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Modeling the distances traveled by flying insects based on the combination of flight mill and mark-release-recapture experiments

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Christelle Robinet, Guillaume David, Herve Jactel. Modeling the distances traveled by flying insects based on the combination of flight mill and mark-release-recapture experiments. *Ecological Modelling*, 2019, 402, pp.85-92. 10.1016/j.ecolmodel.2019.04.006 . hal-02620601

HAL Id: hal-02620601

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Modelling the distances travelled by flying insects

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based on the combination of flight mill and mark-release-recapture

4

experiments

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

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Submitted to Ecological Modelling (Original research paper)

19 **Abstract**

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

39

40 **Key-Words**

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

43 **1. Introduction**

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

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

62 One of the biggest threats of pine forests across the world is the pine wood nematode (PWN),
63 *Bursaphelenchus xylophilus*, as it can potentially kill a pine tree within a few weeks (Suzuki 2002,
64 Webster & Mota 2008, Vicente et al. 2012). Native to North America (Dropkin et al. 1981), it has
65 invaded Japan in 1905 (Yano 1913), China in 1982 (Cheng et al. 1986), Korea in 1988 (Yi et al. 1989),
66 and Portugal in 1999 (Mota et al. 1999), where it has caused extensive mortality. It was also detected
67 in Spain in 2008 (Robertson et al. 2011). To disperse from one tree to another, the pine wood

68 nematode needs an insect vector, which always belongs to the *Monochamus* genus. In Portugal, the
69 pine sawyer beetle, *Monochamus galloprovincialis* (Olivier, 1795), is the only insect known to carry the
70 pine wood nematode (Sousa et al. 2002) but its flight capability is still not well known.

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

82 Several mark-release-recapture experiments have been conducted to determine the dispersal
83 capability of *M. galloprovincialis* in the Iberian Peninsula. The advantage of this method is to measure
84 the dispersal distance of individuals in the field. As they were supposed to have very limited flight
85 capabilities, traps were generally installed in the neighborhood of the release points (e.g., up to 0.5 km
86 and 0.76 km, Etxebeste et al. 2016) and thus most adults have been caught at very short distances.
87 When traps were installed further, some insects were caught at greater distances (at more than 3 km
88 from the release points, with a maximal distance of 5.3 km, Etxebeste et al. 2016; 7.1 km, Hernández
89 et al. 2011; 8.3 km, Gallego et al. 2012; and 22.1 km, Mas et al. 2013). Consequently, it seems that the
90 interception distance can be relatively high in some cases. The variability in recapture distance
91 between these experiments probably reveals the dilemma in placing the traps. When traps are
92 installed close to the release point, they catch more insects but, obviously, long recapture distances

93 cannot be observed (Turchin 1998). When the traps are installed far from the release point, there is
94 low chance to recapture an insect. Insects that were not caught in the traps may have dispersed
95 further, and insects caught in the traps would have perhaps been able to disperse further if they were
96 not caught.

97 Another method commonly used to estimate the flight performance of insects consists in
98 testing individuals on a flight mill. In this method, individuals are placed in artificial conditions and the
99 flight performance recorded on a flight mill may not be fully representative of the dispersal capability
100 in the field. However, it provides an accurate estimate of the probability distribution of flight distances,
101 and thus, of the proportion of beetles that are able to fly further than the others. It also allows
102 recording the distance flown by each individual over its life span under controlled conditions and
103 eventually comparing the effects of different treatments (e.g., according to age, sex and temperature
104 conditions). The flight performance has already been measured in this way for several insect species,
105 such as bark beetle (Jactel & Gaillard 1991), codling moth (Schumacher et al. 1997), mosquito (Briegel
106 et al. 2001), peach fruit moth (Ishiguri & Shirai 2004), monarch butterfly (Bradley & Altizer 2005),
107 emerald ash borer (Taylor et al. 2010), pine processionary moth (Robinet et al. 2012), and predatory
108 ladybirds (Maes et al. 2014). The flight performance of adult beetles of *M. galloprovincialis* was also
109 tested with this method (David et al. 2014, 2015). When emerging from a tree, adult beetles are
110 immature for approximately 20 days (Naves et al. 2006). At this immature stage, they do not respond
111 to sex pheromone attraction and thus cannot be caught by pheromone traps. During this period of
112 sexual maturation, young adults are the main vector responsible for nematode transmission which
113 takes place when insect are feeding on fresh pine twigs (vectors can transmit the nematode for about
114 10 weeks since their emergence; Naves et al. 2007). Using automatically recording flight mills, David
115 et al. (2015) showed that flight distance performed each day by immature beetles increased
116 progressively as beetles were aging, probably as they develop their muscles and accumulate energy
117 when feeding, until reaching a limit. In a second experiment, David et al. (2014) measured the flight
118 performance of mature beetles as 2 km per testing day on average (8 km maximum). However, it is

