

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

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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.

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.

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

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

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

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

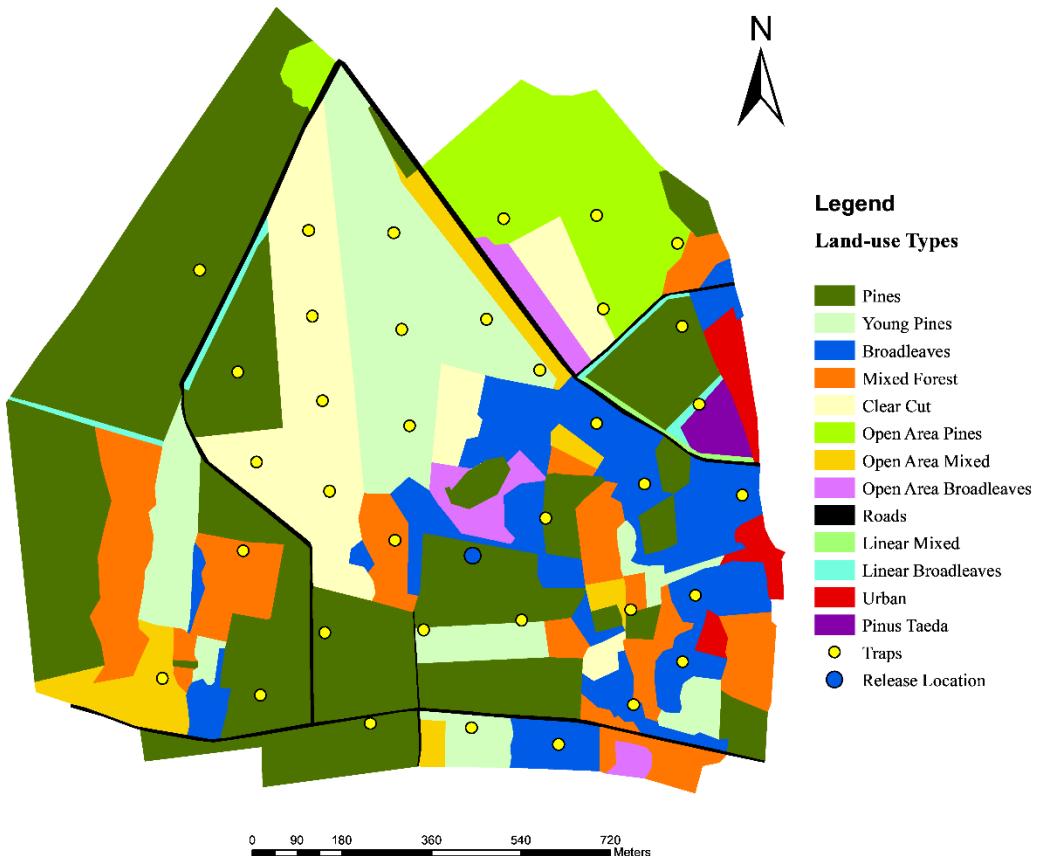
163 We also collected beetles with baited traps in maritime pine stands outside the study area. The
164 age of these beetles was unknown, but they were at least 15 days old since they reacted to the
165 pheromone and were thus sexually mature (Jactel et al. 2019). They were also marked with a
166 painted 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 Km². 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 BRi. We iteratively modified the friction value of the different land-uses until reaching
199 the maximum value of the coefficient of determination R².

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. R² 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 R². 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):

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

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

221

222 With X_B and Y_B being the coordinates of the weighted barycentre, x_i and y_i the coordinates of the
223 points (here of the traps) and w_i the weight of the points, here the recapture of marked beetles in
224 the traps (BRi). 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_i). 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.

