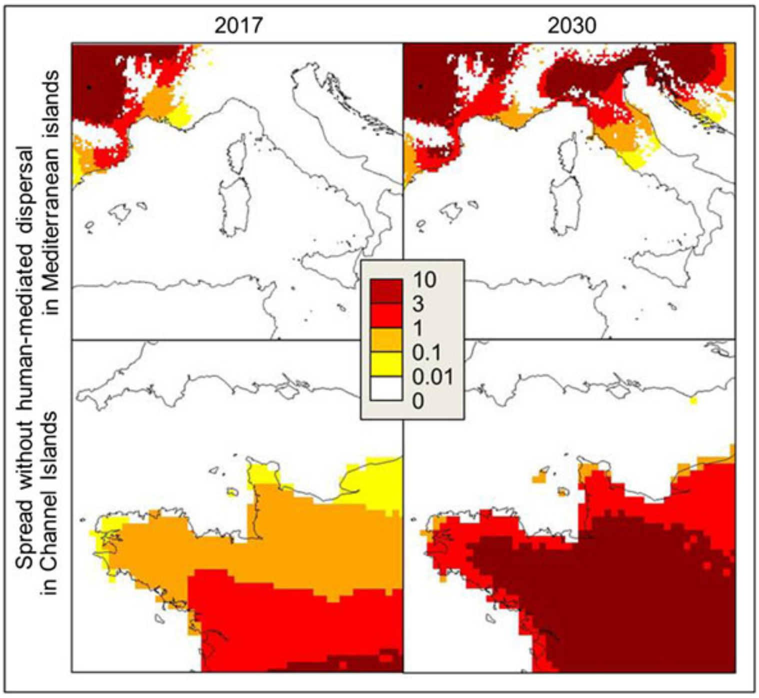

Figure 4. Simulated spread of the yellow-legged hornet in Mediterranean islands and Channel Islands in 2017 and 2030 without human-mediated dispersal. The gradient colours represent the nest density (i.e., number of nests per 10 km ×10 km).