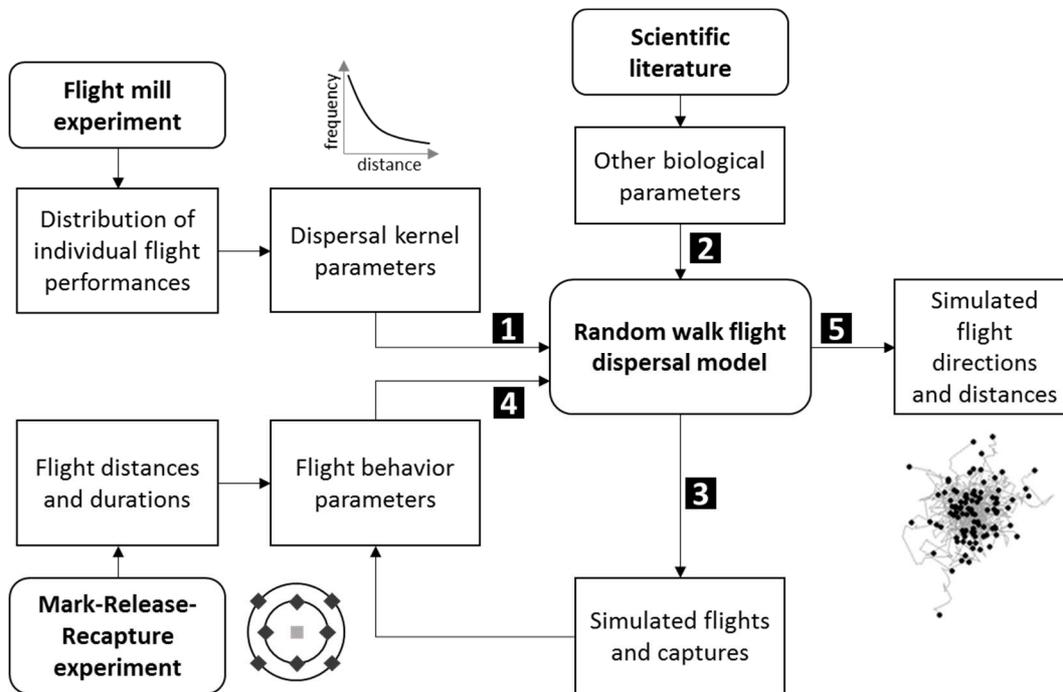
119 unknown whether they can fly these distances every day (2 km per day) or during the whole week (2
120 km/ 7 = 0.3 km per day), as they were tested only once per week. During their entire mature adult
121 lifespan, they could fly 16 km on average (63 km maximum). Although these flight distances are higher
122 than the recapture distances, their direct comparison is impossible because these distances do not
123 represent the same dispersal measure (interception distance *versus* artificial flight performance).

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

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

142 Firstly, we calibrated the individual-based dispersal model using the distances recorded in
143 flight-mill experiments (David et al. 2014, David et al. 2015) to capture the shape of the dispersal

144 distance distribution. Then, we conducted mark-release-recapture experiments with both immature
 145 and mature *M. galloprovincialis* beetles, in a pine plantation landscape, to fine-tune model parameters
 146 (Fig. 1).



147
 148 **Fig. 1.** Conceptual diagram of the modelling approach. Data from flight mill experiments (1; section
 149 2.1) combined with data from literature (2) were used to calibrate the dispersal model. Then, this
 150 model was used to simulate the dispersal of the insect (3) and simulate the mark-release-recapture
 151 experiments (4; section 2.3) to refine the parameters associated with the insect's flight behaviour in
 152 the field. (5; section 2.3).

