

# 1 **Modelling *Monochamus galloprovincialis* dispersal trajectories across a** 2 **heterogeneous landscape to optimize monitoring by trapping networks**

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## 12 13 **Abstract**

### 14 **Context**

15 The pine wood nematode (PWN), is an invasive species which was introduced into Europe in  
16 1999. It represents a major economic and ecological threat to European forests. In Europe, the  
17 maritime pine is the main host and *Monochamus galloprovincialis* is its only vector.

### 18 19 **Objectives**

20 Our goal was to analyze the effect of landscape heterogeneity on the vector's dispersal. We  
21 further aimed at developing a new method to locate the origin of insects captured in a systematic  
22 network of pheromone traps.

### 23 24 **Methods**

25 A mark-release-recapture experiment was carried out in a heterogeneous landscape combining  
26 maritime pine plantations, clear-cuts and isolated patches of broadleaved and mixed forests in  
27 the southwest of France.

28 Least-cost path analysis was used to model dispersal trajectories and assign friction values to  
29 each land-use type in the landscape. We used the trap's geographical coordinates, capture levels  
30 and mean friction values of neighbouring patches to calculate a weighed barycentre and the  
31 position of the release of marked beetles.

33 **Results**

34 Least Cost Path modelling revealed the vector's tendency to avoid habitat patches such as  
35 mixed or deciduous forests and not avoid clear-cuts. The weighted barycentre method was  
36 greatly improved when the friction values of the trap's surrounding land-uses were used.

37

38 **Conclusions**

39 Our study demonstrates the value of applying landscape ecology concepts and methods  
40 to improve our understanding and prediction of pest invasion processes. A practical  
41 application is the design of systematic grids of pheromone traps to locate the infection  
42 focus from which PWN vectors originate in a newly colonized area.

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46 **Keywords**

47 Pine wood nematode, landscape heterogeneity, least cost pathway, barycentre, flight

48

## 49 Introduction

50

51 In the last decades, the number of non-native pest species that have become established outside  
52 their native range has dramatically increased worldwide (Seebens et al. 2017; Walther et al. 2009).  
53 A small portion of these species can become invasive, some with high ecological and economic  
54 costs in the agricultural and forestry sectors (Pimentel et al. 2005; Kenis et al. 2009). The pine  
55 wood nematode (PWN) *Bursaphelenchus xylophilus* (Steiner & Buhrer) is a well-known example  
56 of an invasive species with great ecological and economic impacts (Evans et al. 1996). This  
57 nematode is indigenous to North America, where it causes no noticeable damage to American  
58 pines. On the contrary, the nematode greatly affects non-American pine species (Zhao, 2008),  
59 causing pine wilt disease, which leads to tree death within a few weeks or months. The PWN was  
60 first detected in Japan in 1969 (Tokushige & Kiyohara, 1971), then in China, Taiwan, and South  
61 Korea in the eighties (Yi et al. 1989; Liou et al. 1999; Yi et al. 1989). In Europe, the PWN was  
62 detected in 1999 in Portugal mainland (Burgermeister et al. 1999). A few years later, it was  
63 detected in Madeira islands (Portugal) and Spain (EPPO, 2009; Abelleira, 2011; Fonseca et al.  
64 2012).

65 The pine wood nematode cannot colonize host trees on its own. It needs an insect vector to  
66 transport it from one tree to another and then allow it to be inoculated. In all regions where the  
67 PWN has been introduced, the insect vectors are longhorn beetles of the genus *Monochamus*  
68 (Linit, 1988; Evans et al. 1996). In Europe, only *Monochamus galloprovincialis* (Olivier) has  
69 been reported to be a vector of the PWN (Naves et al. 2001). Young adult beetles feed on pine  
70 shoots of healthy trees for sexual maturation. During this phase, the beetles produce bark wounds,  
71 which are used by the nematodes to penetrate the vascular tissues of the tree (Linit, 1990; Naves  
72 et al. 2007(a)). Gravid beetle females lay eggs in the bark of decaying trees, where they can also  
73 transmit nematodes (Naves et al. 2007(b)). The PWN thus spreads through the dispersal of its  
74 insect vector. On a local scale, dispersal by flight of *M. galloprovincialis* can extend on average  
75 around 16 kilometers during the insect's lifetime (David et al. 2014, Robinet et al. 2019).  
76 However, the spread can be greatly increased by human activities, especially through the transport  
77 of wood containing both the vectors and the nematodes (Robinet et al. 2009). So far, the  
78 eradication of the PWN has been mainly done by the removal of contaminated trees. However, it  
79 was recently demonstrated that clear-cutting susceptible trees 500 m around an infested tree, as  
80 requested by EU regulation to eradicate the PWN, is not effective, mainly due to the high dispersal  
81 capacity of the insect vector (Robinet et al. 2020).

