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To cite this version:

Christelle Robinet, Christelle Suppo, Éric Darrouzet. Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. Journal of Applied Ecology, 2017, 54 (1), pp.205-215. 10.1111/1365-2664.12724 . hal-02625274

HAL Id: hal-02625274
https://hal.inrae.fr/hal-02625274v1

Submitted on 26 May 2020

Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures

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Running title: Rapid spread of invasive yellow-legged hornet

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Summary

1. The invasive yellow-legged hornet was first discovered in Europe, in south-western France, in 2004. It has since spread very rapidly and has caused significant mortality among honey bees and native entomofauna. It also poses a risk to humans because its sting provokes allergic reactions. The objectives of this study were the following: (i) to disentangle the roles played by human-mediated dispersal and self-mediated dispersal in the species' rapid range expansion and (ii) to estimate the intensity of control measures in France and determine what needs to be done to slow the hornet's spread and dramatically reduce its population densities.

2. A mathematical model was developed to describe the hornet's potential spread. This model included parameters describing the population growth rate, carrying capacity, self-mediated dispersal, human-mediated dispersal and the efficacy of control measures (i.e. the destruction of detected nests). Model parameters were estimated using 2004–2009 occurrence data for France and the model was then validated using 2013 occurrence data. Several scenarios were tested: human-mediated dispersal was present or absent and control intensity varied. Then, the species' spread in coming years was simulated (from 2013 to 2020).

3. Despite some uncertainty on the value of the parameters, this model is relatively robust. Human-mediated dispersal may not be necessarily responsible for the hornet's rapid range expansion; the species could spread rapidly on its own. It is likely that, to date, an average of 30–40% of detected nests have been destroyed each year.

4. Increasing the percentage of destroyed nests from 30 to 60% could reduce the species' spread by 17% and its nest density by 29%. If 95% of nests are destroyed, the species' spread and nest density could decline by 43% and 53%, respectively.

5. *Synthesis and applications*. The mathematical model developed in this study shows that human-mediated dispersal of the invasive yellow-legged hornet may not be the only factor explaining the hornet's rapid range expansion and that controlling this invasive pest is still possible. Therefore, there is an urgent need to reduce self-mediated dispersal and to intensify and improve control measures to diminish the species' impact and prevent its further spread. Control measures could combine the mechanical removal and destruction of individuals or infested materials with biological control techniques.

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Key-words:

biological invasion, CLIMEX, insect, dispersal, long distance, nest, reaction-diffusion model, pest management, spread model, *Vespa velutina*

Introduction

The number of biological invasions has grown considerably over recent decades, mainly due to the increased frequency and facility of human travel and international trade (*e.g.*, Levine & D'Antonio 2003; Evans & Oszako 2007). Terrestrial invertebrate species account for a large proportion of the invasions that have occurred in Europe (Hulme *et al*. 2009). Most such species come from Asia and are largely found in France and Italy (Roques *et al*. 2009). Social insects are highly invasive because they can easily adapt their reproductive modes and social structures to match new environments (Beggs *et al*. 2011; Arca *et al*. 2015). For instance, there have been a large number of introductions of *Vespidae* species across the world (n = 34) but only some (n = 9), all of them eusocial, have been found to have negative ecological effects (Beggs *et al*. 2011).

The yellow-legged hornet, *Vespa velutina*, is the first exotic *Vespidae* species to successfully arrive and establish itself in Europe (Beggs *et al*. 2011). It was first discovered in southwestern France in the summer of 2004, and the first individual hornet was caught and identified in 2005 (Haxaire *et al*. 2006; Villemant *et al*. 2006). It was probably introduced via bonsai pots imported from China and, according to genetic analyses, likely came from the eastern Chinese provinces of Jiangsu and Zhejiang (Arca *et al*. 2015). It has since very rapidly expanded its range in France and is now spreading to neighboring European countries. It is found throughout most of France (more than 2/3 of the country has been colonized; Rome *et al*. 2013); it is also present in Spain (López *et al*. 2011), Portugal (Grosso-Silva & Maia 2012), Italy (Federazione Apicoltori Italiani 2013), and Germany (Rome *et al*. 2015). While a single male was observed in Belgium in 2011, very close to the French border (Rome *et al*. 2012), the species does not seem to have established itself in that country yet (pers. com., Dr. J.C. Grégoire, Université Libre de Bruxelles, Belgium, in 2014). A large proportion of Europe, including France, seems to be suitable for the species' establishment (Villemant *et al*. 2011a), and an even larger area could become suitable in the future given various climate change scenarios (Barbet-Massin *et al*. 2013). To more accurately assess the potential spread of an invasive species, it is important to consider the species' dispersal abilities. Along with environmental heterogeneity, dispersal ability can shape a species' distribution and affect population growth (Roques *et al*. 2008). In France, the yellow-legged hornet spreads at a rate of around 100 km/year, and several nests have been found more than 200 km from the invasion front (Villemant *et al*. 2011a; Rome *et al*. 2012). Three locations at which infestations have been observed are thought to have been colonized as a result of long-distance dispersal events (Villemant *et al*. 2011a). It is common to find pioneer colonies of invasive species at such large distances from the invasion front because of accidental transport by humans. Indeed, in models of pest spread, human population density is a key factor that can explain such jumps (*e.g.*, see the European gypsy moth, Sharov & Liebhold 1998; the horse-chestnut leaf miner, Gilbert *et al*. 2004; the emerald ash borer, Muirhead *et al*. 2006; the pine wood nematode, Robinet *et al*. 2009; the pine processionary moth, Robinet *et al*. 2012). However, in case of the yellow-legged hornet, distinguishing between dispersal patterns caused by self-mediated flight versus those caused by human-mediated transport is challenging because the hornet can fly very long distances. Gynes—females destined to become queens and found new colonies—can fly an average of 18 km/day and can cover up to 200 km over 10 days in flight mill experiments (pers. com., Dr. Daniel Sauvard, INRA, France). Although yellow-legged hornet gynes might not have the same flight capabilities in nature, they may cover very long distances over their extensive flight periods (*i.e.*, before and after hibernation).