153

154 2. Materials and methods

155

156 2.1. Calibration of the dispersal kernel with flight mill data

157 The individual-based model describes the dispersal of immature and mature *M. galloprovincialis*
 158 beetles based on a several parameters (Table 1). The shape of the dispersal kernel (negative

159 exponential model; see SM1) was fitted to the flight performance of both mature beetles (35 mature
160 males and 26 mature females) and immature beetles recorded on flight mill (49 immature males and
161 49 immature females) (David et al., 2014, 2015). The beetles used in these experiments were collected
162 in South-Western France, in a pine forest. Each immature beetle was tested during 10 minutes while
163 each mature beetle was tested during 2 hours each week until its death. Hereafter, we present first
164 the model parametrization for mature beetles, and then for immature beetles as the latter was derived
165 from the former. All the simulations were done in R (R Core Team 2015).

166 **2.1.1. Dispersal kernel of mature beetles (age ≥ 20 days)**

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

$$173 \quad k_M(x) = \frac{1}{\alpha} \exp\left(-\left|\frac{x}{\alpha}\right|\right) \quad (\text{Eq. 1})$$

174 where α is the mean daily dispersal distance (in meters). This function was fitted to the flight mill data
175 (David et al., 2014). For that, we calculated the number of flight distances within intervals of 500 m.
176 These distances range from 17 to 8,538 m. To estimate α , we integrated the kernel over the same
177 intervals of 500 m and determined its least-squares estimate in R (using the *nls* function) (R Core Team
178 2015).

179

180

181

182 **2.1.2. Dispersal kernel of immature beetles (age ≤ 20 days)**

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

$$189 \quad k_I(x, t) = \frac{1}{f(t)\alpha} \exp\left(-\left|\frac{x}{f(t)\alpha}\right|\right) \quad (\text{Eq. 2})$$

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

$$194 \quad d(t) = 443.63 + 10.71 \times t \quad (\text{Eq. 3})$$

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

$$197 \quad f(t) = 0.67 + 0.016 \times t \quad (\text{Eq. 4})$$

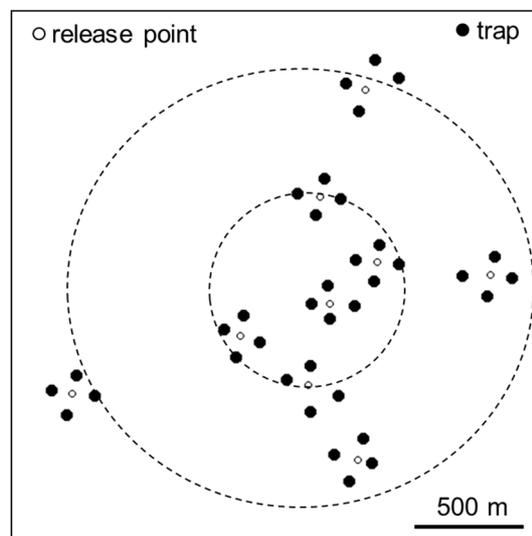
198 with $f(t = 20) = 1$ and $k_I(x, t = 20) = k_M(x)$

199

200 **2.2. Mark-release-recapture experiments**

201 In 2014, 36 traps distributed within nine clusters of four traps (Cross Vane[®] type and GalloProtect Pack
202[®] dispenser) were installed in a maritime pine dominated forest landscape, in south-western France
203 (44.68°N; -0.85°W) (Fig. 2). The traps in the same cluster were separated by 200 m to maximize the

204 chance of recapturing marked beetles (i.e. about twice the attraction distance, Jactel et al. 2018). The
205 clusters were located as far as possible at the center and at the periphery of two concentric circles of
206 300 m and 900 m radius (Fig. 2). Immature and mature beetles were released from the center of each
207 cluster. Mature insects were obtained by pheromone trapping nearby (in the same forest region called
208 “Les Landes de Gascogne”), in the same type of maritime pine forest. Immature insects do not respond
209 to the attraction of pheromones at emergence and the first recaptures generally occur around two
210 weeks after adult emergence. Therefore, immature insects were obtained from pieces of dead wood
211 infested by insect larvae (identified by the presence of characteristic sawdust). Insects were
212 individually marked with numbered tags and dots of color paint on the elytra in a way that enabled
213 tracking of their physiological state upon release (immature *versus* mature), cluster of release and date
214 of release. A total of 499 immature and 3085 mature *M. galloprovincialis* individuals were marked and
215 released in July – August 2014 and the traps were checked three times a week, during 150 days. The
216 date of recapture and the trap that caught each marked insect were recorded.