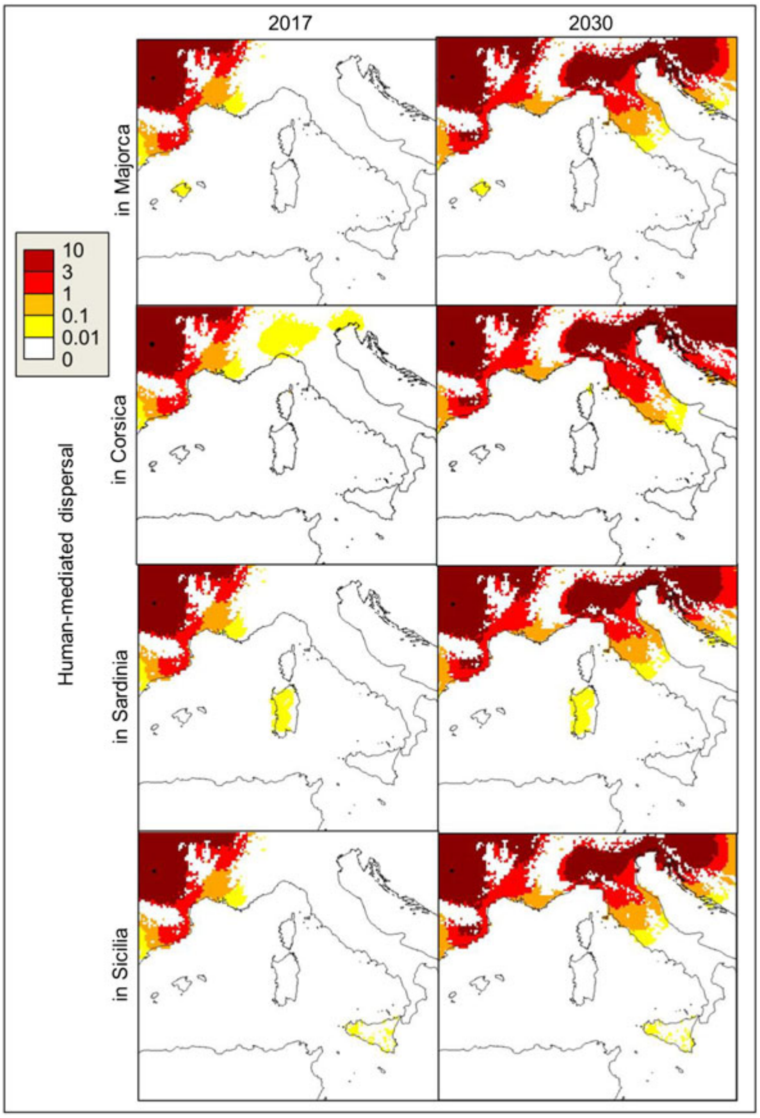

Figure 5. Simulated spread of the yellow-legged hornet on Mediterranean islands in 2017 and 2030 with human-mediated dispersal in each island. The gradient colours represent the nest density (i.e., number of nests per 10 km ×10 km).

2011; Villemant et al. 2011a). It shows that the hornet has few dispersal barriers in these areas.

With the spread model, we have been able to draw conclusions about the means of dispersal across Europe. Obviously, the rapid spread of the yellow-legged hornet throughout Europe is a mix of self-dispersal and human-mediated dispersal. However, we can go further and discriminate the means of dispersal according to the countries and regions and also point out areas where the hornet spread is limited.

Spain, which is very close to the first record of the yellow-legged hornet in Europe, surprisingly appears not highly favourable for the species. This slow spread can be explained by two factors: 1) the Pyrenean mountains could represent a natural barrier for the dispersal of the species (Goldarazena et al. 2015), and 2) central Spain is not very favourable for the species growth (Figure 2). The limited spread predicted by our model is consistent with a niche model previously developed on the Iberian Peninsula (Bessa et al. 2016). Based on a set of 9 predictors (related to vegetation productivity, temperature, precipitation, distance to rivers, and land cover), this previous model also indicated that central Spain was unfavourable for the species establishment. Only small parts of Spain, such as western Galicia, appear highly favourable for the species spread (Rodríguez-Lado 2017).

Spread is relatively limited in Italy too. Like in Spain, there is a high mountainous barrier separating the country from France (the Alps). The north-western part of Italy was likely colonized due to the hornet own dispersal through a narrow corridor close to the seaside (Figure 3; Bertolino et al. 2016) while the infested region in north-eastern Italy probably resulted from an introduction.

The potential spread in Great Britain is very likely because of both, insect dispersal and accidental introductions. It is in agreement with a previous modelling study conducted in Great Britain which shows that the yellow-legged hornet could rapidly colonize a large part of the country, even from a single infested site (Keeling et al. 2017). Genetic analyses revealed that the individuals in Great Britain probably originated from the European population and not from Asia (Budge et al. 2017), confirming bridgehead effects (i.e., human-mediated dispersal within Europe). Furthermore, dead individuals were found in camping equipment that has been previously used in central France and in imported timber products, showing multiple possible pathways for the hornet to cross the English Channel.

Regarding the potential colonization of islands, we have pointed out different cases: the yellow-legged hornet could reach naturally some islands (e.g., Great Britain and the Channel Islands) but not others (e.g. Mediterranean islands). Only an introduction by humans could explain the infestation of Majorca. Although the probability of introducing the hornet in the Mediterranean islands is relatively low, one bias in this analysis is that we used the number of inhabitants per km^2 as a proxy of the probability to accidentally transport the hornet. Yet, a lot of tourists who are not inhabitants of these Mediterranean islands visit these areas and may also carry inadvertently the hornet. The probability of introduction could therefore be underestimated in our study. However, we have shown that, even if introduced, the hornet population could hardly grow and spread on these Mediterranean islands.

Although there are numerous examples of species colonisation in islands because of human-mediated dispersal, it is relatively uncommon to report that some individuals were able to disperse to islands based on their own dispersal capabilities. In the spread model, we made the assumption that the spread mechanism was the same above the ground and overseas. However, this mechanism may not be exactly the same. When flying above the ground, the insects may do one or several stops along their dispersal trajectory, which is clearly not possible overseas. As a result, the species could perhaps spread at shorter distances overseas. Nevertheless, atmospheric conditions above open water can drive the dispersal flight, especially the distance and direction (Wood et al. 2006), and they can eventually enhance the dispersal capability of individuals. Indeed, insects are able to disperse at very long distances above open water. For instance, the dragonfly, *Pantala flavescens*, is able to cross at least 3500 km of ocean from southern India to eastern Africa (Anderson 2009) and the African desert locust, *Schistocerca gregaria*, is able to cross 5000 km of ocean from West Africa to the Caribbean (Lorenz 2009). In our study, the distance travelled above open water is much lower: the hornet was potentially able to fly about 30 km from northern France or Belgium to southern Great Britain and about the same from France to the Channel Islands. The distance to reach the Mediterranean islands is much higher, at least 90 km (except Sicilia which is very close to southern Italy but which is not yet colonized). The spread model shows that the hornet would not be able to fly this distance; however it is unknown whether special atmospheric conditions would permit the hornet to reach occasionally these islands.