At present, France is clearly the most infested country in Europe. Although the full impact of the yellow-legged hornet is not yet known, some concerns are hornet predation of domestic honey bees (*Apis mellifera*) and local entomofauna and the allergic reactions caused by the hornet's sting (Monceau *et al*. 2014). As soon as the yellow-legged hornet was detected in France, beekeepers, among others, became worried about the possible impact the species could have on honey bees and tried to eliminate it by removing and destroying its nests. However, the overall control intensity and efficiency (*e.g.*, the effects on population size over time) of such control efforts remain unclear. Due to the hornet's rapid range expansion in France and the threat it poses, there is an increasing demand for effective control measures. Even if traps and other control methods are available, they remain inefficient and do not exclusively target the yellow-legged hornet. Mass trapping using food baits could have negative impacts on native entomofauna, and it is uncertain how much it would truly affect the yellow-legged hornet (Rome *et al*. 2011; EEA 2012).

Consequently, the objectives of this study were the following: 1) to disentangle the roles played by human-mediated dispersal and self-mediated dispersal in the rapid range expansion of the yellow-legged hornet in France, and 2) to estimate the intensity of control measures in France and determine what needs to be done to slow the hornet's spread and dramatically reduce its population densities. To this end, a spread model was developed and various scenarios were tested.

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Materials and methods

STUDY SPECIES

The yellow-legged hornet produces one generation a year. After hibernation, fertilized queens found new colonies. They build relatively large nests that are around 60–80 cm in diameter and 60–100 cm in length and that can be easily detected (Darrouzet 2013; Rome *et al*. 2015). They are usually located at the tops of trees but can also be found in bushes, in open buildings, or on walls. Since an object of 1 cm x 1 cm can easily be seen from 1 m away and given that nests are generally at least 50 cm x 50 cm, according to the intersect theorem, it should be possible to detect the hornet's nests from up to 50 m away. This detection distance is also the one used when conducting surveys for animals such as rabbits (Mutze *et al.* 1998).

Yellow-legged hornets catch a large range of insect species, but especially domestic honey bees (37%), to feed their larvae (Villemant *et al*. 2011b). Adults mainly consume the sweet liquids and proteinaceous juice produced by the larvae. Workers also gather a variety of suitable materials for nest building and nest maintenance (*i.e.*, plants and water). Because yellow-legged hornets can disperse over long distances, exploit a wide range of prey species, and build/maintain their nests with readily available materials, they likely face few limiting factors as they spread. In addition, they compete very little with other *Vespa* species (Arca *et al*. 2015).

SPECIES OCCURRENCE DATASETS USED IN PARAMETER ESTIMATION AND MODEL VALIDATION

It is difficult to monitor the rapid spread of an invasive species across broad spatial scales. In the case of the invasive yellow-legged hornet in France, this is made in the form of a citizen science project organized by the French Museum of Natural History (MNHN, Paris). General information on the yellow-legged hornet and also a guide that can be used to distinguish it from other species is provided on a special webpage created by the museum (http://frelonasiatique.mnhn.fr/). Anyone can report a species sighting by filling out a form indicating the precise location of the sighting, describing what they observed, and sending either a photograph (of the nest or insect) or sending a dried insect by regular mail. The MNHN then confirms the species' identity, and the record is entered into a database.

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The MNHN provided the 2004–2009 occurrence data used in this study (*e.g.*, number of nests, nest spatial coordinates, and the year of first observation; see maps in the Supplementary Material of Villemant *et al*. 2011a). A total of 4,802 nests were observed between 2004 and 2009 (2 in 2004, 4 in 2005, 257 in 2006, 1,670 in 2007, 1,233 in 2008, and 1,636 in 2009). This dataset was used to estimate the parameters of the spread model (see below).

The map of the species' occurrence in France in 2013 was retrieved from the webpage mentioned above; a total of 1,003 grid cells, each representing an area of 10 km x 10 km, were marked as having been invaded. Since occurrence data for the period between 2010 and 2012 were not available, this second dataset was used to independently validate the results of the model for 2013.

LOCAL DISPERSAL AND POPULATION GROWTH

A reaction-diffusion model was used to simulate local spread of the yellow-legged hornet. This model is commonly used to describe the spatial spread of invasive species (*e.g.*, Shigesada & Kawasaki 1997). The reaction-diffusion model describes not only population dispersal but also population growth. The model can be expressed using the Fisher equation:

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

where N is nest density (km^{-2}) and depends on time t and spatial location (x,y); D is the diffusion coefficient (km^2 year^{-1}); r is growth rate (year^{-1}); and K is carrying capacity (km^{-2}). This model generates a travelling wave that has a constant speed defined by:

$$c = 2\sqrt{rD} \ \text{(km year}^{-1}\text{)} \qquad \text{Equation 2}$$

The parameters c, K, and r were estimated and D was then calculated using those values and Equation 2. Some calculations (see below) were performed at the departmental level: in France, the department is an administrative division that corresponds to the European classification level NUTS3 (http://ec.europa.eu/eurostat/web/nuts/overview).

First, the local rate of spread, c, was estimated by measuring the radial distances between the range edge observed in consecutive years from 2004 to 2009 in southwestern France; the three locations at which hornet presence has been attributed to human-mediated dispersal were excluded (Villemant *et al*. 2011a; Rome *et al*. 2012).

Then, carrying capacity, *K*, was given by the highest nest density in the most infested department of France, which was where the yellow-legged hornet was initially discovered, in the southwest. This value was assumed to represent what the environment can sustain. Since plant resources used in nest building (Monceau *et al*. 2014) and prey are found throughout France, *K* was considered to be homogeneous across the country. Although nests are usually found close to rivers, this factor was not incorporated into the model because its level of spatial resolution was too coarse (*i.e.*, 10 km x 10 km; see the model description below).

Finally, growth rate, *r*, was estimated. Population growth (based on survival and reproduction) may not be homogeneous across France because it usually depends on climatic conditions, and more specifically temperature. Growth index values (*GI*, varying from 0 to 100) were extracted from a CLIMEX model previously developed for the yellow-legged hornet (Sutherst *et al*. 2007; Ibáñez-Justicia & Loomans 2011). This index describes the growth potential of a population during favorable conditions and depends on temperature, moisture, and solar radiation. To obtain a spatial estimate of *r*, we performed a linear regression between *GI* and *r*. For each infested department and for each year *i*, we calculated the annual growth rate:

$$r_i = ln\left(\frac{n_i}{n_{i-1}}\right) \qquad \text{Equation 3}$$

where n_i is the number of nests found in year *i* in the department. Then, we took the mean value of these growth rates r_i over the exponential section of the population growth curve (*i.e.*, before it reaches *K*/2). For each department, we calculated the mean of *GI* and performed the regression. Then, we used the regression equation and the *GI* values to estimate *r* for all of France. These values were then used in the logistic growth (see Equation 1).