217

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

220

221

222 **2.3. Fine-tuning the model parameters using mark-release-recapture data**

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

228 **2.3.1. Simulating the mark-release-recapture experiment when releasing mature beetles**

229 We supposed that mature beetles ($n = 100$) were released at the center of each cluster. Since the
230 beetles tested in this experiment were previously caught in pheromone traps before being marked,
231 they did respond to sex pheromone attraction and were thus considered mature. Their age was not
232 known but it was necessarily above 20 days which is the maturation age (m), and their longevity was
233 assumed to be $l = 120$ days (David et al. 2017). Consequently, the age of the beetles was randomly
234 chosen in a uniform distribution between 20 and 120 days. Since the beetles were recaptured up to
235 70 days after their release, their dispersal was simulated during 70 days. Because the beetles were
236 disturbed (as they were caught in a trap, then marked and released), we considered an initial response
237 time (δ). Since the mean recapture time of mature beetles was 12 days (see results), we tested values
238 going from 4 to 12 days during which the beetles were not supposed to disperse. This delay mainly
239 affected the recapture time in the simulations of mark-release-recapture experiments but it also
240 modified the dispersal distance of beetles at a given time.

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

246 For each flying beetle, we selected at random its dispersal distance from the dispersal kernel
247 of mature beetles previously given, depending on α , the daily mean dispersal distance. The direction
248 of the flight was randomly chosen in a uniform distribution between 0 and 360°. The individual flight
249 trajectory of the beetle was then defined by a straight line between the departure point and the arrival
250 point. If it crosses the attraction area of a trap (disk with a 100 m-radius from the trap, Jactel et al.
251 2018), then the beetle had a given probability (λ) to be caught in the trap. The trap which caught the
252 beetles and the day of capture were recorded to be compared with field observations.

253 ***2.3.2. Simulating the mark-release-recapture experiment when releasing immature beetles***

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

264 ***2.3.3. Fine-tuning parameter estimates***

265 To improve the goodness-of-fit of the dispersal model for field data, we determined the combination
266 of parameters' values that gave the lowest error when comparing simulations to observations. For this
267 comparison, we considered different outputs for both immature and mature beetles: the recapture
268 rate within the same cluster (9 clusters x 2 experiments), the duration between release and recapture
269 within the same cluster (9 clusters x 2 experiments), the recapture rate in other clusters (9 x 8 inter-
270 clusters x 2 experiments), and the duration between release and recapture in other clusters (9 x 8

271 inter-clusters x 2 experiments). The error was measured by two statistics: the relative bias ($RB =$
272 $|\text{mean predicted} - \text{mean observed}| / \text{mean observed}$) and the root mean square error ($RMSE =$
273 $\sqrt{[\text{mean}(\text{predicted value} - \text{observed value})^2]}$).

274 Since α may vary between 300 and 2000 m per day (from David et al., 2014), we tested:
275 $\alpha = 500, 1000, 1500, 2000,$ and 2500 m. In addition to α , additional parameters were necessary to
276 simulate the mark-release-recapture experiment and had to be estimated: λ , the trap efficiency
277 (probability of an insect being caught by the pheromone trap given that its trajectory crosses the area
278 of trap attraction); δ , the delay response time (in days); and β , the rest duration between two
279 consecutive flights (in days) (Table 1). Based on preliminary simulations, we tested the following
280 values: $\lambda = 0.005, 0.01$ and 0.02 ; $\delta = 4, 8$ and 12 days; $\beta = 0, 1, 2, 3$ days.

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

291 **2.3.4. Simulation of insects' dispersal**

292 Finally, the potential dispersal of emerging *M. galloprovincialis* adults ($n = 100$) was simulated
293 accounting for the best combination of parameters' value (Table 1), from adult emergence to 20 days
294 after emergence (corresponding to the end of the immature stage), 70 days after emergence
295 (corresponding approximately to the maximum date of pine wood nematode transmission), and 120

296 days (corresponding to the maximal adult longevity). A sensitivity analysis was also done on the
297 parameter α . The dispersal simulations were done in R (Robinet et al. 2018) and we assumed that
298 insects dispersed within a homogeneous landscape representative of a non-fragmented pine forest.

