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Number of figures: 5; Number of Tables:3 ; Number of references: 54.

Submitted to Ecological Modelling (Original research paper)

Abstract

The number of invasive species is increasing throughout the world. One of the corner stones to successfully control them is to better estimate their dispersal capabilities. For flying insects, dispersal performance is commonly estimated through flight mill and mark-release-recapture experiments. However, each approach has its own bias, over- and under-estimating flying distances respectively. The objective of this study was to develop an individual-based dispersal model to circumvent these drawbacks. The shape of the dispersal kernel was calibrated on distances recorded in flight mill experiments (previously done) and then model parameters were fine-tuned based on mark-release-recapture experiments (presented in this study). The pine sawyer beetle, *Monochamus galloprovincialis*, was used as case study because it is the European vector of the invasive pine wood nematode, *Bursaphelenchus xylophilus*, recognized as one of the biggest threats to pine forests worldwide. The best fitted model to mark-release-recapture data was parametrized with a mean flying distance of 2000 m per day, which is consistent with flight mill data. It was used to further simulate the dispersal of 100 beetles in non-fragmented pine forests. The cumulative flight distance was 63 km on average at the end of their adult life stage, and the mean dispersal distance as the crow flies was of ca. 13 km. At the end of the maturation period, when most nematodes have been already transmitted to host pines via shoot feeding, about 80% of the insects were located at more than 500 m from the emergence point. These outcomes clearly question the relevance of clear-cut zones of 500 m radius required by the European regulation for the eradication of the invasive nematode. Such dispersal model could be used to support decision-making for eradication programs.

Key-Words

Bursaphelenchus xylophilus; dispersal model; flight distance; *Monochamus galloprovincialis;* pine wood nematode; mark release recapture.

1. Introduction

Due to the ecological damage and economic impacts caused by invasive species, various management and control measures have to be implemented, ranging from early detection, eradication, containment, “slow the spread” and biological control (Wittenberg & Cock 2001, Sharov et al. 2002, Meentemeyer et al. 2008). A corner stone for the success of invasive pests control is to better know their biology and behavior. In particular, a better estimation of their dispersal capacity is crucial as it affects both their establishment capability (Robinet & Liebhold 2009, Tobin et al. 2011) and spread rate (Turchin 1998).

Although radio tracking is the most accurate method for monitoring animal dispersal in the wild, it is often impossible to track small-sized species, as they cannot carry heavy equipment compared to their own weight or because they can disperse over large areas. In this case, indirect measures are generally used. For insect species that disperse by flying, mark-release-recapture experiments and flight mill experiments are commonly used (Turchin 1998, Martí-Campoy 2016). However, each method has its own bias: data recorded on flight mills represent artificial flight performance and usually overestimate dispersal capacities while data recorded in mark-release-recapture (hereafter MRR) experiments represent interception distances and are limited by the number of traps and the distance between the release point and the furthest trap, thus resulting in underestimation of flight performance. Therefore, precisely estimating the dispersal capabilities of insects is often challenging.

One of the biggest threats of pine forests across the world is the pine wood nematode (PWN), *Bursaphelenchus xylophilus*, as it can potentially kill a pine tree within a few weeks (Suzuki 2002, Webster & Mota 2008, Vicente et al. 2012). Native to North America (Dropkin et al. 1981), it has invaded Japan in 1905 (Yano 1913), China in 1982 (Cheng et al. 1986), Korea in 1988 (Yi et al. 1989), and Portugal in 1999 (Mota et al. 1999), where it has caused extensive mortality. It was also detected in Spain in 2008 (Robertson et al. 2011). To disperse from one tree to another, the pine wood nematode needs an insect vector, which always belongs to the *Monochamus* genus. In Portugal, the pine sawyer beetle, *Monochamus galloprovincialis* (Olivier, 1795), is the only insect known to carry the pine wood nematode (Sousa et al. 2002) but its flight capability is still not well known.

To prevent the spread of the pine wood nematode within the European Union, the European Union regulation (Implementing Decision 2012/535/EU) requires the Member States to implement emergency measures. The current contingency plan consists of surveys for nematode detection, eradication measures to eliminate the nematode where it is present, and containment measures to prevent a further spread of the nematode where it cannot be eradicated. The requested eradication measure is to fell, remove and dispose of all susceptible plants within a zone, called clear cut zone (CCZ), of a minimum radius of 500 m (that may be reduced to 100 m subject to conditions) around any infected tree. Despite the regulation measures imposed by the European Union, the PWN has spread to a large part of Portugal and has been repeatedly detected in Spain (Abelleira et al. 2011, Vicente et al. 2012). Assessing the dispersal distance of the insect vector is therefore a crucial step to improve the management strategy of the PWN where it has been introduced.

Several mark-release-recapture experiments have been conducted to determine the dispersal capability of *M. galloprovincialis* in the Iberian Peninsula. The advantage of this method is to measure the dispersal distance of individuals in the field. As they were supposed to have very limited flight capabilities, traps were generally installed in the neighborhood of the release points (e.g., up to 0.5 km and 0.76 km, Etxebeste et al. 2016) and thus most adults have been caught are very short distances. When traps were installed further, some insects were caught at greater distances (at more than 3 km from the release points, with a maximal distance of 5.3 km, Etxebeste et al. 2016; 7.1 km, Hernández et al. 2011; 8.3 km, Gallego et al. 2012; and 22.1 km, Mas et al. 2013). Consequently, it seems that the interception distance can be relatively high in some cases. The variability in recapture distance between these experiments probably reveals the dilemma in placing the traps. When traps are installed close to the release point, they catch more insects but, obviously, long recapture distances cannot be observed (Turchin 1998). When the traps are installed far from the release point, there is low chance to recapture an insect. Insects that were not caught in the traps may have dispersed further, and insects caught in the traps would have perhaps been able to disperse further if they were not caught.