The diffusion coefficient, *D*, was assumed to be homogeneous across France because of the fast spread rate (and thus likely few local barriers) and no evidence of a spatial heterogeneity in terms of invaded areas per unit of time. However, since *r* and *c* likely vary, *D* was estimated using the values of *r* and *c* for southwestern France (the Aquitaine region). First, we calculated the mean value of *r* using the *r* values that had been estimated for each department in southwestern France. Second, we calculated *D* for each department using Equation 2 and the previously determined value of *c*. Finally, we calculated the mean value of *D* across all these departments.

Based on the results of bioclimatic envelope models (Ibáñez-Justicia & Loomans 2011; Villemant *et al*. 2011a), most of France is suitable for the establishment of the yellow-legged hornet and the least suitable areas in Europe seem to be mainly located in mountainous regions (Péré & Kenis 2011). Therefore, we defined an elevation limit *E* above which the yellow-legged hornet should

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not be able to establish itself; we used the highest elevation at which it was found between 2004 and 2009 (dataset used for parameter estimates). Climate change could possibly affect the elevational threshold. However, in this study, we did not explore this possibility as the hornet's spread is relatively fast compared to the effects of climate change.

LONG-DISTANCE DISPERSAL

Points where hornets occurred at distances greater than the local dispersal distance from their nearest neighbors were identified. In addition, a subset of points with the highest dispersal distances which fell within the same range than the three points thought to result from long-distance dispersal (according to Villemant *et al*. 2011a) was also identified. For all these locations, the effects of human population density (retrieved from CIESIN & CIAT 2005) on long-distance dispersal were analyzed. We obtained estimates of human density at the points and compared those values with the values associated with 100 randomly chosen points found both within habitat favorable to hornets (where elevation < *E*) and outside the short-distance dispersal range. Since the data were not normally distributed, a Wilcoxon test was used to compare human population densities between the two sets of points (Millot 2011). A threshold value for human population density (*H*) above which long-distance dispersal events could be observed was defined. This threshold distinguished the long-distance dispersal points from the randomly chosen points.

Then, to simulate human-mediated dispersal, we defined a yearly probability of observing a long-distance dispersal event, denoted as *Pldd*, which was based on the number of occurrences observed every year between 2004 and 2009 that likely resulted from human-mediated dispersal. Then, for each event, we randomly chose a nest founding point within the area where human population density and elevation were suitable (above *H* and below *E*). Since the model was stochastic, we ran 100 replicate simulations to obtain result convergence (see Appendix S1 in Supplementary Information).

CONTROL MEASURES

Control measures (*e.g.*, nest removal and destruction) may affect the range expansion of the yellow-legged hornet. Their effects in the form of nest density reduction were included in the model for two reasons: 1) to determine the percentage of nests removed and destroyed in the past in France and 2) to explore the possible effects in the future if control efforts increased. Since some control measures

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have been applied since the species was detected in France, the model had to account for them both in the model calibration and validation.

Control measures are likely not uniformly applied across France because their application largely depends on the likelihood of encountering nests. The nests can be detected by chance or when yellow-legged hornets are reported and then the nests are searched for destruction. Beekeepers face some dramatic problems in rural areas but anyone living in urban areas can also face important problems because the yellow-legged hornet also occurs there, it can be aggressive toward humans and its colony size is relatively large (Choi *et al*. 2012). Since there is a high number of potential observers and a high number of people likely to get stung in urban areas, we assumed that the probability of applying control measures is greater in these areas.

In the model, we assumed that people can detect a yellow-legged hornet nest from within a 50-m radius ($d = 0.05$ km). We then defined the parameter ρ as the proportion of a given area that one person can observe, where $\rho = (\pi \times d^2)/A$. For a cell of 10 km x 10 km ($A = 100$ km²), the area observed is $\pi \times d^2 = 7.85\ 10^{-3}$ km². Therefore $\rho = 7.85\ 10^{-5}$ for that cell. The intensity of control measures, $C(h)$, is given by (**Figure 1**):

$$C(h) = \frac{\alpha h}{\frac{1}{2\rho} + h} \qquad \text{Equation 4}$$

where h is the number of humans associated with the cell (*i.e.*, human population density) and α is the maximal control intensity if all nests were detected ($0 \leq \alpha \leq 1$, where $\alpha = 0$ means that no nest is destroyed and $\alpha = 1$ means that all the detected nests are destroyed). As human population densities increase, $C(h)$ approaches α. Control intensity describes the proportion of nests that are destroyed. Although actual control efforts are more complex, this simple function based on the detection radius and human population density likely captures the main pattern that explains heterogeneity in attempts to control the yellow-legged hornet.

MODEL DESCRIPTION, VALIDATION, UNCERTAINTY ANALYSIS AND PREDICTIONS

We combined estimates of local spread and growth with estimates of long-distance dispersal and control intensity. We applied these models to a grid that covered France with a spatial resolution of 10 km x 10 km; implementation took place in R (R Development Core Team 2014; Robinet *et al*. 2016; see also Appendix S1). The simulations began with the two nests that were present in 2004 at the location where the hornet first appeared in France (**Figure 2**).

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To validate the model and identify the most likely dispersal and control scenarios, the species' spread between 2004 and 2013 was simulated with and without long-distance dispersal events (representing human-mediated dispersal). Different levels of control intensity were also used; α ranged from 0 to 1 and varied by increments of 0.1. The simulated results obtained for 2013 were compared with actual observations from that year (**Figure 2**). We calculated the percentage of departments for which hornet presence/absence was correctly predicted.

Due to uncertainty on the value of some parameters, we did an uncertainty analysis. First, we identified the possible range of the parameters' values for the local spread rate (c), the carrying capacity (K), the growth rate (r) and the detection radius (d). Then, we simulated the potential spread of the yellow-legged hornet between 2004 and 2013 using these values to obtain the possible range of the model outputs. We considered no long-distance dispersal and $\alpha = 0.30$, and we calculated the percentage of departments correctly predicted.

To predict the effects of future control efforts, we took into account the simulated spread in 2013 (as initial conditions) and the most likely dispersal scenario (spread without human-mediated dispersal; see results). We then simulated the species' potential spread through 2020. The effects of control intensity were tested (at $\alpha = 0.3$, 0.6, and 0.95, which represent the current control intensity, a doubling of control efforts, and nearly maximal control efforts, respectively).