299

300 **3. Results**

301

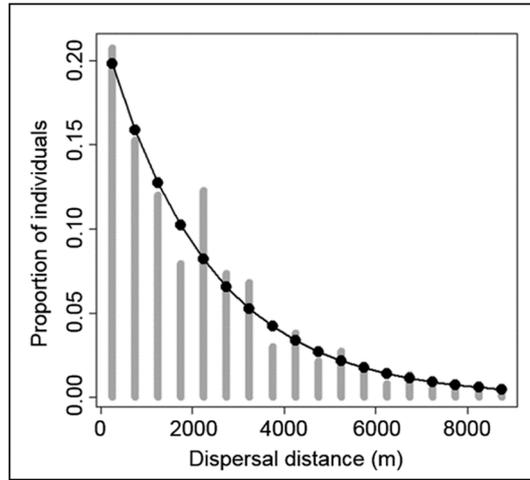
302 **3.1. Mark-release-recapture experiments**

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

311

312 **3.2. Model calibration and fine-tuning**

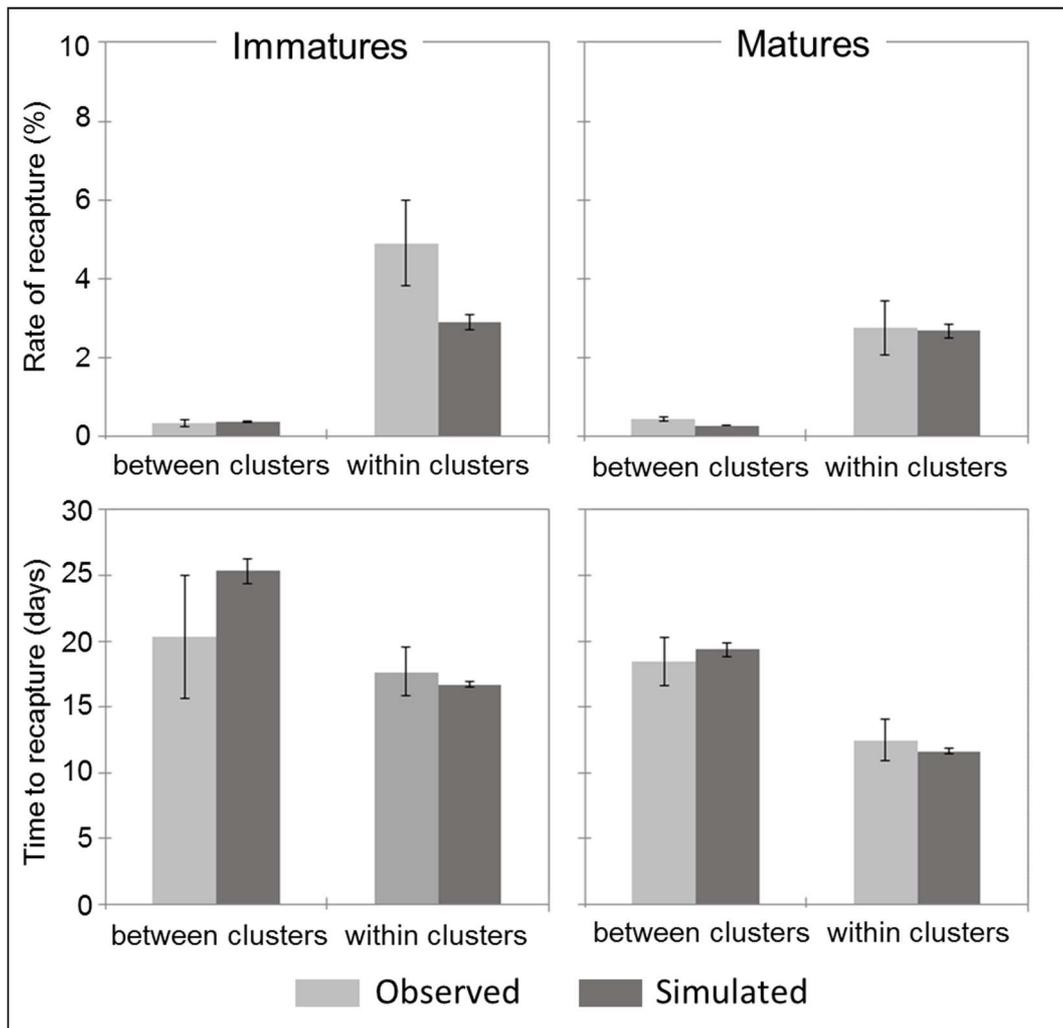
313 The estimate of mean dispersal distance based on flight mill data was $\alpha = 2268$ m ($t.test = 17.73$,
314 $P < 0.001$) and the negative exponential kernel fitted very well the distances recorded in the flight mill
315 experiment (Fig. 3; SM1).