82 It is therefore of paramount importance to better understand the behavior and dispersal capabilities  
83 of the insect vector in order to predict the location of new foci of PWN infestation, or to slow  
84 down its spread if eradication of new foci fails. During their dispersal phase, insects generally

85 react to landscape elements. Some types of land use can enhance dispersal, while others slow it  
86 down or even hinder it. According to the concept of functional landscape connectivity  
87 (Tischendorf & Fahrig, 2000), land use types have different friction values which result in  
88 different levels of dispersal inhibition (Zeller et al. 2012). This concept has been mainly applied  
89 for organisms of conservation interest and much less for pest insects (Bunn et al. 2000; Ferreras,  
90 2001; Wang et al. 2009). In general, it is assumed that land-use types corresponding to the species  
91 habitat facilitate dispersal, but several studies indicate the opposite (Crone et al. 2019, Lutscher  
92 et al. 2017), because individuals might prefer to stay in favorable habitat patches while moving  
93 faster through unfavorable ones. It is therefore likely that landscape heterogeneity can have a  
94 significant role in slowing down (Rigot et al. 2004) or accelerating the dispersal of insect species.  
95 Different methods exist to study insect dispersal in the field such as observation of flying insects,  
96 telemetry, mark-release-recapture (MRR) experiments, colonization patterns or genetic studies  
97 (Ranius, 2006). Telemetry has been tested recently for *Monochamus alternatus*, but it was found  
98 to be unable to track over long distances (Zhang et al. 2020). MRR with baited traps was found  
99 to be relevant for *M. galloprovincialis* although within a short spatial range (Álvarez et al. 2015;  
100 Sanchez-Husillos et al, 2015, Jactel et al. 2019). In addition, MRR data alone do not permit a  
101 functional interpretation of flight behavior through different landscape elements since it only  
102 provides information on the release and recapture points. To determine the effect of landscape  
103 composition and configuration on dispersal behavior, MRR data should be combined with  
104 modelling tools, such as Least Cost Path analyses (LCP). These tools allow testing the effect of  
105 different land-use friction values on recapture rates (Adriaensen et al. 2003).

106 A major step forward in controlling the spread of PWN would be the early detection of insect  
107 vectors carrying the nematode, which can be achieved using pheromone traps (Álvarez et al.  
108 2016), and then the location of the infestation site from which they originated. This could involve  
109 the implementation of trapping networks, allowing the triangulation of an area of probable origin  
110 of insects trapped in the surrounding landscape (e.g. fixed grid triangulation, Pierce 1994,  
111 Arbogast et al. 1998). Even though the use of monitoring traps for the early detection of the PWN  
112 is currently mandatory to all EU members (Commission Implementing Decision 2012/535/EU of  
113 26 September 2012), so far there were very few scientific contributions towards the optimization  
114 of monitoring trapping networks, especially regarding trap density (Torres-Vila et al. 2015).

115 In this study, we organized a mark-release-recapture experiment of *M. galloprovincialis* beetles,  
116 using a systematic grid of pheromone traps deployed in a heterogeneous forest landscape.  
117 Recapture data were used to fit an LCP model to assess the friction value of different types of  
118 land use, with respect to flight dispersal of the insect vector. We estimated correlations between  
119 insect recapture rates and i) the distance of a direct flight trajectory from the release point to the  
120 trap position or ii) the distance of a longer flight trajectory but minimizing dispersal costs. Our

121 hypothesis was that the insects would avoid flying through non-habitat patches represented by  
122 e.g. broadleaved or mixed-species woodlands.

123 We then used the evaluated friction value for each land use type to calculate an average friction  
124 value in a buffer around each trap. We calculated the coordinates of the barycenter of the trap's  
125 positions in the grid, weighted by the recapture levels and the average value of friction around the  
126 traps. Our hypothesis was that by proceeding in this way we could approach the coordinates of  
127 the point of insect release and thus propose a method of predicting the location of the original  
128 focus of the captured insects.

129 This study therefore represents an original application of landscape ecology concepts to better  
130 study and predict the risk of spread of an invasive alien species in realistic forest landscapes.

131

## 132 **2. Material and Methods**

### 133 Study area

134 The study was carried out in the south-west of France in the 'Landes de Gascogne' forest. This  
135 region of one million ha is dominated by even-aged plantations of the native maritime pine *Pinus*  
136 *pinaster* Ait, which is the main host tree of the pine wood nematode in Europe (Naves et al. 2016).  
137 Broadleaved woodlands are rare and found along rivers or as scattered patches of a few hectares.  
138 They are generally dominated by oak species (*Quercus robur* or *Quercus pyrenaica*). Open areas  
139 in the landscape are mainly represented by pine clear-cuts, maize fields, firebreaks and  
140 powerlines. The local climate is temperate oceanic Sub-Mediterranean with mean annual  
141 temperature of 14°C and a mean total annual precipitation of 944 mm.

### 142 Site selection and landscape mapping

143 Within the Landes de Gascogne forest we selected a study site of 183 ha in the municipality of  
144 Saint Jean d'Illac, with a heterogeneous landscape composed of different land-uses (different ages  
145 of pine stands, clear-cuts, mixed forests and broadleaved forests (coordinates of the centre  
146 44°48'16.721"N, 0°51'2.329"W).