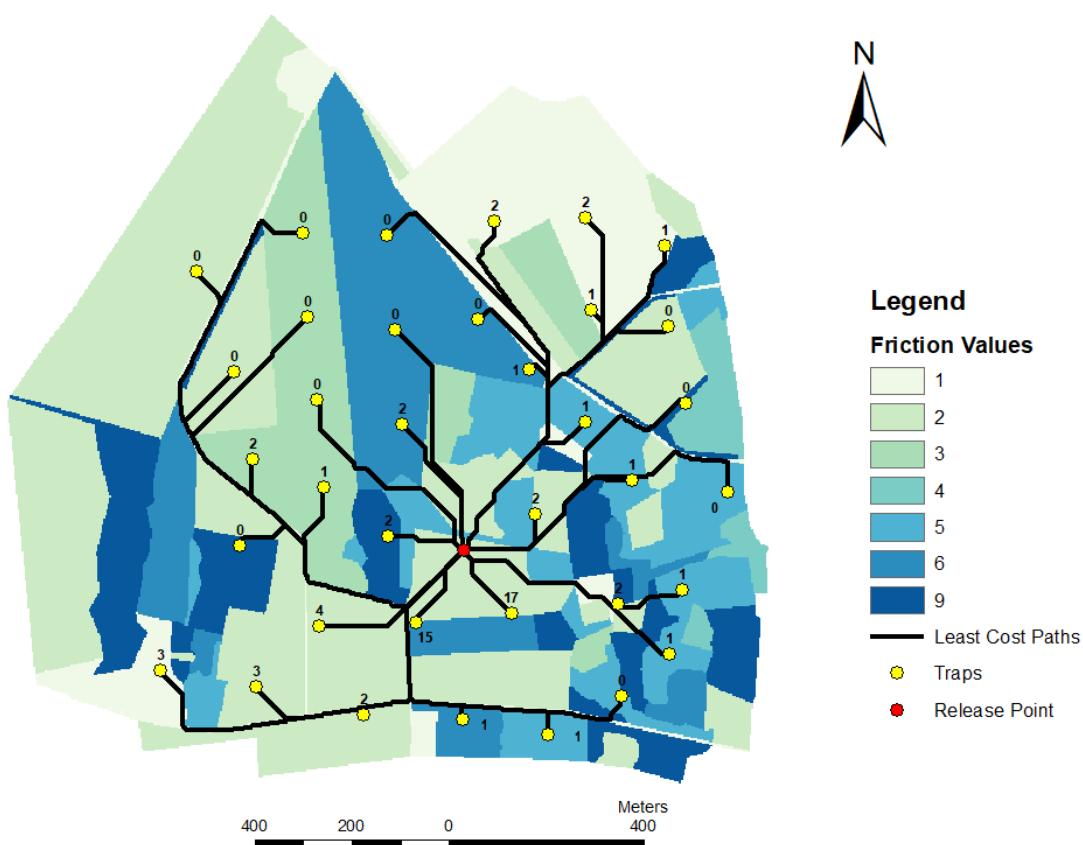
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261 **3. Results**

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.



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 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.

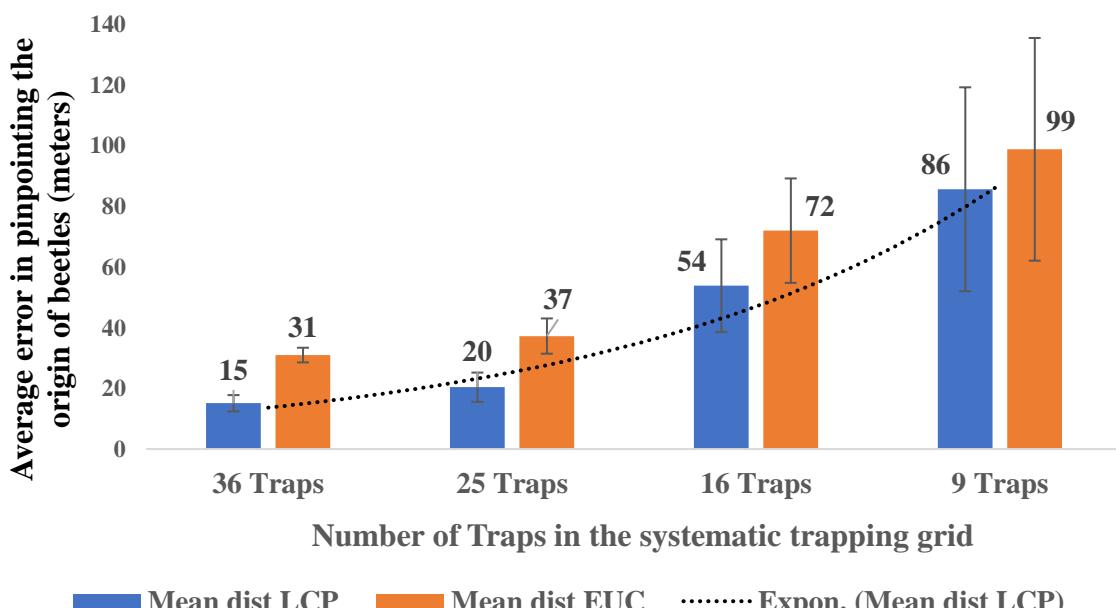
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285 Re-finding the position of the release point using the recapture levels in the grid of traps

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. Etxeberria 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, Etxebeeste 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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383

384 Systematic trapping networks for the monitoring of the insect vector of the pine wood nematode
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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

441 Acknowledgements

442 We would like to thank Victor Rebillard and Fabrice Vétillard very much for their help in
443 collecting, rearing, marking, releasing and recapturing the beetles.