316

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

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



326

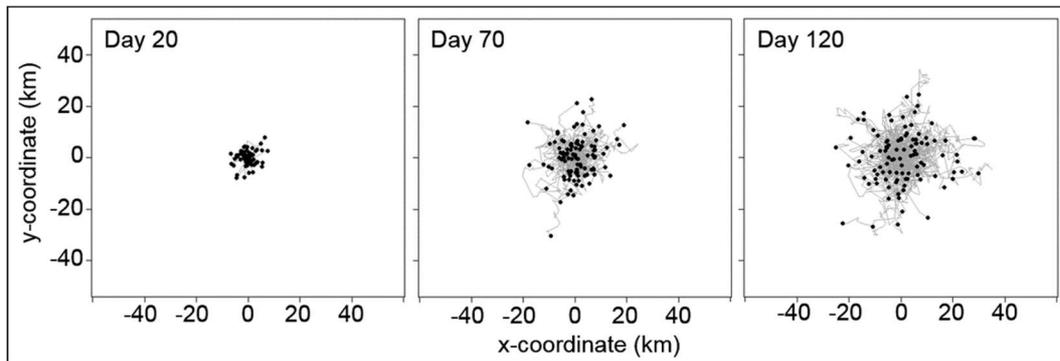
327 **Fig. 4.** Comparison of mean (\pm SE) rate and time of recapture for immature and mature *Monochamus*
 328 *galloprovincialis* beetles, within- and between-clusters of traps, observed in the mark-release-
 329 recapture experiments and simulated by the dispersal model with the best combination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

330

331 3.3. Simulation of the insect dispersal

332 We simulated the insect dispersal using the best combination of parameter values (Fig. 5; see also the
 333 video in Robinet et al. 2018). A substantial proportion of daily flights (>20% for mature beetles and
 334 >5% for immature beetles) could reach at least 500 m. The cumulative distance travelled by 100 insects
 335 between their emergence point and the final destination point (on day 120) was 63,464 m on average
 336 (SD = 15,907 m). However, the dispersal distance “as the crow flies” between the origin and the

337 destination point was lower, but still of 13,219 m on average (SD = 7,313 m) due to non-unidirectional
338 trajectories (fig.5; see also Table 3 for dispersal distances on day 20 and 70, and for the median). When
339 considering a change +/- 10% in the value of α , the cumulative dispersal distance until day 120 was
340 within the interval [56,071 m; 69,170 m] and the distance “as the crow flies” from the origin was within
341 [11,968 m; 13,903 m].



342
343 **Fig. 5.** Simulated dispersal of 100 individuals from a release point at the origin (0, 0) at 20 days, 70 days
344 and 120 days after the adult emergence. Each black dot represents an insect and the grey lines
345 represent their trajectory.