Results

LOCAL DISPERSAL AND POPULATION GROWTH

The yellow-legged hornet spread over a radius of 112 km during 2004-2005, 75 km during 2005-2006, 89 km during 2006-2007, and 75 km during 2008-2009; a pioneer population spread by 30 km during 2007-2008. Therefore, the rate of spread ranged between 75 and 112 km/year. Given that the yellow-legged hornet was discovered in 2004 but had probably arrived before then and needed time to build up and spread (*i.e.*, spreading less rapidly, possibly by around 30 km for the first year, like the pioneer population above), the local rate of spread was more likely between 75 and 82 km/year. In the simulations, we considered that $c = 78$ km/year in southwestern France (Table 1).

In the department with the greatest infestation levels, the highest number of nests was about 330. Since the area of this department is 5,361 km², we estimated K at 0.06 nest/km².

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There was a weak positive correlation between r and GI ($R^2 = 0.11$; $F_{1,19} = 2.347$, $P > 0.05$) (**Figure 3**). The growth rate was defined by the following formula:

$$r = -1.29593 + 0.09502 \times GI \qquad \text{Equation 5}$$

D was estimated for each department in the Aquitaine region using their respective r values (r = 1.35, 1.80, 2.39, 1.08, and 1.65). Given that c = 78 km/year, the mean value of D was 984 km² year^{-1} (Table 1).

Between 2004 and 2009, the highest elevation where the yellow-legged hornet was found was E = 791.5 m. Consequently, this was the threshold used in the simulations.

LONG-DISTANCE DISPERSAL

A total of 30 occurrence points were found further than 78 km (the mean radial distance) from their nearest neighbors. Distances ranged almost continuously from 78 km to 327 km (**Figure 4**), including the three furthest points generally attributed to human-mediated dispersal in the literature; they are located in Côte d'Or (point number 1), Ille-Et-Vilaine (point number 2), and Seine-Saint-Denis (point number 3) (**Figure 4**). Since the distance distribution was rather continuous, there was no clear threshold separating short-distance events from long-distance events, which calls into question previous assumptions regarding human-mediated dispersal.

At these 30 occurrence points, human population densities were higher than at the 100 randomly selected points (W = 2034, P < 0.001) (average of 322.3 and 86.9 inhabitants/km², respectively). There were a subset of two to five points located further than the others, at the periphery of the species' range (**Figure 4**), which were therefore more likely associated with long-distance dispersal events. At these points, human population densities were the following: 126.3 (point 1), 566.1 (point 2), 1,490.4 (point 3), 228.9 (point 4), and 19.0 (point 5). We chose H = 125 inhabitants/km² for the threshold above which the yellow-legged hornet arrives via human-mediated dispersal. Four of the five extreme points were above this distance threshold. Although point 5 had a relatively low human population density, it was located very close to point 4. The yellow-legged hornet was observed at points 4 and 5 the same year, in 2007, so it is possible that it actually arrived before then and spread from one point to the other.

A stochastic approach was used to simulate human-mediated dispersal. As the number of points discovered at very long distance and possibly resulting from human-mediated dispersal events was possibly between two and five for a 6-year period (2004-2009) (**Figure 4**) and a large proportion

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of France is suitable for species establishment (meaning that most human-mediated dispersal events could result in establishment), we estimated that the yearly probability of hornets being accidently dispersed by humans in France, denoted as P_{ldd}, ranged from 0.3 to 0.8. A Bernoulli distribution with probability P_{ldd} was used to simulate the occurrence of human-mediated dispersal. In case of long-distance events, we randomly selected a nest founding location within suitable habitat (where $E \leq 791.5$ m) that was not yet invaded and where human population density was above H.

MODEL VALIDATION: ROLE OF HUMAN-MEDIATED DISPERSAL AND CURRENT CONTROL INTENSITY

A higher percentage of departments had their statuses correctly predicted (*i.e.*, hornet presence/absence) in the simulations without human-mediated dispersal and when control intensity was intermediate (α = 0.3-0.4; **Figure 5**). When human-mediated dispersal was present, the model overestimated the hornet's spread, especially in northern and eastern France (**Figure 6; Figure S1 in SM1**). In simulations without human-mediated dispersal but with higher control intensity ($\alpha \geq 0.6$), spread was underestimated (**Figure 6; Figure S1 in SM1**) and predictions were less accurate (**Figure 5**). These results suggest that past control efforts have been moderate. In addition, when control intensity was maximal ($\alpha = 1$), all the dispersal scenarios converged. This finding makes sense since, in the model, colonies dispersed by humans arrive in urban areas and most are destroyed ($C(h) \approx \alpha$).

UNCERTAINTY ANALYSIS

Uncertainty on the local spread rate (c from 75 to 82 km/ year) and on the carrying capacity (K from 0.06 to 0.18 nests/km²) impacted the percentage of departments correctly predicted by -3.1 to +1.1 %. Uncertainty on the detection radius (d from 10 to 1000 m) impacted this percentage by 0 to -5.2%, with a best fit for values ranging from 40 to 70 m, which includes the default value (50 m). The model output was mostly sensitive to the population growth (r). To estimate this parameter, we calculated the observed growth rate each year (before it reached half of the carrying capacity), and then these values were averaged for each invaded department. In this uncertainty analysis, we considered the lower and upper limit of the 95% confidence interval of this mean, and we considered the following linear regressions:

$$r_{inf} = -1.45386 + 0.07018 \times GI \qquad \text{Equation 6}$$

$$r_{sup} = -1.13801 + 0.11985 \times GI \qquad \text{Equation 7}$$

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for the lower limit of the 95% confidence interval (r_{inf}) and the upper limit of the 95% confidence interval (r_{sup}), respectively. The percentage of correctly predicted departments decreased by 7.3% when considering r_{inf} and by 31.5% when considering r_{sup}. The spread model developed in this study was relatively robust, even if there was some uncertainty associated with the estimations of certain parameters (see Appendix S2 for more details).

MODEL PREDICTIONS: EFFECTS OF INCREASING CONTROL INTENSITY

Based on the simulations run for the period between 2013 and 2020 in which human-mediated dispersal events were excluded, the yellow-legged hornet could continue to expand its range in the future (**Figure 7**). When control intensity was increased from 30 to 60%, the hornet's spread was reduced by 17.1% (453,400 versus 375,800 km² of total invaded area) and nest density was reduced by 27.9% (from 16,249 to 11,708 nests). When control intensity was raised even further, to 95%, the hornet's spread was reduced by 42.7% (to 259,900 km² of invaded area) and nest density was reduced by 53.3% (to 7,587 nests).