Another method commonly used to estimate the flight performance of insects consists in testing individuals on a flight mill. In this method, individuals are placed in artificial conditions and the flight performance recorded on a flight mill may not be fully representative of the dispersal capability in the field. However, it provides an accurate estimate of the probability distribution of flight distances, and thus, of the proportion of beetles that are able to fly further than the others. It also allows recording the distance flown by each individual over its life span under controlled conditions and eventually comparing the effects of different treatments (e.g., according to age, sex and temperature conditions). The flight performance has already been measured in this way for several insect species, such as bark beetle (Jactel & Gaillard 1991), codling moth (Schumacher et al. 1997), mosquito (Briegel et al. 2001), peach fruit moth (Ishiguri & Shirai 2004), monarch butterfly (Bradley & Altizer 2005), emerald ash borer (Taylor et al. 2010), pine processionary moth (Robinet et al. 2012), and predatory ladybirds (Maes et al. 2014). The flight performance of adult beetles of *M. galloprovincialis* was also tested with this method (David et al. 2014, 2015). When emerging from a tree, adult beetles are immature for approximately 20 days (Naves et al. 2006). At this immature stage, they do not respond to sex pheromone attraction and thus cannot be caught by pheromone traps. During this period of sexual maturation, young adults are the main vector responsible for nematode transmission which takes place when insect are feeding on fresh pine twigs (vectors can transmit the nematode for about 10 weeks since their emergence; Naves et al. 2007). Using automatically recording flight mills, David et al. (2015) showed that flight distance performed each day by immature beetles increased progressively as beetles were aging, probably as they develop their muscles and accumulate energy when feeding, until reaching a limit. In a second experiment, David et al. (2014) measured the flight performance of mature beetles as 2 km per testing day on average (8 km maximum). However, it is unknown whether they can fly these distances every day (2 km per day) or during the whole week (2 km/ 7 = 0.3 km per day), as they were tested only once per week. During their entire mature adult lifespan, they could fly 16 km on average (63 km maximum). Although these flight distances are higher than the recapture distances, their direct comparison is impossible because these distances do not represent the same dispersal measure (interception distance *versus* artificial flight performance).

Individual movement is the result of a complex combination of four basic components: internal state of the individual (e.g., its physiology), its motion and navigation capacities, and external factors (e.g., environmental conditions) (Nathan et al. 2008, Baguette et al. 2014). This movement can be seen as a sequence of several paths going from one point to another. Each path is generally characterized by a straight line between these two points, which can be fully described either by the Cartesian coordinates of these two points or by their polar coordinates, reporting their distance and angle (Nathan et al. 2012). We used this classical framework of movement ecology to design an individual-based dispersal model.

To simulate the movement of individuals, various dispersal models has been developed (Turchin 1998). Some models described the spread of a population such as reaction-diffusion models (Shigesada & Kawasaki 1997) whilst other models based on random walks were able to simulate individuals' trajectories. In the latter case, successive dispersal distances and directions were then randomly chosen to characterize the individual's path (Turchin 1998). For instance, these dispersal distances can be chosen from a dispersal kernel providing the probability distribution of dispersal distances. The shape of the dispersal kernel is important to define the proportion of individuals able to disperse at long distance (Klein et al. 2006, Nathan et al. 2012). In this study, we developed such an individual-based model using both dispersal measures (flight mill and mark-release-recapture data) to determine the potential dispersal capability of the insect vector of the pine wood nematode in Europe.

Firstly, we calibrated the individual-based dispersal model using the distances recorded in flight-mill experiments (David et al. 2014, David et al. 2015) to capture the shape of the dispersal distance distribution. Then, we conducted mark-release-recapture experiments with both immature and mature *M. galloprovincialis* beetles, in a pine plantation landscape, to fine-tune model parameters (Fig. 1).

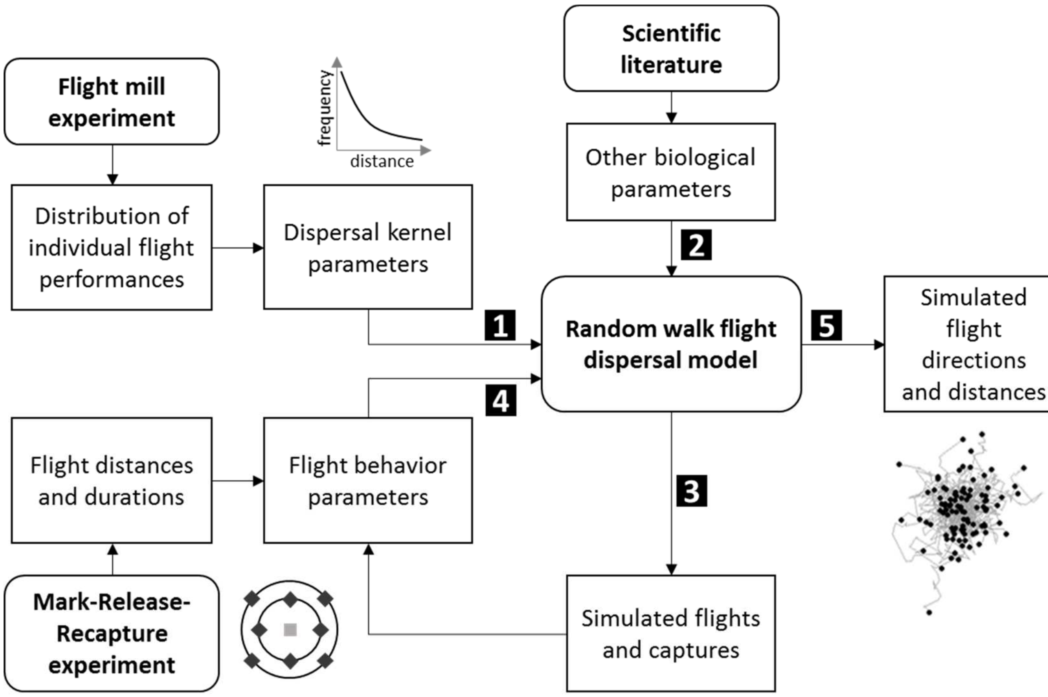

Fig. 1. Conceptual diagram of the modelling approach. Data from flight mill experiments (1; section 2.1) combined with data from literature (2) were used to calibrate the dispersal model. Then, this model was used to simulate the dispersal of the insect (3) and simulate the mark-release-recapture experiments (4; section 2.3) to refine the parameters associated with the insect's flight behaviour in the field. (5; section 2.3).