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

351

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354

355 **4. Discussion**

356

357 **4.1. Dispersal modelling: a new approach to conciliate dispersal distance from flight mill** 358 **experiments and mark-release-recapture experiments**

359 Many studies focus on one method to assess the potential dispersal of insect species such as flight mill
360 experiments (e.g., Jactel & Gaillard 1991, Schumacher et al. 1997, Briegel et al. 2001, Ishiguri & Shirai
361 2004, Bradley & Altizer 2005, Robinet et al. 2012, Maes et al. 2014) and mark-release-recapture
362 experiments (e.g., Turchin & Thoeny 1993, Marini et al. 2010, Margaritopoulos et al. 2012). The
363 number of species for which the dispersal capabilities have been recorded with different methods is
364 relatively low and these measures generally differed (e.g., from tens of kilometers *versus* hundreds of
365 meters for *M. galloprovincialis*). However, it is not possible to compare directly these distances since
366 they represent different measures of the dispersal distance. Data from flight mill experiments may
367 provide overestimated flight performance but they allowed determining the dispersal kernel, i.e. the
368 shape of distances distribution and the proportion of individuals able to fly long distances (e.g., those
369 mainly contributing to the population range expansion). Data from mark-release-recapture
370 experiments provided an interception distance. Although they were based on individuals' dispersal in
371 the field, the traps potentially captured individuals that could be able to disperse further.

372 Until now, there was no study comparing dispersal measures based on the same source of
373 population. In this study, insects tested on the flight mill and in the mark-release-recapture
374 experiments all originated from a maritime pine dominated forest of south-western France. Therefore,
375 variability in dispersal distances may not be attributed to intra-specific variability. The dispersal model
376 that we developed reveals that the distances recorded in the two types of experiment were actually in
377 good agreement. The estimate of the daily mean dispersal distance ($\alpha = 2.0$ km) was consistent with
378 the flight distance data estimated on the flight mill once per week (1.93 km for females and 2.14 km

379 for males; David *et al.*, 2014) and with the distance flown between the release point and the most
380 distant trap (1.8-1.9 km).

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

390

391 **4.2. Reconsideration of control measures for the pine wood nematode**

392 It has been suggested to use mass trapping for the control of *M. galloprovincialis* (Sanchez-Husillos et
393 al. 2015) to reduce the transmission and the spread of PWN. We are aware of five previous mark-
394 release-recapture experiments with the pine sawyer beetle in the Iberian Peninsula (Gallego et al.
395 2012, Hernandez et al. 2011, Mas et al. 2013, Torres-Villa et al. 2015, Etxebeste et al. 2016). Although
396 the landscape context, the number of traps and the distance between traps differed and the
397 populations do not belong to the same genetic clade (Haran et al. 2018), these experiments were all
398 conducted in similar conditions (similar traps and lures) as our MRR study. Interestingly they provide
399 consistent estimate of recapture rates. Using immature beetles, Etxebeste et al. (2016) obtained a
400 mean recapture rate per trap of 1.25% (in 2010) and 0.52% (in 2011) which is very close to the 1.23%
401 immature beetles recaptured per trap within clusters in our experiment. Likewise, using mature
402 beetles (first trapped then marked and released), Gallego et al. (2012) obtained a rate of recapture per
403 trap of 0.66%, Hernandez et al. (2011) 0.62%-0.67%, Mas et al. (2013) 0.83%-1.83%, Torres-Villa et al.

404 (2015) 0.67%, which is very similar to the 0.69% mature beetles recaptured per trap within clusters in
405 our experiment. Due to these very low levels of trap efficiency, one would need a very high density of
406 traps per hectare for capturing enough beetles to impede the reproduction success and thus durably
407 reduce the population density of the insect vector. Even more problematic, it took on average 18 days
408 to recapture the released immature beetles, while Etxebeste et al. (2016) indicated that recaptures
409 occurred 7–14 days after their release. This means that they would have had ample time to transmit
410 most of their nematode load while feeding on shoot for sex maturation. When considering the high
411 density of traps needed, that should be deployed on very large areas (e.g. the pine forest at high risk
412 of invasion in southwestern France covers ca. 1 million hectares) with the incapacity of trapping
413 immature beetles that transmit PWN, it clearly appears that mass trapping should not be
414 recommended as control measure.

415 According to the simulated dispersal of *M. galloprovincialis*, a substantial proportion of daily
416 flights (>20% for mature beetles and >5% for immature beetles) could reach at least 500 m, which is
417 the radius of the clear-cut imposed by the European regulation. In addition, most of insects (about
418 80%) have already gone further than 500 m a few days after their emergence (Table 3). So far, there is
419 no evidence that the flight performance of *M. galloprovincialis* carrying the pine wood nematode is
420 different from those free from the nematode (flight distance of 15 infested insect tested on flight mill
421 was not significantly different from those not infested but further studies are needed; David 2014).
422 Based on these results and the continuous spread of the pine wood nematode in the Iberian Peninsula
423 despite the European regulation (Rodrigues et al. 2015), it is legitimate to question the effectiveness
424 of the clear-cut measure. However further research is needed to better assess this effectiveness,
425 accounting for the transmission of the pine wood nematode along the adult life span of *M.*
426 *galloprovincialis*. Here again a dispersal model would be relevant to simulate the effects of clear-cuts
427 on PWN dissemination and transmission.