147 Land-use types of the study site were mapped in ArcGIS using aerial photos of 2018 (i.e. the year  
148 of the study) with a pixel size of 50 cm as background layer. We distinguished 13 land-use types  
149 that could be recognized on these photos and that could be of ecological relevance for the dispersal  
150 behaviour of *Monochamus* beetles (see Appendix 1 for land-use description and Fig.1).  
151 Landscape mapping was checked in the field for the patches visible from forest roads.

### 152 Beetle's origin and releases

153 We released marked *M. galloprovincialis* adults reared from infested logs (i.e. adult immatures)  
154 or collected in traps in pine stands (i.e. adult matures).

155 Maritime pine logs or branches infested with *M. galloprovincialis* larvae were collected in spring  
156 2018 and stored outside in tents. From Mid-May on, tents were inspected daily to collect newly

157 emerged adult beetles. They were kept in the laboratory in plastic boxes separated by sex and fed  
158 until release with fresh maritime pine shoots. The released beetles had an age of one to seven days  
159 and are hereafter called “immatures”. They were marked with POSCA® paint on the elytra using  
160 a different code for each release date and a mark on the thorax coding for ‘immature beetle’.  
161 Previous release studies (Robinet et al. 2019) showed that marks did not affect beetle flight  
162 performances.

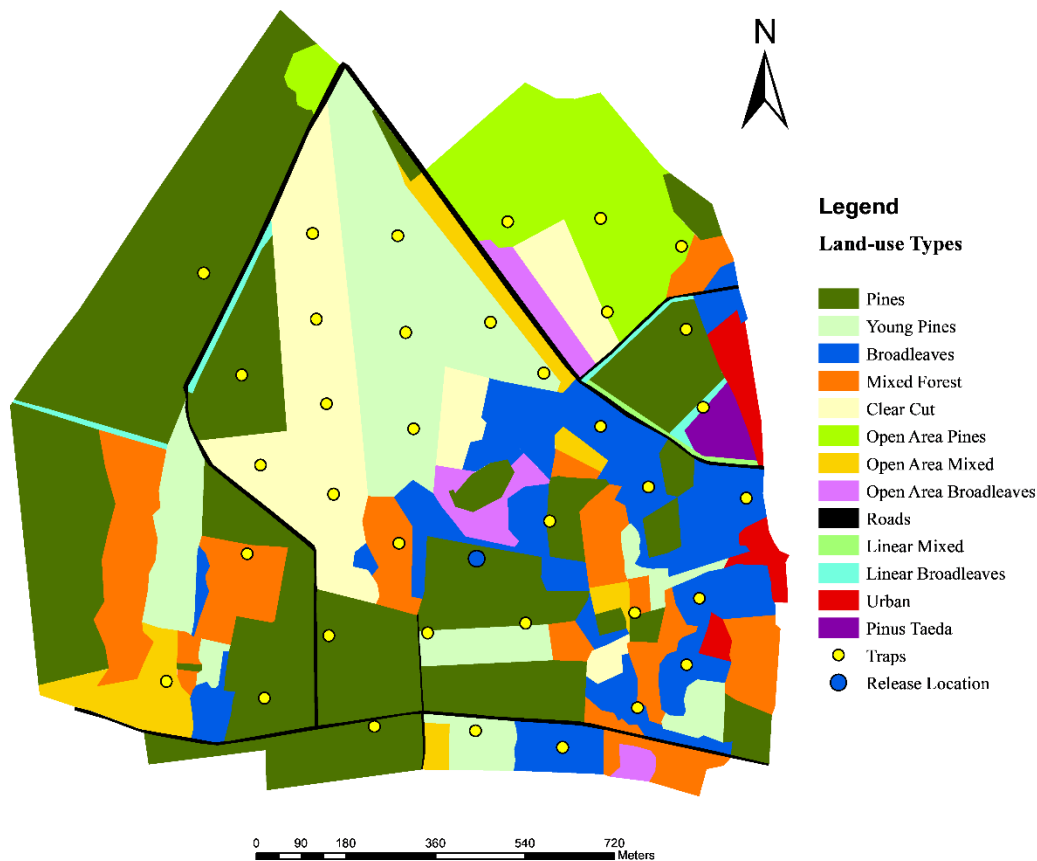
163 We also collected beetles with baited traps in maritime pine stands outside the study area. The  
164 age of these beetles was unknown, but they were at least 15 days old since they reacted to the  
165 pheromone and were thus sexually mature (Jactel et al. 2019). They were also marked with a  
166 painted code for each release date and a code for ‘mature beetle’.

167 All marked beetles were released at a fixed point in a mature maritime pine stand in the centre of  
168 the study landscape. In total 3162 beetles were released (2747 immature and 415 mature).