Discussion

YELLOW-LEGGED HORNET INVASIVENESS IS TIED TO DISPERSAL AND ESTABLISHMENT ABILITIES

This study presents the first evidence that the rapid spread throughout France of the yellow-legged hornet may not be necessarily mediated by humans. Although the model used was stochastic and may not precisely predict the area to be invaded, it nonetheless performed better than a purely random model (see Appendix S1). It was clear that including human-mediated dispersal in the model resulted in less accurate predictions than when only dispersal over "short" distances was allowed. In fact, such "short-distance" dispersal could represent self-mediated dispersal by the yellow-legged hornet and occur over relatively large distances: the average was 78 km/year in this study. How can this unexpected result be explained?

First, founder females are capable of flying very long distances (Beggs *et al*. 2011). They can cover 200 km in several days in flight mill experiments (Pers. Com., Dr. Daniel Sauvard, INRA, Orléans, France). Despite the possible bias of such experiments, the distances recorded fit with the rate of spread observed for some species in the field. Indeed, species range expansion can result from the

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long-distance dispersal of just a few individuals with extreme dispersal abilities (*e.g.*, around 5 km/year for the pine processionary moth, Battisti *et al*. 2005; Robinet *et al*. 2012). The overall flight period of yellow-legged hornet gynes is relatively long because they may fly before hibernation (*i.e.*, while looking for a hibernation site) and after hibernation (*i.e.*, while building new nests and thus founding new colonies). This long flight period could therefore translate into long dispersal distances.

Second, the yellow-legged hornet is extremely successful at establishing new colonies. The invasion in France probably resulted from the introduction of no more than a few and perhaps even just one mated female (Arca *et al*. 2015). If so, it means that if a mated female manages to fly a hundred kilometers and arrives in favorable habitat, then there is a high probability that she will succeed in founding a new population. The fact that a single individual can give rise to a whole population makes the yellow-legged hornet a formidable invader (EEA 2012). Because of the species' high degree of establishment success, only a few females need to disperse long distances to create satellite colonies far from the species' main range.

DISENTANGLING HUMAN-MEDIATED DISPERSAL FROM SELF-MEDIATED LONG-DISTANCE DISPERSAL

This study suggests that individual hornets would be able to disperse long distances on their own and thus generate stochastic patterns of spread similar to those resulting from human-mediated dispersal. If the patterns they produce are similar, it is difficult to discriminate between the two potential scenarios. This study therefore differs from other studies of invasive species in which the long-distance dispersal events associated with rapid range expansion are mainly attributed to human activities. For instance, human-mediated dispersal was considered as the factor explaining long-distance dispersal and the subsequent rapid spread of the following species: (i) the pine processionary moth, *Thaumetopoea pityocampa*, whose spread across France was hypothesized to result from the transport and planting of large potted trees whose soil was infested (Robinet *et al*. 2012); (ii) the horse-chestnut leafminer, *Cameraria ohridella*, whose spread across Europe was attributed to the transport of infested leaves via car traffic (Gilbert *et al*. 2004); (iii) the pine wood nematode, *Bursaphelenchus xylophilus*, which is thought to have spread across China because of the transport of infested wood material (Robinet *et al*. 2009); and (iv) the emerald ash borer, *Agrilus planipennis*, which may have spread across North America because of the transport of infested firewood (Muirhead *et al*. 2006). The results of this study therefore indicate that greater caution is needed when interpreting the mechanisms explaining long-distance dispersal events.

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FUTURE RESEARCH: APPLYING THE MODEL TO OTHER COUNTRIES

It is not known whether there have been other, more recent introductions of the yellow-legged hornet from Asia to Europe. The model presented here was developed to describe the potential spread of the yellow-legged hornet in France. However, due to the species' ability to spread rapidly and effectively, it is now necessary to assess its potential spread across Europe. This same model could be used to predict the hornet's spread in Spain, Portugal, and Italy, countries where the hornet is already present. The estimates of the model parameters could be adjusted and the model eventually refined with these additional datasets. This model can also be used as a companion to genetic studies, which are commonly used to trace the origins of populations (*e.g.*, Arca *et al*. 2015); simulations can be used to test whether the yellow-legged hornet likely arrived from neighboring countries (if the simulation results fit with observations) or following other introduction events (if the simulation results do not fit with observations). It is also possible to determine the likelihood that the species will spread to uninvaded neighboring countries with favorable climates, such as Switzerland, Belgium, and the United Kingdom.

COMBINING CONTROL METHODS TO IMPROVE EFFICIENCY

Insect eradication may be possible when the invasion is confined to small areas or a sharply delimited breeding habitat (Pluess *et al*. 2012). Since the yellow-legged hornet has already spread throughout most of France, it is no longer possible to eradicate it. Instead, the best strategy would be to slow its spread and reduce its population densities at large scale. Control measures could combine the mechanical removal and destruction of individuals or infested materials with biological control techniques. For example, such an approach was successfully used to control the spruce beetle, *Dendroctonus micans* (Fielding & Evans 1997; Pauly & Meurisse 2007). In the United Kingdom and France, clearcutting infested trees and releasing a natural predator, *Rhizophagus grandis*, caused the population to decline; it ultimately reached a low-level equilibrium, particularly in recently colonized areas and areas experiencing outbreaks. Combining control measures in this way could also be useful when dealing with rapidly spreading invaders. For instance, removing leaves infested by the horse-chestnut leafminer, *Cameraria ohridella*, and releasing one of the insect's generalist predators could cause populations to reach an economically acceptable threshold (Aniţa *et al*. 2014).