2. Materials and methods

2.1. Calibration of the dispersal kernel with flight mill data

The individual-based model describes the dispersal of immature and mature *M. galloprovincialis* beetles based on a several parameters (Table 1). The shape of the dispersal kernel (negative exponential model; see SM1) was fitted to the flight performance of both mature beetles (35 mature males and 26 mature females) and immature beetles recorded on flight mill (49 immature males and 49 immature females) (David et al., 2014, 2015). The beetles used in these experiments were collected in South-Western France, in a pine forest. Each immature beetle was tested during 10 minutes while each mature beetle was tested during 2 hours each week until its death. Hereafter, we present first the model parametrization for mature beetles, and then for immature beetles as the latter was derived from the former. All the simulations were done in R (R Core Team 2015).

2.1.1. Dispersal kernel of mature beetles (age ≥ 20 days)

Following the flight mill experiment with mature beetles, 77% of adults flew at least once and only these individuals were considered hereafter. Among these fliers, 61 % of flight mill trials showed flight activity long enough (30 s) to be considered dispersal flights (derived from David et al., 2014). In the simulation model, we considered that the daily probability of a mature beetle flying was $p_{fm} = 0.61$. Then, we considered a negative exponential kernel (k_M such as $\int_{x=0}^{+\infty} k_M(x)dx = 1$) to determine the probability to disperse at a given distance x (in meters) during one day (Klein et al. 2006):

$$k_M(x) = \frac{1}{\alpha} exp\left(-\left|\frac{x}{\alpha}\right|\right) \quad \text{(Eq. 1)}$$

where α is the mean daily dispersal distance (in meters). This function was fitted to the flight mill data (David et al., 2014). For that, we calculated the number of flight distances within intervals of 500 m. These distances range from 17 to 8,538 m. To estimate α, we integrated the kernel over the same intervals of 500 m and determined its least-squares estimate in R (using the *nls* function) (R Core Team 2015).

2.1.2. Dispersal kernel of immature beetles (age ≤ 20 days)

Following the flight mill experiment on immature beetles, 45 % of them showed some flight activity (David et al., 2015). In the simulation model, we considered that the daily probability of an immature beetle flying was p_{fi} = 0.45. For immature beetles, we assumed that the shape of the kernel was the same as that of mature beetles but, according to the results on flight mills (David et al., 2015), we set the mean dispersal distance to linearly increase with beetle age. Therefore, we considered the following dispersal kernel (k_I):

$$k_I(x,t) = \frac{1}{f(t)\alpha} exp\left(-\left|\frac{x}{f(t)\alpha}\right|\right) \qquad \text{(Eq. 2)}$$

where x is a given distance (in meters), t is the age of the immature beetle (in days since adult emergence; between 1 and 20), α the mean daily dispersal distance of mature beetles (in meters), and f is an increasing function ranging from 0 to 1. Following David et al. (2015), the distance flown by immature beetles (*d* in m) within 10 minutes of test was:

$$d(t) = 443.63 + 10.71 \times t \qquad \text{(Eq. 3)}$$

Since immature beetles were supposed to have their full dispersal performance when they become mature, then we should have $f(t) = d\,(t)/d\,(t = 20)$ and thus:

$$f(t) = 0.67 + 0.016 \times t \qquad \text{(Eq. 4)}$$

with $f(t = 20) = 1$ and $k_I(x, t = 20) = k_M(x)$

2.2. Mark-release-recapture experiments

In 2014, 36 traps distributed within nine clusters of four traps (Cross Vane ® type and GalloProtect Pack ® dispenser) were installed in a maritime pine dominated forest landscape, in south-western France (44.68°N; -0.85°W) (Fig. 2). The traps in the same cluster were separated by 200 m to maximize the chance of recapturing marked beetles (i.e. about twice the attraction distance, Jactel et al. 2018). The clusters were located as far as possible at the center and at the periphery of two concentric circles of 300 m and 900 m radius (Fig. 2). Immature and mature beetles were released from the center of each cluster. Mature insects were obtained by pheromone trapping nearby (in the same forest region called "Les Landes de Gascogne"), in the same type of maritime pine forest. Immature insects do not respond to the attraction of pheromones at emergence and the first recaptures generally occur around two weeks after adult emergence. Therefore, immature insects were obtained from pieces of dead wood infested by insect larvae (identified by the presence of characteristic sawdust). Insects were individually marked with numbered tags and dots of color paint on the elytra in a way that enabled tracking of their physiological state upon release (immature *versus* mature), cluster of release and date of release. A total of 499 immature and 3085 mature *M. galloprovincialis* individuals were marked and released in July – August 2014 and the traps were checked three times a week, during 150 days. The date of recapture and the trap that caught each marked insect were recorded.

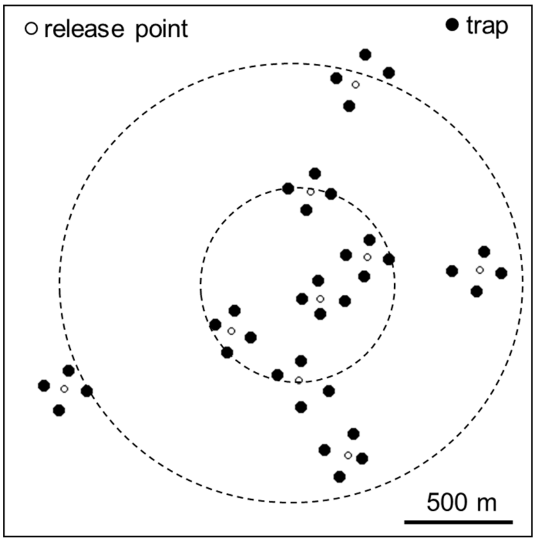

Fig. 2. Spatial distribution of nine clusters of four traps at the centre and at the periphery of two concentric circles of 300 m and 900 m radius for the mark-release-recapture experiment.