169

#### 170 Recaptures

171 We placed 36 traps (Cross Vane® type) in a regular grid pattern within the study landscape, with  
172 a mean distance of 170 m between traps in a total area of about 1 Km<sup>2</sup>. Because of field conditions  
173 the distance between traps varied somewhat (between 130 and 220 m). The 36 cross traps were  
174 baited with Galloprotect 2D®, a commercial product that includes the aggregation pheromone  
175 (2-undecyloxy-1-ethanol) and kairomonal substances (2-undecyloxy-1-ethanol, ipsenol and 2-  
176 methyl-3-buten-1-ol) (Jactel et al. 2019), the lures were replaced once in the summer. The  
177 collecting vial contained an insecticide. Traps were checked twice a week, between 13 June and  
178 8 August 2018.



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183 Fig 1 – Map of the study landscape and its classification in 13 different land-use classes (see SM1  
184 for detailed definition), the 36 trap positions for recapturing the beetles, *Monochamus*  
185 *galloprovincialis*, and the release point of the beetles.

186

### 187 Creating the Least Cost Distance Model

188 We calculated Least Cost Pathways from the release point to all 36 traps in ArcMap using the  
189 “cost path polyline function”. This procedure provides for each trap (i) a value representing the  
190 minimum total cost to reach it (i.e. Path Cost i, PathCi). The cost depends on the distance and the  
191 friction value of each land-use type between the release point and the trap (Adriaensen et al.  
192 2003). The algorithm calculates the path through the landscape with the lowest total cost. To find  
193 the friction value (Fi) of each land use type, we went through a model optimization process. We  
194 assumed that the number of catches in each trap (beetles’ recapture value of trap i, BRi) would  
195 depend on the least cost pathway between the release point and this trap. Multiple scenarios with  
196 different friction values for the different land use types were used to calculate the corresponding  
197 PathCi. For each scenario, we calculated the correlation between PathCi and log transformed

198 values of BR<sub>i</sub>. We iteratively modified the friction value of the different land-uses until reaching  
199 the maximum value of the coefficient of determination R<sup>2</sup>.

200 First we tested scenarios for which each land use type was tested separately for low, medium and  
201 high friction values (“1”, “4”, “8”) respectively (within a scale of 1 to 9), while keeping the other  
202 land-uses at value 1. We also tested friction values higher than 9, but they did not change the  
203 resulting paths. Second, according to the results (i.e. R<sup>2</sup> value), land-use types were grouped into  
204 three categories of friction values (1 - Low, 4 - Medium, 8 - High). Third, within each of the three  
205 categories, we incrementally changed the friction values (e.g. ±1), keeping the values constant in  
206 the other two categories, until we reached the maximum value of R<sup>2</sup>. Last, we repeated the  
207 procedure for the other two categories. The complete optimization process is described in detail  
208 in the supplementary material ([Appendix 2](#)).

209

#### 210 Re-finding the position of the release point using the recapture levels in the grid of traps

211 We investigated whether we could re-find the position of the release point of marked beetles using  
212 the location of the traps and their level of recapture. The objective of this computation was to  
213 simulate a situation where a grid of traps was set up to detect the position of a focus of infested  
214 trees (from which beetles originate) in the landscape. To estimate the coordinates of the release  
215 point (simulating beetles’ emergence from the infestation focus), we used the method of weighted  
216 barycentre that is commonly applied to find the centroid of a system of several points in a given  
217 two-dimensions space, taking into account the weight (or size) of the points. Here we used the  
218 trap recaptures as weight. The general formula is (eqn1):

$$219 \quad X_B = \frac{\sum_{i=1}^n x_i \cdot w_i}{\sum_{i=1}^n w_i}$$

$$220 \quad Y_B = \frac{\sum_{i=1}^n y_i \cdot w_i}{\sum_{i=1}^n w_i}$$

221

222 With X<sub>B</sub> and Y<sub>B</sub> being the coordinates of the weighted barycentre, x<sub>i</sub> and y<sub>i</sub> the coordinates of the  
223 points (here of the traps) and w<sub>i</sub> the weight of the points, here the recapture of marked beetles in  
224 the traps (BR<sub>i</sub>). This method based on Euclidian distances between traps is further called the  
225 EUC-method.

226 In a second step, we tested whether we could improve the estimation of the coordinates of the  
227 release point (barycentre of the traps) by taking into account the difficulty of the beetles to reach  
228 the traps, according to the friction value of the surrounding land-uses. For that, we used our best  
229 estimates of friction values per land-use type to calculate the mean friction value in a buffer radius  
230 around each trap (F<sub>i</sub>). For this, we tested the results between different buffer radius values of 50,  
231 100, 150 and 200 meters and compared the accuracy of resulting estimations. The results were  
232 compared with an ANOVA type 1 analysis.



233 We thus adapted the calculation of the coordinates of the barycentre using the following formula  
234 (eqn2):

$$235 X_B = \frac{\sum_{i=1}^n x_i \cdot BR_i \cdot F_i}{\sum_{i=1}^n BR_i \cdot F_i}$$

$$236 Y_B = \frac{\sum_{i=1}^n y_i \cdot BR_i \cdot F_i}{\sum_{i=1}^n BR_i \cdot F_i}$$

237

238 With  $F_i$  being the mean value of friction values in a buffer around each trap ( $i$ ). This method based  
239 on Euclidian distances between traps and the results of Least Cost Pathway analysis for  
240 surrounding trap friction was further called the LCP method.