Another type of uncertainty is the effect of climate warming on the ability of species to reach further locations. Temperature is known to affect the insect flight performance. For instance, the nocturnal flight activity of females of the pine processionary moth, *Thaumetopoea pityocampa*, linearly increases with the mean night temperature (Battisti et al. 2006). In southern Great Britain, the continuous increase of the number of migratory Lepidoptera species (moths and butterflies) reported each year is likely attributed to climate warming (Sparks et al. 2007). Until now, there is no evidence of such effects on the yellow-legged hornet. However, further studies on the effects of temperature on flight performance could be done in flight-mill experiments at various temperature conditions. If such effects occur, then the diffusion coefficient in the spread model can be modulated by temperatures in future modelling studies.

In the spread model, we assumed that the maximal elevation limit was 791.5 m asl since this was the highest elevation where the hornet was found following the calibration dataset previously used (occurrence data between 2004 and 2009; Robinet et al. 2017). However, this limit is relatively uncertain. Even if the hornet could be found much higher, the mountainous areas would remain important dispersal barriers and the potential spread throughout Europe would probably not be impacted so much.

Although there is an uncertainty about the validity of the spread model outside France (where it has been originally validated), this study provides a first exploratory analysis about the potential spread of the yellow-legged hornet throughout Europe and especially in some islands. It also illustrates how we could clarify the role of human-mediated dispersal in the spread of a fast invader.

7. Consequences in terms of pest management

Following this study, we can differentiate: (i) areas that could be colonized by the yellow-legged hornet because of its own flight capabilities, (ii) areas that could be colonized because of human-mediated dispersal, and (iii) areas that could be colonized due to these two dispersal means. Consequences in terms of pest management are quite different.

In the first case, it is difficult to prevent the arrival of the invasive species because the pressure of the population density will inevitably push this colonisation wave. However, it is possible to reduce the population density and slow the spread (see Robinet et al. 2017). The control of nest density could be the best solution. However, the main problem is to locate *V. velutina* colonies. Although some areas could be more attractive for the yellow-legged hornet (Monceau and Thiéry 2017), at the present day, we do not have efficient tools to locate their nests. We are able to locate nests in top of trees only when leaves fall in autumn. Nevertheless, when it is possible to eliminate such colonies, it is too late for an efficient control of this invasive species as several gynes have already left their colonies to reproduce and to disperse. It is thus necessary to develop new tools to locate colonies before the departure of these gynes. Some scientific projects try to resolve this problem by using drones and thermic camera to locate colonies in trees, by using a harmonic radar to track hornets and to locate their colonies (Milanesio et al. 2016, 2017).

In the second case, the date of arrival of the invasive species is highly stochastic and no one can currently predict when it can invade this area. However, it is possible to reduce the risk of entry by alerting importers of this risk and by eventually re-enforcing visual checks and treatments of products coming from an infested area and products which have transited in such area.

In the third case, both types of pest management should be considered.

Moreover, in all cases, it could be important to use also selective traps to capture hornets. Baited traps are generally regarded as the best means for controlling wasps and are commonly used. However, concerns about their use have been raised because they can have significant effects on non-target species (Rome et al. 2011) when they are constituted by food baits (proteins, carbohydrates). To maximize captures of *V. velutina* while minimizing captures of non-target species, traps must be selective: for example, some traps incorporate holes allowing small insects to escape and employ pheromone-based baiting. Pheromones are generally used in insect pest management and provide significant financial and environmental benefits. Indeed, pheromones have been identified in several types of insects and are the safest of all currently available insect control products (Minks and Kirsch 1998). Several successful pheromone-based methods for directly controlling insect pests work at least as well as the conventional pesticides they have replaced (Cardé and Minks 1995). Our study raises the importance to develop such selective traps.

Disclosure statement

No potential conflict of interest was reported by the authors.

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