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

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

450

451 **Acknowledgments**

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

456 **Funding**

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

461 **SUPPORTING INFORMATION**

462 **SM1: Comparison of the exponential and Gaussian kernels**

463 MS-MG-Dispersal-SM1.docx

464 **SM2. Results of the mark-release-recapture experiments**

465 MS-MG-Dispersal-SM2.xlsx

466 **SM3. Results of the Multi-Criteria Decision Analysis**

467 MS-MG-Dispersal-SM3.xlsx

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605 **TABLES**

606

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

Parameter	Definition	Values	FM	MRR	SIM
α	Mean daily dispersal distance (in meters)	500 – 2500	X	X	X
<i>r</i>	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
<i>n</i>	Number of beetles released	100		X	X
<i>l</i>	Adult longevity (in days since adult emergence)	120 days	X	X	X
<i>m</i>	Maturation age (in days since adult emergence)	20 days	X	X	X
ρ_{fm}	Daily probability of flying for mature beetles	0.61	X	X	X
ρ_{fi}	Daily probability of flying for immature beetles	0.45	X	X	X

612

613

614 **Table 2.** Relative bias (*RB*) and root mean square error (*RMSE*) of the model simulating the Mark-
 615 Release-Recapture experiment for the parameters corresponding to the best fit model ($\alpha = 2000$ m,
 616 $\lambda = 0.01$, $\delta = 12$ days, $\beta = 1$ day for immature beetles and $\alpha = 2000$ m, $\lambda = 0.01$, $\delta = 8$ days, $\beta = 1$
 617 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	<i>RB</i> = 0.778 <i>RMSE</i> = 0.406	<i>RB</i> = 0.665 <i>RMSE</i> = 0.028
	Inter-cluster	<i>RB</i> = 2.353 <i>RMSE</i> = 0.167	<i>RB</i> = 0.945 <i>RMSE</i> = 0.360
Time of recapture	Intra-cluster	<i>RB</i> = 0.296 <i>RMSE</i> = 0.054	<i>RB</i> = 0.378 <i>RMSE</i> = 0.065
	Inter-cluster	<i>RB</i> = 0.643 <i>RMSE</i> = 0.246	<i>RB</i> = 0.667 <i>RMSE</i> = 0.047

618

619

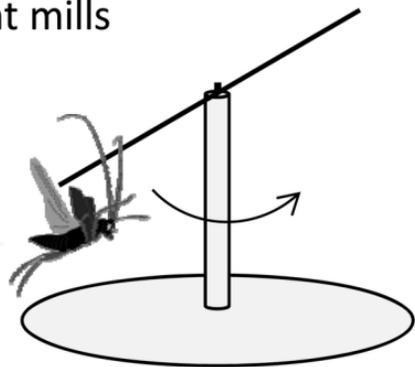
620

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

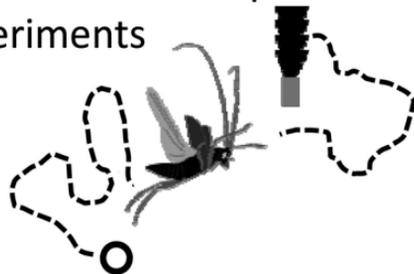
Time after adult emergence	Dispersal distance (m)			Percentage (%) of individuals dispersed at			
	Mean	SE	Median	≥ 500 m	≥ 5 000 m	≥ 10 000 m	≥ 20 000 m
Day 20	2 507	2 384	1 790	78	15	1	0
Day 70	8 898	5 552	7 806	100	78	33	5
Day 120	13 219	7 313	11 395	99	92	56	23

623

Flight mills



Mark-release-recapture experiments



Calibrating the shape

Fine-tuning the parameters

Individual-based dispersal model