2.3. Fine-tuning the model parameters using mark-release-recapture data

We used the dispersal model for simulating both mark-release-recapture experiments, with immature and mature beetles, in order to compare the simulations and the field data, and then fine-tune the estimate of model parameters. Since immature beetles become mature during the experiment, the corresponding model was more complex. Therefore, we present first the dispersal of mature beetles and then of immature beetles.

2.3.1. Simulating the mark-release-recapture experiment when releasing mature beetles

We supposed that mature beetles (n = 100) were released at the center of each cluster. Since the beetles tested in this experiment were previously caught in pheromone traps before being marked, they did respond to sex pheromone attraction and were thus considered mature. Their age was not known but it was necessarily above 20 days which is the maturation age (m), and their longevity was assumed to be l = 120 days (David et al. 2017). Consequently, the age of the beetles was randomly chosen in a uniform distribution between 20 and 120 days. Since the beetles were recaptured up to 70 days after their release, their dispersal was simulated during 70 days. Because the beetles were disturbed (as they were caught in a trap, then marked and released), we considered an initial response time (δ). Since the mean recapture time of mature beetles was 12 days (see results), we tested values going from 4 to 12 days during which the beetles were not supposed to disperse. This delay mainly affected the recapture time in the simulations of mark-release-recapture experiments but it also modified the dispersal distance of beetles at a given time.

Each day after the initial response time, the flying beetles were randomly chosen from a binomial distribution with probability p_{fm} among those which were not dead (*i.e.*, beetles which have not been already caught in a trap and which have not reached their maximal longevity) and which did not rest. To match the time of recapture in experiments, we added a parameter to account for a period when beetles rest and feed between two consecutive flights (β) ranging from 0 to 3 days.

For each flying beetle, we selected at random its dispersal distance from the dispersal kernel of mature beetles previously given, depending on α, the daily mean dispersal distance. The direction of the flight was randomly chosen in a uniform distribution between 0 and 360°. The individual flight trajectory of the beetle was then defined by a straight line between the departure point and the arrival point. If it crosses the attraction area of a trap (disk with a 100 m-radius from the trap, Jactel et al. 2018), then the beetle had a given probability (λ) to be caught in the trap. The trap which caught the beetles and the day of capture were recorded to be compared with field observations.

2.3.2. Simulating the mark-release-recapture experiment when releasing immature beetles

The dispersal model was very similar when simulating the mark-release-recapture of immature beetles. Only few changes were done. First, their initial age was randomly chosen in a uniform distribution ranging from 0 to 7 days after adult emergence because newly emerged beetles were released once per week. During the experiment, beetles were getting older and they were supposed to become mature on day 20. Each day, we therefore differentiated immature beetles from mature beetles. As long as beetles were immature, they had a given probability to fly (p_{fi}) and following their age, we considered the corresponding dispersal kernel (k_I) and daily mean dispersal distance ($f(t)\alpha$). We also considered an initial response time (δ), but for immature beetles, this time did not represent a time to recover from their manipulation (as they directly emerged in laboratory) but to the time required to respond to the pheromone.

2.3.3. Fine-tuning parameter estimates

To improve the goodness-of-fit of the dispersal model for field data, we determined the combination of parameters' values that gave the lowest error when comparing simulations to observations. For this comparison, we considered different outputs for both immature and mature beetles: the recapture rate within the same cluster (9 clusters x 2 experiments), the duration between release and recapture within the same cluster (9 clusters x 2 experiments), the recapture rate in other clusters (9 x 8 inter-clusters x 2 experiments), and the duration between release and recapture in other clusters (9 x 8 inter-clusters x 2 experiments). The error was measured by two statistics: the relative bias (*RB* = |mean predicted - mean observed| / mean observed) and the root mean square error (*RMSE* = √[mean (predicted value - observed value)²]).

Since α may vary between 300 and 2000 m per day (from David et al., 2014), we tested: α = 500, 1000, 1500, 2000, and 2500 m. In addition to α, additional parameters were necessary to simulate the mark-release-recapture experiment and had to be estimated: λ, the trap efficiency (probability of an insect being caught by the pheromone trap given that its trajectory crosses the area of trap attraction); δ, the delay response time (in days); and β, the rest duration between two consecutive flights (in days) (Table 1). Based on preliminary simulations, we tested the following values: λ = 0.005, 0.01 and 0.02; δ = 4, 8 and 12 days; β = 0, 1, 2, 3 days.

Consequently, a total of 180 combinations of parameters' values was considered ((5 values for α) × (3 values for λ) × (3 values for δ) × (4 values for β) = 180 values) for each of the two models (mature and immature beetles). We had at our disposal 8 criteria to identify the best parameters, i.e. those which would provide the lowest error statistics for the relative bias (*RB*) and the root mean square error (*RMSE*) in recapture rate and duration, within and between clusters of pheromone traps. We used a Multi Criteria Decision Analysis approach, based on the PROMETHEE algorithm, and developed on the Visual-PROMETHEE 1.4.0.0® platform, to identify the best combination of parameters (e.g. "actions" in the PROMETHEE vocabulary). The complete outranking method was applied (Mareschal et al. 1984), with equal weight for all criteria, which were set to be minimized, using a preference value of 0.01.

2.3.4. Simulation of insects' dispersal

Finally, the potential dispersal of emerging *M. galloprovincialis* adults (*n* = 100) was simulated accounting for the best combination of parameters' value (Table 1), from adult emergence to 20 days after emergence (corresponding to the end of the immature stage), 70 days after emergence (corresponding approximately to the maximum date of pine wood nematode transmission), and 120 days (corresponding to the maximal adult longevity). A sensitivity analysis was also done on the parameter α. The dispersal simulations were done in R (Robinet et al. 2018) and we assumed that insects dispersed within a homogeneous landscape representative of a non-fragmented pine forest.