Combining different approaches—such as (1) removing and destroying hornet nests, (2) trapping hornets with more selective traps and more specific attractant, and (3) releasing natural enemies—could be highly valuable in efforts to control the yellow-legged hornet in France and in

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Europe in general. Although none of these methods would be 100% effective, they might be more efficient when combined, applied at larger scales, and coupled with certain phenomena, such as inbreeding, that naturally reduce the population sizes of invaders (Darrouzet *et al*. 2015a). Nest removal and destruction can be performed more frequently if they are required by a country's regulations. Trapping yellow-legged hornets is not yet efficient since traps and attractants are not selective enough (Monceau *et al.* 2012; Goldarazena *et al*. 2015). Reducing nest density should be possible if traps catch gynes. There is therefore an urgent need to develop selective traps. In addition, choosing appropriate locations at which to set traps (*e.g.*, not necessarily near hives) could improve trapping efficiency (Monceau *et al*. 2012). Since gynes are trapped under certain climatic conditions, removing or closing traps when these conditions are not present could help prevent the capture of non-target species (Monceau *et al*. 2012). Another promising control method that merits further study is the use of biological control agents. These agents include the endoparasitoid, *Conops vesicularis*, which was recently observed in dead queens in France (Darrouzet *et al*. 2015b) and parasitic nematodes such as *Pheromermis vesparum*, which were collected from adult hornets in France (Villemant *et al.* 2015). Although these biological agents by themselves would hardly hamper the invasion (Villemant *et al.* 2015), if more efficient natural enemies were found, especially in the yellow-legged hornet's native range, they could be used to weaken populations. Nevertheless, like for any intentional release of natural enemies, caution is needed as these controlling agents themselves could have unexpected impact on the environment (Hajek *et al*. 2016). Some infamous examples are: the marine cane toad, *Bufo marinus*, introduced in Australia to control cane beetles, which has rapidly spread for unclear reasons and caused severe problems (Shanmuganathan *et al.* 2010), and the Harlequin ladybird, *Harmonia axyridis*, an Asian coccinellid introduced in America, Europe and Africa to control aphids, which became invasive after some admixture with bridgehead populations (Lombaert *et al*. 2010).

Combining different control methods in these ways, whilst preventing potential side effects, could be the best approach to reduce the yellow-legged hornet's impact and slow its spread in France and in Europe in general. To this end, species-specific management policies should be adopted in France and Europe in addition to the recent EU regulations instituted regarding invasive alien species (see Regulation 1143/2014; http://ec.europa.eu/environment/nature/invasivealien/index_en.htm). European countries should anticipate the potential spread of invaders, especially given climate warming (Barbet-Massin *et al.* 2013), such that appropriate regulations are in place prior to the arrival of invasive species. In France, the yellow-legged hornet has been considered a noxious species since 2012, yet prevention, monitoring, and/or management efforts are still not mandatory (Monceau *et al*. 2014). The results of

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this study (which underscore that it is possible to slow the spread and reduce the nest densities of the yellow-legged hornet if stronger control measures are deployed), and the development of new control techniques (such as selective traps) will encourage decision makers to adopt stronger pest management policies to control the invasive yellow-legged hornet and thereby reduce its impact on honey bees, native entomofauna, and humans.

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Acknowledgments

We gratefully acknowledge Claire Villemant, Quentin Rome, and Franck Muller (Museum of Natural History, Paris, France) for kindly providing the 2004–2009 hornet occurrence data for France; Daniel Sauvard (INRA, URZF, Orléans, France) for providing preliminary flight mill data about the flight capabilities of the yellow-legged hornet; Jean-Claude Grégoire (Université Libre de Bruxelles, Belgium) for providing the latest information about the invasion in Belgium; Sylvie Augustin and Annie Yart (INRA, URZF, Orléans, France) for describing examples of successful control efforts. This study was supported by funding from the region Centre-Val de Loire, namely the awarding of a French regional grant for our "FRELON" project ("Frelon asiatique: étude et lutte ciblée contre une espèce invasive prédatrice des abeilles"; 2011-2014).

Data accessibility

The R script and the data needed to use this script are available at https://zenodo.org/record/49021 (Robinet *et al*. 2016). The R code of the core function and 2013 occurrence data are provided in the Appendix S1of this manuscript. Occurrence data for 2004 to 2009 are provided in the Supplementary Material in Villemant *et al.* (2011b).

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TABLES

Table 1. Estimates of model parameters. (*) Since parameters *c* and *r* vary across France, the estimates provided are those for southwestern France.

Parameter	**Symbol**	**Estimate**
Rate of spread	c	78 km year^{-1} (*)
Carrying capacity	K	0.06 nest km^{-2}
Growth rate	r	1.66 (*)
Diffusion coefficient	D	984 km^2 year^{-1}
Maximum elevation above sea level where hornets are found	E	791.5 m
Annual probability of long-distance dispersal	P_{LDD}	0.3-0.8
Threshold of human population density	H	125 km^{-2}

FIGURES

Figure 1. Control intensity as a function of human population density (given by the number of inhabitants within 10 km x 10 km cells) when $\alpha = 1$. The map shows the corresponding control intensity throughout France which goes from low (less than 10%) in light gray areas to high (more than 90%) in black areas. The dark gray polygons delineate the borders of the French departments.

Figure 2. Distribution of the yellow-legged hornet in 2013 (source: INPN website). The data are projected onto a grid with a resolution of 10 km x 10 km (on the left) and depicted per department (on the right). The black point in southwestern France indicates where the yellow-legged hornet was first found in 2004.

Figure 3. Growth rate. (a) Correlation between the observed growth rates (r) and the growth index values estimated from the CLIMEX model (GI) (one point per department). (b) Predicted growth rates estimated from the GI values across France (10-km grid resolution).

Figure 4. Long-distance dispersal. (A) Number of hornet occurrence points found more than 78 km from their nearest neighbors. (B) Locations of these long-distance dispersal events (black dots). The most extreme points (largest black dots) are numbered so their distances can be identified in (A). In the literature, points 1, 2, and 3 are hypothesized to have resulted from long-distance dispersal (Villemant *et al*. 2011a). The gray dots are points located less than 78 km from their nearest neighbors.

Figure 5. Percentage of departments for which the model correctly predicted the presence/absence of the yellow-legged hornet in 2013 at different control intensities (α from 0 to 1). Several dispersal scenarios were tested—the yearly probability of human-mediated dispersal events varied ($Pldd$ = 0.3, 0.5, and 0.8) and human-mediated dispersal events were also excluded. In gray are the 95% confidence intervals for each human-mediated dispersal scenario.

Figure 6. Potential spread in 2013 for simulations under different control intensities (α) and different human-mediated scenarios (without human-mediated dispersal “no LDD” and with different yearly probability of human-mediated dispersal event, $Pldd$). The color gradient expresses differences in nest density (yellow: 0.01–0.1 nests per cell; orange: 0.1– 1 nests per cell; red: 1–3 nests per cell; and dark red: more than 3 nests per cell).

Figure 7. Potential spread in 2020 for different control intensities (α =0.3, 0.6, and 0.95) where long-distance, human-mediated dispersal was excluded. The color gradient expresses the differences in

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hornet population density as estimated via the number of nests in each grid cell (cell size = 10 km x 10 km).

Figure 1.