241 The accuracy of the barycentre estimation methods was calculated as the distance (Dist), in  
242 meters, from the estimated barycentre to the real release point. The precision of each method was  
243 calculated as the 95% confidence interval of the Dist values, also calculated for all possible trap  
244 subsets of  $n-1=35$  traps (Jackknife resampling technique).

245

246 Effect of reducing the number of traps on the accuracy of estimating the location of the release  
247 point

248 We studied the effect of reducing the number of traps on the accuracy of barycentre estimation.  
249 Following the same approach of a systematic trapping grid, we calculated the barycentre  
250 estimations for subsets of 5x5, 4x4, and 3x3 traps. In addition, we took the precaution of evenly  
251 distributing the traps across the landscape. For that, we divided the study landscape in 25, 16 or  
252 9 quadrants, and we re-sampled one trap per quadrant. All possible combinations of one trap per  
253 quadrant were considered, resulting in 2049, 93312 and 230400 combinations respectively for the  
254 25, 16 and 9 trap grids. For each trap combination, we calculated the barycentre coordinates, using  
255 the EUC and the LCP methods. The mean distance between the estimated barycentre coordinates  
256 and the release point (Dist) was then calculated for each density of traps in the systematic grid as  
257 a measure of accuracy and the precision of each method was calculated as the 95% confidence  
258 interval of the Dist values. These and the previous calculations were all done with Microsoft  
259 Excel, using the “list all combinations” function from the Kutools add-on.

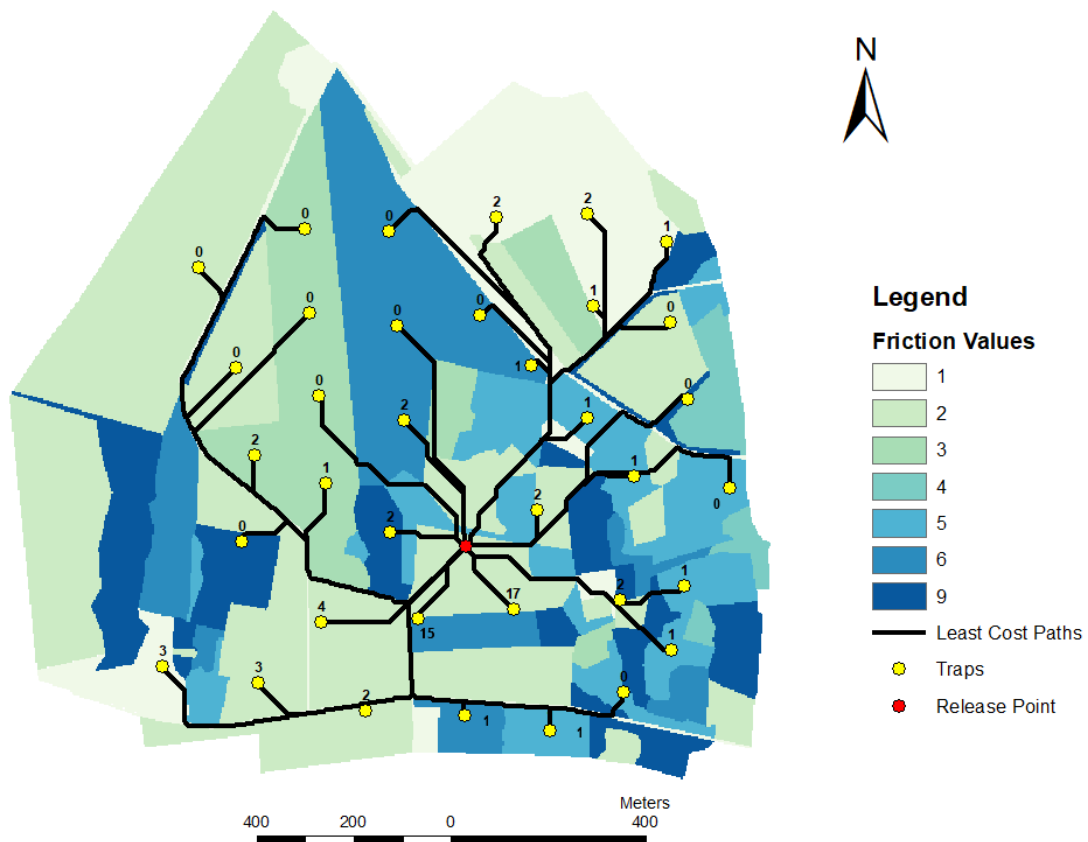
260

### 261 **3. Results**

#### 262 Recaptures and Least Cost Path model

263 In the 36 traps, 68 marked beetles were recaptured (i.e. 2.2 % of total number of released beetles),  
264 53 immature and 15 mature beetles. The recaptures were unevenly distributed across the study  
265 area with 13 traps with no beetles recaptured and two traps with 17 and 15 recaptured beetles  
266 (47%).