3. Results

3.1. Mark-release-recapture experiments

In the MRR experiments, the 36 traps distributed into 9 clusters caught a total of 37 marked immatures out of 499 released and 193 marked matures out of 3085 released (SM2). The mean recapture rate of immature beetles was ca. 5% within trap clusters and ca. 0.3% between trap clusters. They took at least 18 days on average to be recaptured. The mean recapture rate of mature beetles was ca. 3% within, and 0.4% between clusters of traps. They were on average recaptured within 12 days. The maximum dispersal distance recorded was 1,754 m for immature and 1,886 m for mature insects, which corresponded more or less to the distance between two most distant clusters. The longest recapture time was 61 days for immature and 70 days for mature beetles.

3.2. Model calibration and fine-tuning

The estimate of mean dispersal distance based on flight mill data was α = 2268 m (*t.test* = 17.73, $P < 0.001$) and the negative exponential kernel fitted very well the distances recorded in the flight mill experiment (Fig. 3; SM1).

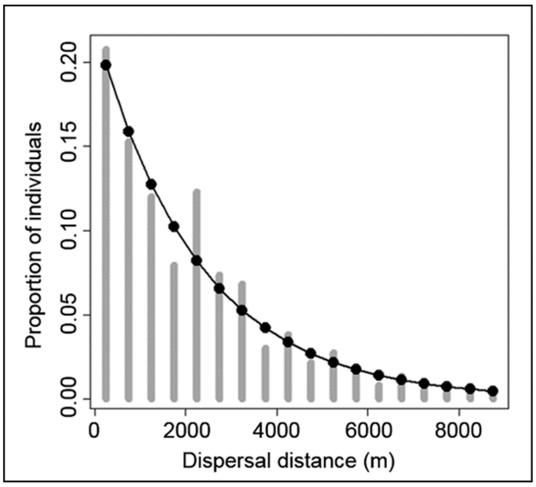

Fig. 3. Negative exponential kernel fitted to the dispersal capabilities of *Monochamus galloprovincialis* mature adults on flight mills.

When fine-tuning the dispersal model, the parameter settings were consistent with each other. The best fit to MRR data for the dispersal model was obtained with the combination of the following parameters: α = 2000 m, λ = 0.01, δ = 12 days, β = 1 day for the release of immature beetles, and α = 2000 m, λ = 0.01, δ = 8 days, β = 1 day for the release of mature beetles (Table 2; SM3). With this parameterization, the recapture rates and the times of recapture were very similar in simulations and observations (Fig. 4). Only the recapture rate of immatures within the cluster of traps was substantially different, nevertheless the absolute value differed by approximately 2.0% only.

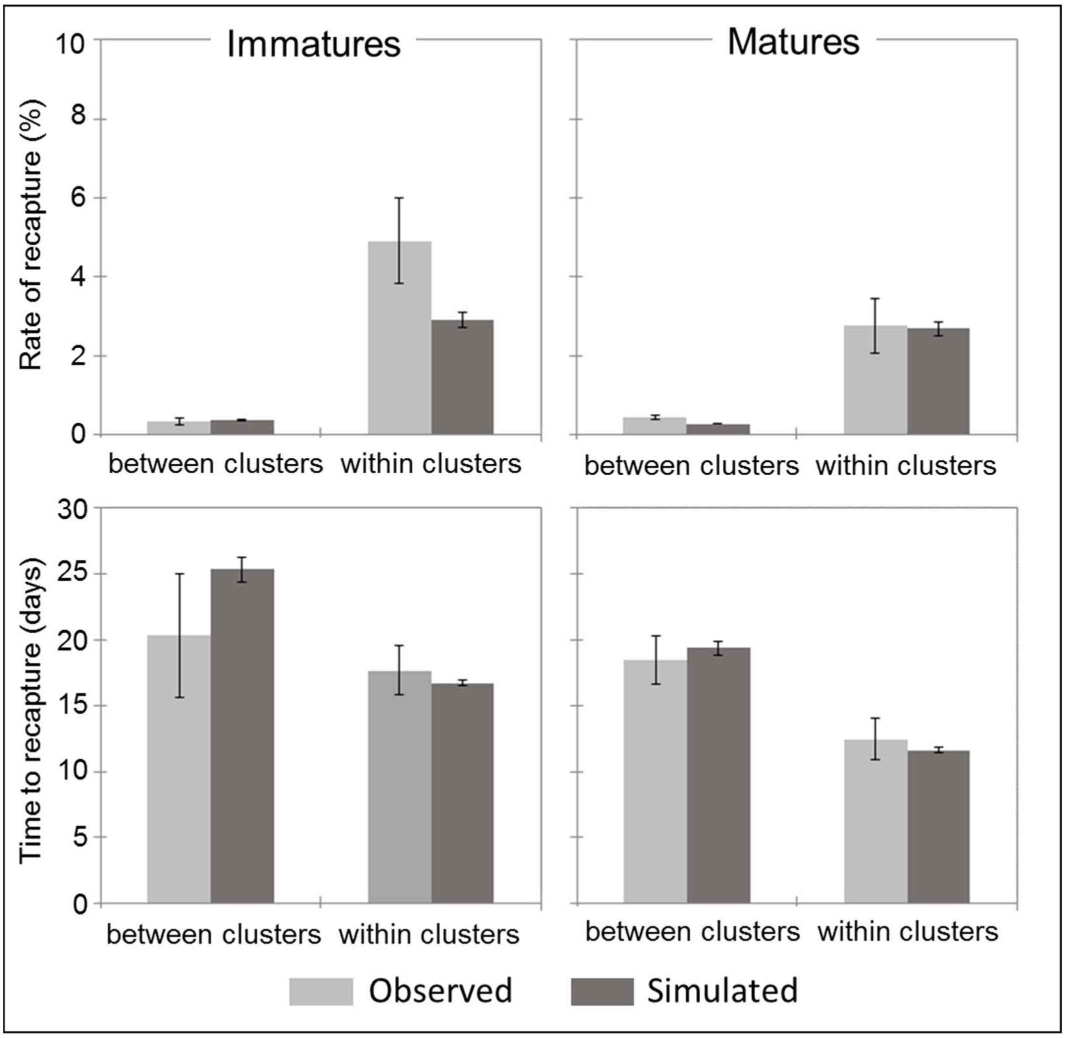

Fig. 4. Comparison of mean (± SE) rate and time of recapture for immature and mature *Monochamus galloprovincialis* beetles, within- and between-clusters of traps, observed in the mark-release-recapture experiments and simulated by the dispersal model with the best combination of values.