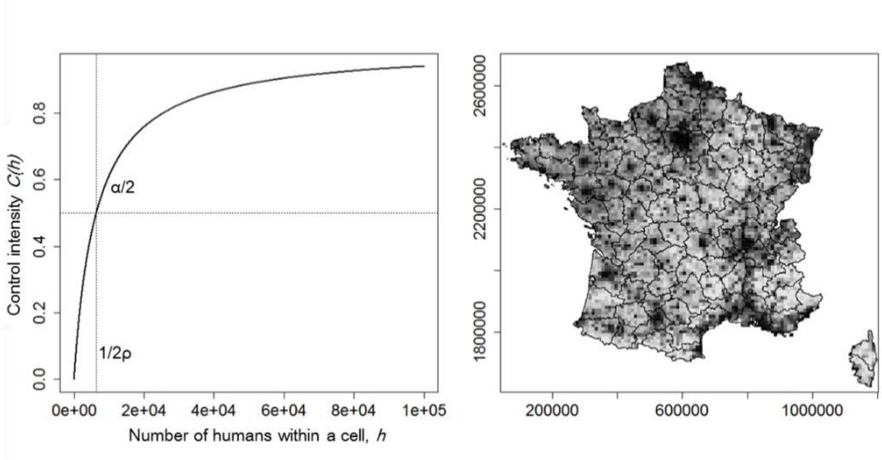

Figure 2.

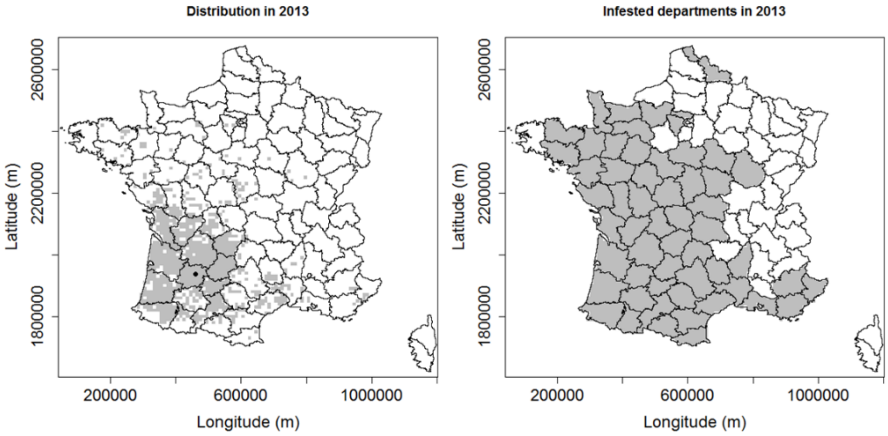

Figure 3.

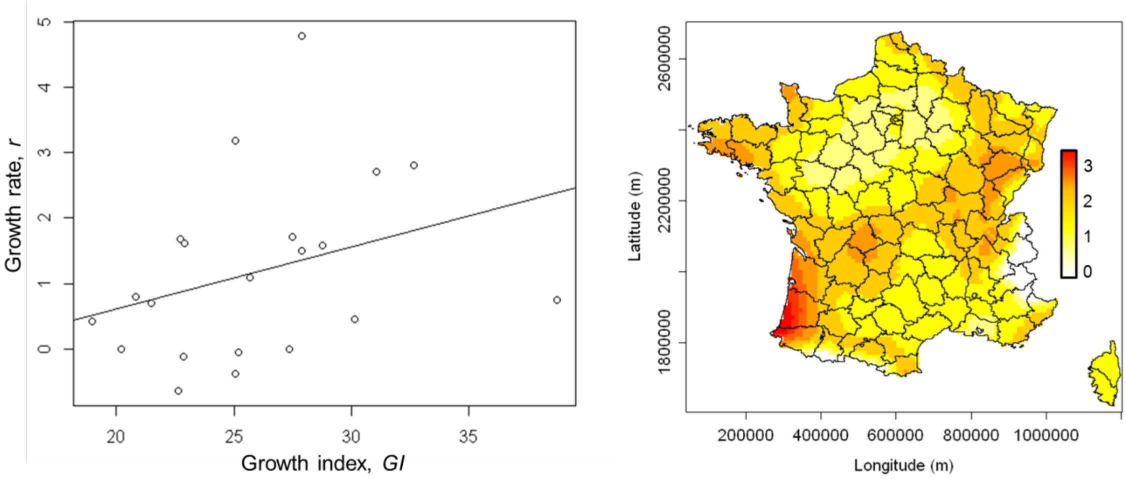

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Figure 4.

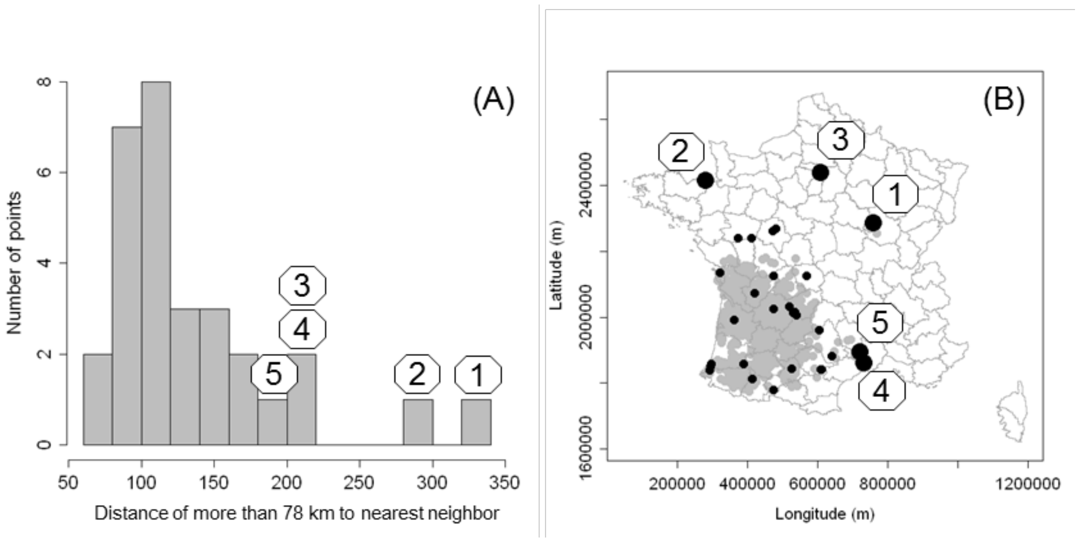


Figure 5.