267 The optimization process for determining land-use friction values based on the highest  $R^2$  between  
 268 the least cost path costs (PathCi) of the traps and their recapture values (BRi) resulted in the  
 269 selection of the best scenario (P19), with a  $R^2$  of 0.63, P-value < 0.0001 (SM2). The  $R^2$  using the  
 270 Euclidean distance method was much lower (0.27). The corresponding friction values for each  
 271 land use type are shown in Fig. 3. Open areas and mature pine stands had the lowest friction  
 272 values (1-2), clear-cuts of pine stands, young pine plantations, broadleaves, urban and *Pinus taeda*  
 273 had intermediate frictions values (3-5) while linear woodlands with broadleaves and mixed pine  
 274 and broadleaved forest had the highest values (9). These friction values were used for the rest of  
 275 LCP analyses.



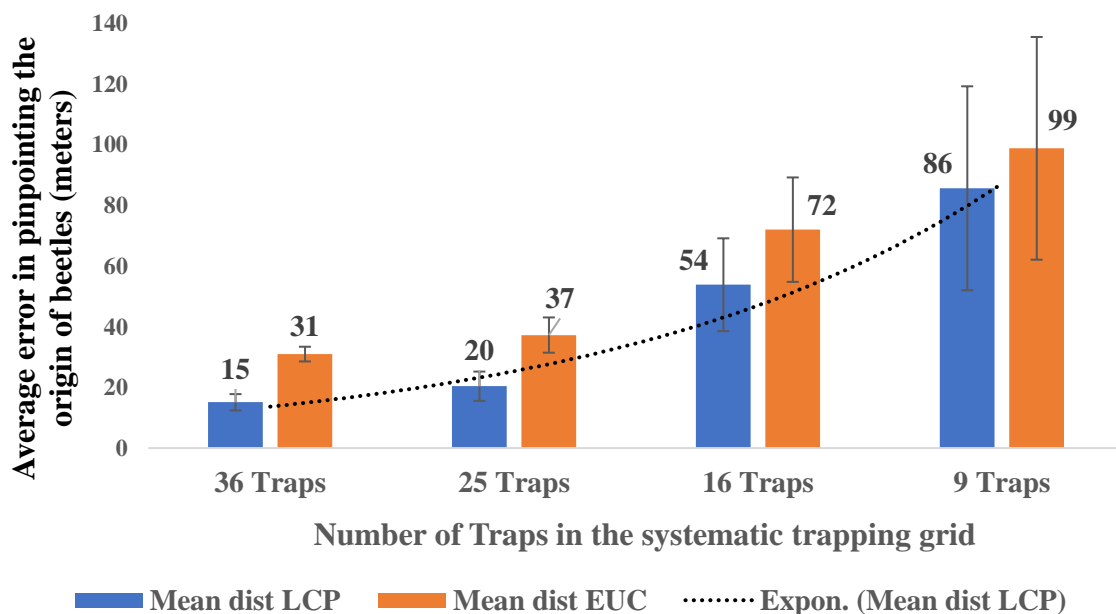
276  
 277  
 278 Fig. 2 - The least cost paths between the release point and each of the 36 traps calculated with the  
 279 least cost pathway model using the set of land-use type friction values from scenario P19. Friction  
 280 values of each land-use type: 1 – Open Area Mixed, Open Area Pines and Roads; 2 – Pines and  
 281 Open Area Broadleaves; 3 – Clear Cut; 4 – Urban and *Pinus taeda* 5 – Broadleaves; 6 – Young  
 282 Pines; 9 – Linear Broadleaves, Linear Mixed and Mixed Forest. The number of captured beetles  
 283 is indicated per trap.

284

285 Re-finding the position of the release point using the recapture levels in the grid of traps

286 We verified that the buffer radius values had no significant effect on the accuracy of barycenter  
 287 estimates (Dist) with the LCP method (P-value > 0.995, Appendix 3). Thereafter, the LCP results  
 288 used will be those based on a buffer radius of 100 m. This allowed including a larger number of  
 289 surrounding land-uses, without overlapping between surrounding buffers of two adjacent traps.  
 290 Using only the coordinates and recapture data of the 36 traps to calculate weighted barycenter's,  
 291 the accuracy was Dist = 31.0 m (Euclidean distance estimation method). The accuracy was  
 292 improved with a reduction of Dist to 15.1 m when the friction values of the surrounding landscape  
 293 (within a buffer of 100 m) were considered, (the Least Cost Path estimation method) (Fig 3).  
 294 Using the jackknife resampling method for the 36 traps trial, both estimation methods offered  
 295 similar precision, with 95% confidence intervals of 2.7 and 2.4 meters respectively for the LCP  
 296 and EUC method (Fig 3).  
 297 For both estimation methods, the accuracy (Dist) sharply decreased as the number of traps  
 298 decreased (Fig. 3). LCP method always provided higher accuracy over EUC method. Yet, the  
 299 gain in accuracy of the LCP method over the EUC method decreased with the reduction of trap  
 300 number, from 51%, 30%, 25% to 13% for grids of 36, 25, 16 and 9 traps respectively (Fig. 3).  
 301 The two estimation methods had similar precision values (Fig. 3).