3.3. Simulation of the insect dispersal

We simulated the insect dispersal using the best combination of parameter values (Fig. 5; see also the video in Robinet et al. 2018). A substantial proportion of daily flights (>20% for mature beetles and >5% for immature beetles) could reach at least 500 m. The cumulative distance travelled by 100 insects between their emergence point and the final destination point (on day 120) was 63,464 m on average (SD = 15,907 m). However, the dispersal distance "as the crow flies" between the origin and the destination point was lower, but still of 13,219 m on average (SD = 7,313 m) due to non-unidirectional trajectories (fig.5; see also Table 3 for dispersal distances on day 20 and 70, and for the median). When considering a change +/- 10% in the value of α, the cumulative dispersal distance until day 120 was within the interval [56,071 m; 69,170 m] and the distance "as the crow flies" from the origin was within [11,968 m; 13,903 m].

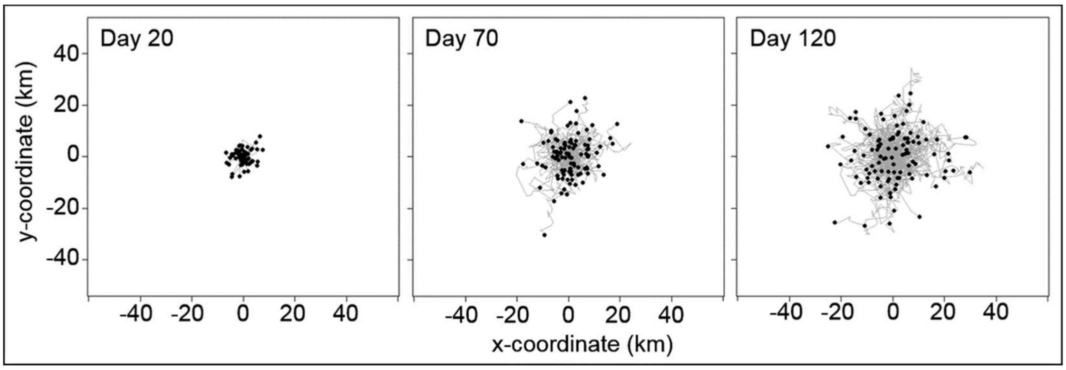

Fig. 5. Simulated dispersal of 100 individuals from a release point at the origin (0, 0) at 20 days, 70 days and 120 days after the adult emergence. Each black dot represents an insect and the grey lines represent their trajectory.

On day 20, about 80% of insects were located at more than 500 m from the emergence point, and 1% even reached more than 10 km (Table 3), showing that they could potentially disperse rapidly even during the immature stage. At the end of their life-span, on day 120, more than half of the insects could potentially be located at more than 10 km (Table 3) and even 23% at more than 20 km from there emergence point.

4. Discussion

4.1. Dispersal modelling: a new approach to conciliate dispersal distance from flight mill experiments and mark-release-recapture experiments

Many studies focus on one method to assess the potential dispersal of insect species such as flight mill experiments (e.g., Jactel & Gaillard 1991, Schumacher et al. 1997, Briegel et al. 2001, Ishiguri & Shirai 2004, Bradley & Altizer 2005, Robinet et al. 2012, Maes et al. 2014) and mark-release-recapture experiments (e.g., Turchin & Thoeny 1993, Marini et al. 2010, Margaritopoulos et al. 2012). The number of species for which the dispersal capabilities have been recorded with different methods is relatively low and these measures generally differed (e.g., from tens of kilometers *versus* hundreds of meters for *M. galloprovincialis*). However, it is not possible to compare directly these distances since they represent different measures of the dispersal distance. Data from flight mill experiments may provide overestimated flight performance but they allowed determining the dispersal kernel, i.e. the shape of distances distribution and the proportion of individuals able to fly long distances (e.g., those mainly contributing to the population range expansion). Data from mark-release-recapture experiments provided an interception distance. Although they were based on individuals' dispersal in the field, the traps potentially captured individuals that could be able to disperse further.

Until now, there was no study comparing dispersal measures based on the same source of population. In this study, insects tested on the flight mill and in the mark-release-recapture experiments all originated from a maritime pine dominated forest of south-western France. Therefore, variability in dispersal distances may not be attributed to intra-specific variability. The dispersal model that we developed reveals that the distances recorded in the two types of experiment were actually in good agreement. The estimate of the daily mean dispersal distance (α = 2.0 km) was consistent with the flight distance data estimated on the flight mill once per week (1.93 km for females and 2.14 km for males; David *et al*., 2014) and with the distance flown between the release point and the most distant trap (1.8-1.9 km).

Another interesting convergence point is that i) many marked beetles remained within the same small forest area (the one delimited by trap locations, ca. 1000 hectares) for several weeks (up to 7 weeks), ii) the flight mill experiment showed that most of the individual flights were of short duration (i.e. mean individual flight of ca. 1km, David et al. 2014) and iii) the dispersal model revealed that the zig-zag trajectories led to a majority of beetles remaining within a much smaller area than predicted with unidirectional flights. All these observations are consistent with *M. galloprovincialis* mainly performing foraging flights, *i.e.* those necessary to find suitable host pine trees for feeding on fresh shoot or laying eggs on dead branches, and not migratory flights, those required when feeding or ovipositing resources are scarce in space or time.