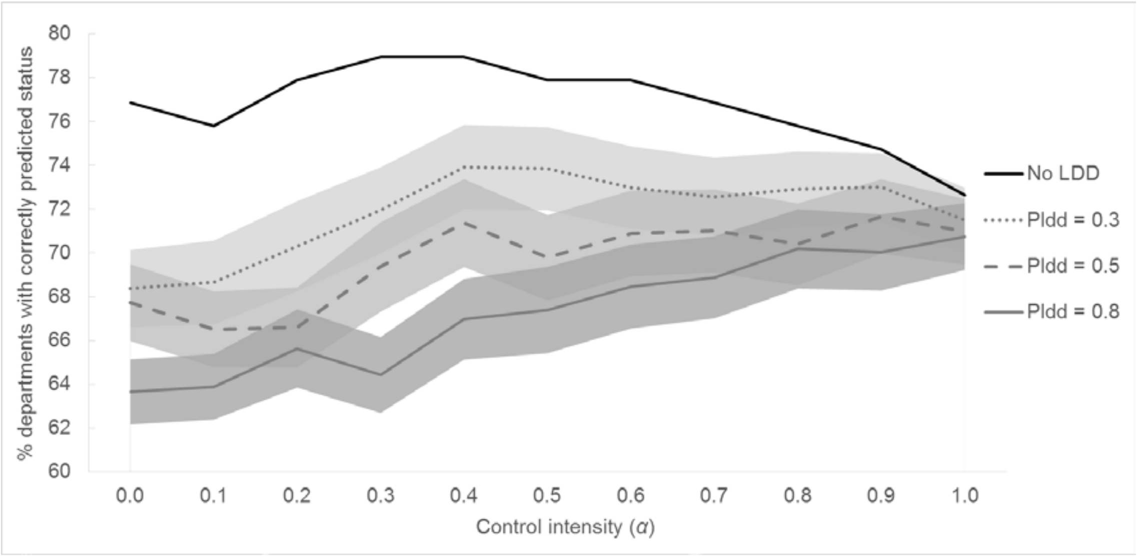


Figure 6.

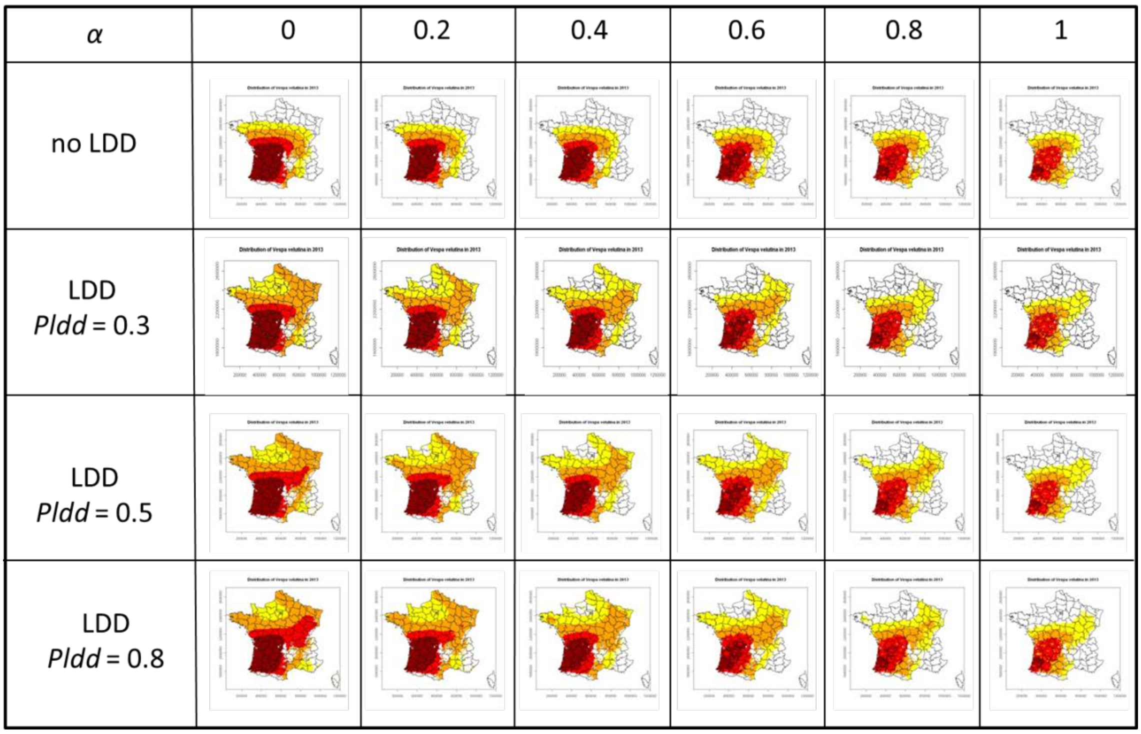
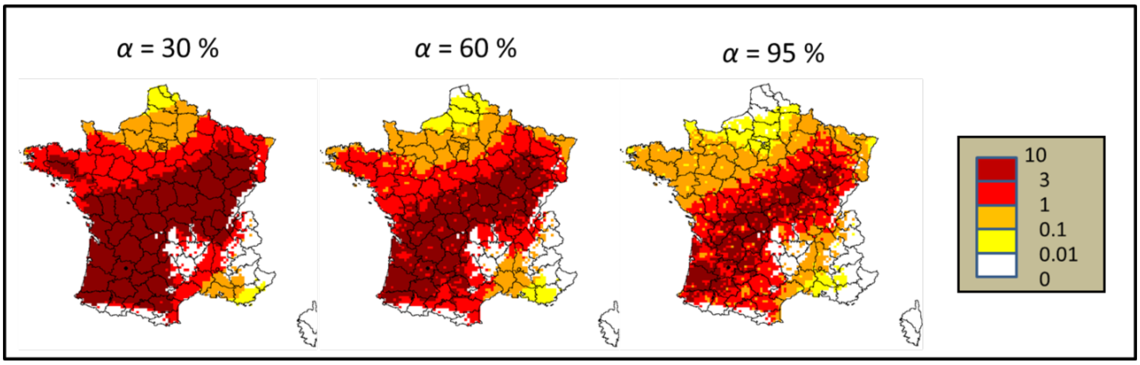


Figure 7.



Supporting Information

Appendix S1. Technical description of the model and additional supporting results.

Appendix S2. Uncertainty analysis.

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