444 We gratefully acknowledge support for this work from the project PINASTER (French Ministry
445 of Agriculture), the EU project REPHRAME KBBE.2010.1.4- 09 (FP7 Project), the EU project
446 HOMED (H2020, grant agreement no. 771271) and from the PESSOA project (TC-05/10).

447 P. Nunes was supported by SUSFOR (PD/00157/2012) doctoral grant funded by the Foundation
448 for Science and Technology (FCT) (PD/BD/142960/2018). Both P. Nunes and M. Branco are
449 supported by CEF, a research unit funded by Foundation for Science and Technology (FCT),
450 Portugal (UID/AGR/00239/2019 and UIDB/00239/2020).

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455 **References**

- 456
- 457 Abelleira A, Picoaga A, Mansilla JP, Aguin O (2011). Detection of *Bursaphelenchus xylophilus*,
458 causal agent of pine wilt disease on *Pinus pinaster* in Northwestern Spain. *Plant
disease*, 95(6), 776-776. <https://doi.org/10.1094/PDIS-12-10-0902>
- 459
- 460 Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulnick H, Matthysen E (2003).
461 The application of 'least-cost' modelling as a functional landscape model. *Landscape and
urban planning*, 64(4), 233-247. [https://doi.org/10.1016/S0169-2046\(02\)00242-6](https://doi.org/10.1016/S0169-2046(02)00242-6)
- 462
- 463 Álvarez G, Etxeberri I, Gallego D, David G, Bonifacio L, Jactel H, Sousa E, Pajares JA (2015).
464 Optimization of traps for live trapping of Pine Wood Nematode Vector *Monochamus
galloprovincialis*. *Journal of Applied Entomology*, 139(8), 618-626.
465 <https://doi.org/10.1111/jen.12186>
- 466
- 467 Álvarez G, Gallego D, Hall DR, Jactel H, Pajares JA (2016). Combining pheromone and
468 kairomones for effective trapping of the pine sawyer beetle *Monochamus
galloprovincialis*. *Journal of applied entomology*, 140(1-2), 58-71.
469 <https://doi.org/10.1111/jen.12297>
- 470
- 471 Arbogast RT, Weaver DK, Kendra PE, Brenner RJ (1998). Implications of spatial distribution
472 of insect populations in storage ecosystems. *Environmental Entomology*, 27(2), 202-216.
473 <https://doi.org/10.1093/ee/27.2.202>
- 474
- 475 Augustin S, Guichard S, Svatoš A, Gilbert M (2004). Monitoring the regional spread of the
476 invasive leafminer *Cameraria ohridella* (Lepidoptera: Gracillariidae) by damage assessment
477 and pheromone trapping. *Environmental Entomology*, 33(6), 1584-1592.
<https://doi.org/10.1603/0046-225X-33.6.1584>
- 478
- 479 Bakke A (1985). Deploying pheromone-baited traps for monitoring *Ips typographus* populations
1. *Zeitschrift für angewandte Entomologie*, 99(1-5), 33-39. <https://doi.org/10.1111/j.1439-0418.1985.tb01956.x>
- 480
- 481 Bunn AG, Urban DL, Keitt TH (2000). Landscape connectivity: a conservation application of
482 graph theory. *Journal of environmental management*, 59(4), 265-278.
483 <https://doi.org/10.1006/jema.2000.0373>
- 484
- 485 Burgermeister W, Braasch H, Sousa E, Penas AC, Mota M, Metge K, Bravo MA (1999). First
486 report of *Bursaphelenchus xylophilus* in Portugal and in Europe. *Nematology*, 1(7), 727-
734. <https://doi.org/10.1163/156854199508757>
- 487
- 488 Yi CK, Byun BH, Park JD, Yang SI, Chang KH (1989). First finding of the pine wood
489 nematode, *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle and its insect vector in
Korea. *Research Reports of the Forestry Research Institute* (Seoul), (38), 141-149.