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306 Figure 3 – Average error in pinpointing the origin of beetles, i.e. distance between the real location  
 307 of the release point of marked beetles and the estimated location (mean and standard error of Dist)  
 308 using a weighted barycentre calculation with trap recapture data only (EUC method, orange bars)  
 309 or trap recapture data and friction values of surrounding landscape (using the 100m radius buffer)  
 310 around traps (LCP method, blue bars), for different trap densities.

311

312

## 313 **4. Discussion**

314

315 Combining a mark-release-recapture experiment in a heterogeneous landscape and least-cost  
316 pathways simulations, we were able to show that *Monochamus galloprovincialis*, the insect vector  
317 of the pine wood nematode, modifies its flight behavior in response to certain elements of the  
318 landscape and that this information can be used to improve the design of a trapping network to  
319 find the localization of infestation sites. The uneven distribution of the captured beetles in the  
320 trapping grid (Fig 2.) was in agreement with the heterogeneity of the landscape surrounding the  
321 site of release and the distance to the release point.

322

323

### 324 *Dispersal of the insect vector of the pine wood nematode across realistic landscapes*

325

326 More specifically, it emerged from our modelling analysis that some habitat types would offer a  
327 greater resistance to *M. galloprovincialis* movement than others. Open areas with scattered pine  
328 trees received the lowest friction value (=1), suggesting that beetles move fast through these types  
329 of land uses, perhaps due to reduced obstacles to flight.

330 Mature pines had a slightly higher friction value (=2). They represent the main habitat of the  
331 insect vector and are therefore not avoided by dispersing beetles. However, favorable habitats  
332 with abundant feeding resources may also slow down the insect dispersal due to feeding stops  
333 (Crone et al. 2019, Lutscher et al. 2017).

334 Interestingly clear-cuts of former pine plantations had a friction value (=3) only slightly higher  
335 than the one of mature pine stands, which indicates that they are not avoided by flying beetles.

336 This result is consistent with the findings of Bakke (1985) and Schroeder (2013) for the conifer  
337 bark beetle *Ips typographus*. Schroeder (2019) obtained similar trap captures of *M.*  
338 *galloprovincialis* in clear-cut areas and pine stands. Etxebeste et al. (2016) also reported longer  
339 flight distances of *M. galloprovincialis* in fragmented than in continuous pine landscapes. The *M.*  
340 *galloprovincialis* non-avoidance of clear-cuts by flight, has important implications for the  
341 eradication strategy of the pine wood nematodes as it confirms that EU recommendation for  
342 clearcutting 500m around infected trees would not prevent the insect vectors from dispersing  
343 (Robinet et al. 2020).

344 Young pine stands had a relatively high resistance value (=6) in our study. Their dense structure  
345 may impede insect dispersal and they do not provide reproduction resources.

346 All the land-use types containing high density of non-host tree species, principally broadleaved  
347 trees like oaks, had high friction values for the dispersal of *M. galloprovincialis*. The avoidance

348 of patches of non-habitat maybe explained by the lack of attractive chemical cues for the beetles,  
349 as they are attracted to pine terpenes, particularly during the maturation phase of young adults  
350 (Giffard et al. 2017). In addition, broadleaved trees might emit non-host volatiles that are  
351 commonly used by conifer-specialist insects to identify and avoid non-habitats (Jactel et al. 2011),  
352 according to the semiochemical diversity hypothesis (Zhang and Schlyter 2004).

353

354 However, our study had some limitations. Only one landscape was used to calculate LCP, which  
355 might reduce the generality of our results. Replicating the mark-release-recapture experiments in  
356 different landscapes of different configuration would obviously be of interest to better ascertain  
357 our estimates of friction values, although these experiments are very work intensive, especially  
358 because the recapture rates are always low for *M. galloprovincialis* (see Robinet et al. 2019 and  
359 2020, Etxebeste et al. 2016). Another approach would be sensitivity tests based on merging certain  
360 types of land use (similar in terms of vegetation cover) to verify their effects on the estimation of  
361 friction values. Additionally, behavioral experiments, with radio telemetry, would be necessary  
362 to fully disentangle the effect of friction caused by a non-suitable habitat and the retention effect  
363 caused by an attractive habitat. Finally, the activation of pheromone traps in different land-use  
364 types, coupled with an analysis of trap captures taking into account the amount of habitat and  
365 non-habitat patches in their surroundings (Martin-Garcia et al. 2011) could provide an indirect  
366 verification of friction values.