4.2. Reconsideration of control measures for the pine wood nematode

It has been suggested to use mass trapping for the control of *M. galloprovincialis* (Sanchez-Husillos et al. 2015) to reduce the transmission and the spread of PWN. We are aware of five previous mark-release-recapture experiments with the pine sawyer beetle in the Iberian Peninsula (Gallego et al. 2012, Hernandez et al. 2011, Mas et al. 2013, Torres-Villa et al. 2015, Etxebeste et al. 2016). Although the landscape context, the number of traps and the distance between traps differed and the populations do not belong to the same genetic clade (Haran et al. 2018), these experiments were all conducted in similar conditions (similar traps and lures) as our MRR study. Interestingly they provide consistent estimate of recapture rates. Using immature beetles, Etxebeste et al. (2016) obtained a mean recapture rate per trap of 1.25% (in 2010) and 0.52% (in 2011) which is very close to the 1.23% immature beetles recaptured per trap within clusters in our experiment. Likewise, using mature beetles (first trapped then marked and released), Gallego et al. (2012) obtained a rate of recapture per trap of 0.66%, Hernandez et al. (2011) 0.62%-0.67%, Mas et al. (2013) 0.83%-1.83%, Torres-Villa et al.

(2015) 0.67%, which is very similar to the 0.69% mature beetles recaptured per trap within clusters in our experiment. Due to these very low levels of trap efficiency, one would need a very high density of traps per hectare for capturing enough beetles to impede the reproduction success and thus durably reduce the population density of the insect vector. Even more problematic, it took on average 18 days to recapture the released immature beetles, while Etxebeste et al. (2016) indicated that recaptures occurred 7–14 days after their release. This means that they would have had ample time to transmit most of their nematode load while feeding on shoot for sex maturation. When considering the high density of traps needed, that should be deployed on very large areas (e.g. the pine forest at high risk of invasion in southwestern France covers ca. 1 million hectares) with the incapacity of trapping immature beetles that transmit PWN, it clearly appears that mass trapping should not be recommended as control measure.

According to the simulated dispersal of *M. galloprovincialis*, a substantial proportion of daily flights (>20% for mature beetles and >5% for immature beetles) could reach at least 500 m, which is the radius of the clear-cut imposed by the European regulation. In addition, most of insects (about 80%) have already gone further than 500 m a few days after their emergence (Table 3). So far, there is no evidence that the flight performance of *M. galloprovincialis* carrying the pine wood nematode is different from those free from the nematode (flight distance of 15 infested insect tested on flight mill was not significantly different from those not infested but further studies are needed; David 2014). Based on these results and the continuous spread of the pine wood nematode in the Iberian Peninsula despite the European regulation (Rodrigues et al. 2015), it is legitimate to question the effectiveness of the clear-cut measure. However further research is needed to better assess this effectiveness, accounting for the transmission of the pine wood nematode along the adult life span of *M. galloprovincialis*. Here again a dispersal model would be relevant to simulate the effects of clear-cuts on PWN dissemination and transmission.

Assessing the potential dispersal capability is also useful to improve the layout of a network of pheromone traps as required by the European Union for the surveillance of the pine wood nematode. Based on the spatial distribution of dispersal probabilities derived from the model and a given number of traps, it is possible to optimize the trapping network so that: 1) infested beetles have a good chance to be captured and thus the nematode to be detected as early as possible, and 2) the origin of the infestation (i.e., contaminated trees from which the insects emerged) could be easily delimited by triangulation.

However, for both objectives, it will be necessary to improve the realism of the dispersal model by taking into account landscape compositional heterogeneity as *M. galloprovincialis* might modify its dispersal behavior to cross or avoid non-habitat patches, like broadleaved forests or crop fields. Most of mathematical approaches related to population spread in heterogeneous environment have focused on periodic environments alternating very and less favorable areas for survival and dispersal (Shigesada & Kawasaki 1997; Berestycki et al. 2005). These studies provide important insights into the role of periodic heterogeneity in spread dynamics but are not relevant to determine accurately the effects of real landscapes. In addition, they are mainly based on the reaction-diffusion model (Fisher-KPP), which is analog of a Gaussian dispersal kernel. In our case, we have shown that the negative exponential kernel fits better the dispersal of *M. galloprovincialis*, with higher proportion of individuals able to disperse at long distance. Rather, we suggest collecting field data on insect dispersal behavior (e.g., using MRR experiments) in landscapes of different heterogeneities to to test whether some particular configurations can significantly accelerate or impede individuals' dispersal. By adapting the model to those features, we will provide a more effective tool to predict the dispersal capability of the insect vector of one of the most damaging forest pests, in realistic environments.

Acknowledgments

We are grateful to Inge van Hader, Elorri Segura, Fabrice Vétillard and Nils Préat for their invaluable help with field work. We sincerely thank Philippe Castagnone-Sereno, Manuel Mota, Géraldine Roux, Corinne Sarniguet, Xavier Tassus for fruitful discussions in the working group on pine wood nematode of ANSES.

Funding

We acknowledge support for this work from the EU project REPHRAME KBBE.2010.1.4-09 (FP7 Project, Analysis of the potential of the pine wood nematode (*Bursaphelenchus xylophilus*) to spread, survive and cause pine wilt in European coniferous forests in support of EU plant health policy) and to ANSES (French Agency for Food, Environmental and Occupational Health & Safety).

SUPPORTING INFORMATION

SM1: Comparison of the exponential and Gaussian kernels

MS-MG-Dispersal-SM1.docx

SM2. Results of the mark-release-recapture experiments

MS-MG-Dispersal-SM2.xlsx

SM3. Results of the Multi-Criteria Decision Analysis

MS-MG-Dispersal-SM3.xlsx

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TABLES

Table 1. Parameters used in the model. Parameters given in Greek letters are parameters which are estimated in the present study. Values of parameters in Roman letters are derived from literature *(l, m)*, previous experiments (*r*, p_{fm}, p_{fi}), or arbitrary (*n*). These parameters are used to calibrate the model on flight mill data (FM), to validate the model on mark-release-recapture data (MRR) and/or to simulate the insect dispersal (SIM).