367

368 Nevertheless, our study clearly showed that landscape composition has an effect on *Monochamus*  
369 dispersal. The effect of landscape heterogeneity on dispersal will however depend on the presence  
370 of landscape elements promoting or impeding movement and the configuration of these elements  
371 in the landscape. In theory, landscape heterogeneity can stimulate or slow down the dispersal of  
372 invasive species, depending not only on the proportion and distribution of different habitat types  
373 in the landscape but also on the variability of dispersal parameters, including the existence of  
374 long-distance dispersal events (O'Reilly-Nugent et al, 2016). However, very few empirical studies  
375 exist to validate these hypotheses. For example, Rigot et al (2014) showed that the rate of spread  
376 of the invasive scale *Matsucoccus feytaudi* was slowed by the heterogeneity of the forest  
377 landscape using long-term monitoring of the invasion front. Another possible approach is the use  
378 of process-based dispersion models. For instance, integrating behavioral aspects such as the  
379 avoidance of non-habitat patches, would improve the realism of the individual-based model of  
380 the flight dispersal of *M. galloprovincialis* (Robinet et al. 2019), which could be then used to  
381 simulate flight trajectories in more or less heterogeneous landscapes.

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385

386 In the management of invasive species, early detection is a key element for successful eradication  
387 and containment. Soon after the arrival of a species into a new area, starts the establishment phase  
388 (Simberloff, 1997, Liebhold & Tobin, 2008) and it is well recognized that control actions need to  
389 be taken during this phase, while the invasive population has a limited distribution, in order to  
390 increase their cost-effectiveness (Simberloff, 1997). Therefore, there is a pressing need to improve  
391 the early detection of invasive species and the ability to predict the most likely locations where  
392 alien species are established in surveyed landscapes. For forest pests, this means to detect the  
393 individual trees or cluster of trees that are being colonized. This is particularly important for  
394 invasive forest pests because eradication methods often rely on the removal of host trees in  
395 demarcated areas. In the particular case of PWN, EU regulations require the felling of all  
396 susceptible trees within a buffer zone of 500 m around any infected tree but it was recently  
397 suggested to rather focus on the cutting of individual trees (Robinet et al. 2020).

398

399 To improve the capacity for early detection of the arrival of PWN in new forest areas we made  
400 two assumptions: 1) it will be useful to detect the nematode as carried by its insect vector, which  
401 can be trapped, in complement with the detection of the first infected trees, which are likely to be  
402 isolated in the landscape and difficult to spot; 2) the setting up of a systematic grid of traps will  
403 make it possible not only to capture the first *Monochamus* carrying the invasive nematode but  
404 also to locate the source of infestation from which they originate, thanks to a triangulation method.  
405 Using a mark-release recapture trial with a systematic grid of traps and a calculation of the  
406 Euclidean weighted barycenter using trap coordinates and catches, it was possible to pinpoint the  
407 origin of the beetles with good accuracy (31 meters). However, the method was significantly  
408 improved when the landscape composition around each trap was taken into consideration by  
409 assigning different levels of resistance (friction) to beetle dispersal to different land-use types.  
410 The location of the release point was then predicted with a remarkable accuracy of 13m.

411

412 Establishing high-density trap grids is not realistic given the cost of installation and assessments.  
413 By simulating a reduction in trap density in systematic grids, we showed that with only 9 traps  
414 spread over 180 ha, i.e. one trap per 20 ha, we could still predict the location of the original insect  
415 outbreak with an accuracy of 86 m, i.e. in an area of about 2.5 ha. We believe that restricting the  
416 search area for infected trees with PWN dieback symptoms to an area of 2.5 ha instead of 180 ha  
417 is a real progress in optimizing the early detection of infestation spots. However, further  
418 simulations in a larger array of landscape configurations, and taking into account installation and  
419 maintenance costs, still need to be carried out to optimize an operational detection method based  
420 on systematic trap networks (Augustin et al. 2004; Mercader et al. 2013; Elkinton et al. 2014;

421 Wilson et al. 2017; Sylla et al. 2017). This approach is likely to be particularly relevant for the  
422 surveillance of risk areas, including buffer zones established in the periphery of contaminated  
423 regions, such as those currently located on the border of Portugal and Spain.

424

## 425 Conclusions

426 Our study demonstrates the value of applying landscape ecology concepts and methods to  
427 improve our understanding and prediction of pest invasion processes. By using the least cost  
428 pathway method to analyze the results of a mark release-recapture experiment, we were able to  
429 demonstrate the importance of landscape composition and configuration for the dispersal of the  
430 PWN insect vector. The two main findings are that clear cuts of pine plantations did not disturb  
431 its flight path and that patches of non-habitat, composed mainly of broadleaved species, were  
432 avoided, imposing longer flight trajectories and probably reducing the spread of the disease. A  
433 practical application of these results is that we can now better design systematic trap networks  
434 and interpret their results, taking into account the composition of the surrounding landscape. We  
435 thus propose an innovative method to locate the most likely area of origin in the landscape of  
436 trapped insects that carry the nematode. This approach should now be applied in a wider range of  
437 landscape composition, with other types of land-uses and landscapes, with different degrees of  
438 compositional and configurational heterogeneity, in order to be able to generalize its application,  
439 especially in the main areas at risk of nematode establishment.

440

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