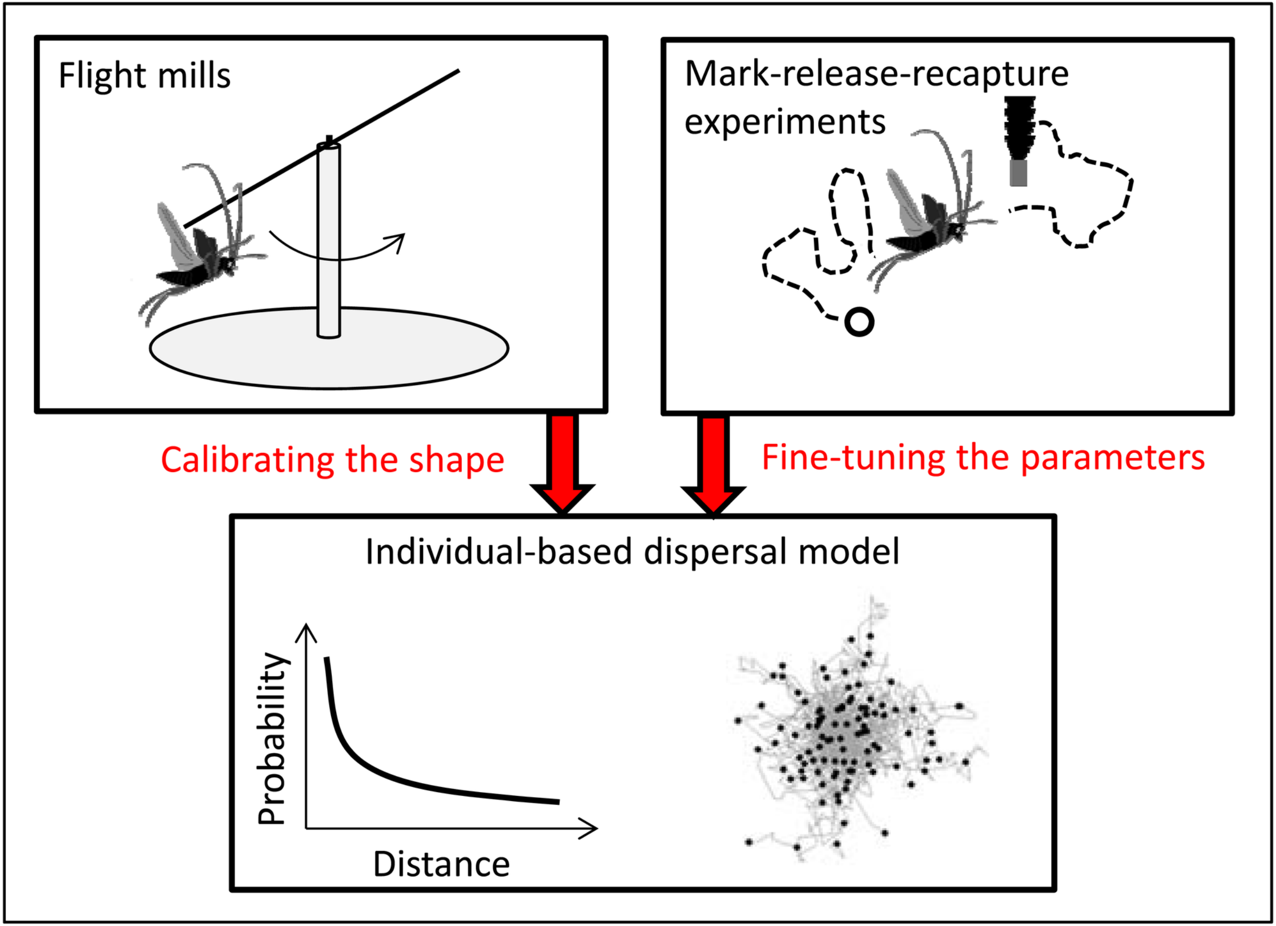
Parameter	Definition	Values	FM	MRR	SIM
α	Mean daily dispersal distance (in meters)	500 – 2500	X	X	X
r	Attraction distance of the trap (in meters)	100		X	
λ	Trap efficiency (rate)	0.005 – 0.02		X	
δ	Delay response time (in days)	4 – 12 days		X	X
β	Rest between two flights (in days)	0 – 3 days		X	X
n	Number of beetles released	100		X	X
l	Adult longevity (in days since adult emergence)	120 days	X	X	X
m	Maturation age (in days since adult emergence)	20 days	X	X	X
p_{fm}	Daily probability of flying for mature beetles	0.61	X	X	X
p_{fi}	Daily probability of flying for immature beetles	0.45	X	X	X

Table 2. Relative bias (*RB*) and root mean square error (*RMSE*) of the model simulating the Mark-Release-Recapture experiment for the parameters corresponding to the best fit model (α = 2000 m, λ = 0.01, δ = 12 days, β = 1 day for immature beetles and α = 2000 m, λ = 0.01, δ = 8 days, β = 1 day for mature beetles). See SM3 for the fitting success related to all parameters' values.

Variable		**Immature beetles**	**Mature beetles**
Rate of recapture	Intra-cluster	*RB* = 0.778 *RMSE* = 0.406	*RB* = 0.665 *RMSE* = 0.028
	Inter-cluster	*RB* = 2.353 *RMSE* = 0.167	*RB* = 0.945 *RMSE* = 0.360
Time of recapture	Intra-cluster	*RB* = 0.296 *RMSE* = 0.054	*RB* = 0.378 *RMSE* = 0.065
	Inter-cluster	*RB* = 0.643 *RMSE* = 0.246	*RB* = 0.667 *RMSE* = 0.047

Table 3. Results of the dispersal model when simulating the dispersal of 100 insects with the best fitted parameters values.

Time after adult emergence	**Dispersal distance (m)**			**Percentage (%) of individuals dispersed at**			
	Mean	SE	Median	≥ 500 m	≥ 5 000 m	≥ 10 000 m	≥ 20 000 m
Day 20	2 507	2 384	1 790	78	15	1	0
Day 70	8 898	5 552	7 806	100	78	33	5
Day 120	13 219	7 313	11 395	99	92	56	23


Flight mills
Mark-release-recapture experiments
Calibrating the shape
Fine-tuning the parameters
Individual-based dispersal model
Probability
Distance