- 490 Crone EE, Brown LM, Hodgson JA, Lutscher F, Schultz CB (2019). Faster movement in
491 nonhabitat matrix promotes range shifts in heterogeneous landscapes. *Ecology*, 100(7), 1–
492 10. <https://doi.org/10.1002/ecy.2701>
- 493 David G, Giffard B, Piou D, Jactel H (2014). Dispersal capacity of *Monochamus*
494 *galloprovincialis*, the European vector of the pine wood nematode, on flight mills. *Journal*
495 *of Applied Entomology*, 138(8), 566–576. <https://doi.org/10.1111/jen.12110>
- 496 Elkinton JS, Liebhold A, Boettner GH, Sremac M (2014). Invasion spread of *Operophtera*
497 *brumata* in northeastern United States and hybridization with *O. bruceata*. *Biological*
498 *invasions*, 16(11), 2263–2272. <https://doi.org/10.1007/s10530-014-0662-9>
- 499 EPPO (2009): Diagnostic protocols for regulated pests: *Bursaphelenchus xylophilus*. *Bulletin*
500 OEPP/EPPO, 31: 61 – 69
- 501 Etxebeste I, Sanchez-Husillos E, Álvarez G, Mas i Gisbert H, Pajares J (2016). Dispersal of
502 *Monochamus galloprovincialis* (Col.: Cerambycidae) as recorded by mark–release–
503 recapture using pheromone traps. *Journal of applied entomology*, 140(7), 485–499.
504 <https://doi.org/10.1111/jen.12278>
- 505 Evans HF, McNamara DG, Braasch H, Chadoeuf J, Magnusso C. (1996). Pest Risk Analysis
506 (PRA) for the territories of the European Union (as PRA area). *Bulletin OEPP/EPPO*, 26,
507 199–249. <https://doi.org/10.1111/j.1365-2338.1996.tb00594.x>
- 508 Ferreras P (2001). Landscape structure and asymmetrical inter-patch connectivity in a
509 metapopulation of the endangered Iberian lynx. *Biological Conservation*, 100(1), 125–136.
510 [https://doi.org/10.1016/S0006-3207\(00\)00213-5](https://doi.org/10.1016/S0006-3207(00)00213-5)
- 511 Fonseca L, Cardoso JMS, Lopes A, Pestana M, Abreu F, Nunes N, Mota M, Abrantes, I (2012).
512 The pinewood nematode, *Bursaphelenchus xylophilus*, in Madeira Island. *Helminthologia*,
513 49(2), 96–103. <https://doi.org/10.2478/s11687-012-0020-3>
- 514 Giffard B, David G, Joubard B, Piou D, Jactel H (2017). How do sex and sexual maturation
515 influence the response of *Monochamus galloprovincialis* to host odours?. *Journal of*
516 *applied entomology*, 141(7), 551–560. <https://doi.org/10.1111/jen.12374>
- 517 Jactel H, Birgersson G, Andersson S, Schlyter F (2011). Non-host volatiles mediate
518 associational resistance to the pine processionary moth. *Oecologia*, 166(3), 703–711.
519 <http://doi.org/10.1007/s00442-011-1918-z>
- 520 Jactel H, Bonifacio L, Van Halder I, Vétillard F, Robinet C, David G (2019). A novel, easy
521 method for estimating pheromone trap attraction range: application to the pine sawyer
522 beetle *Monochamus galloprovincialis*. *Agricultural and Forest Entomology*, 21(1), 8–14.
523 <https://doi.org/10.1111/afe.12298>
- 524 Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Péré C, Cock MJ, Settele J, Augustin
525 J, Lopez-Vaamonde C (2009). Ecological effects of invasive alien insects. *Biological*
526 *Invasions*, 11(1), 21–45. <https://doi.org/10.1007/s10530-008-9318-y>

- 527 Liebhold AM, Tobin PC (2008). Population ecology of insect invasions and their
528 management. *Annu. Rev. Entomol.*, 53, 387-408.
529 <http://doi.org/10.1146/annurev.ento.52.110405.091401>
- 530 Linit MJ (1988). Nematode-vector relationships in the pine wilt disease system. *Journal of*
531 *Nematology*, 20(2), 227. PMID: 19290206
- 532 Linit MJ (1990). Transmission of pinewood nematode through feeding wounds of Monochamus
533 carolinensis (Coleoptera: Cerambycidae). *Journal of Nematology*, 22(2), 231. PMID:
534 19287715
- 535 Lutscher F, Musgrave JA (2017). Behavioral responses to resource heterogeneity can accelerate
536 biological invasions. *Ecology*, 98(5), 1229-1238. <https://doi.org/10.1002/ecy.1773>
- 537 Martín-García J, Jactel H, Diez JJ (2011). Patterns and monitoring of Sesia apiformis
538 infestations in poplar plantations at different spatial scales. *Journal of Applied Entomology*,
539 135(5), 382-392. <https://doi.org/10.1111/j.1439-0418.2010.01562.x>
- 540 Mercader R, McCullough DG, Bedford JM (2013). A comparison of girdled ash detection
541 trees and baited artificial traps for Agrilus planipennis (Coleoptera: Buprestidae) detection.
542 *Environmental entomology*, 42(5), 1027-1039. <https://doi.org/10.1603/EN12334>
- 543 Naves P, Camacho S, Sousa EM, Quartau JA (2007) (a). Transmission of the pine wood
544 nematode Bursaphelenchus xylophilus through feeding activity of Monochamus
545 galloprovincialis (Col, Cerambycidae). *Journal of Applied Entomology*, 131(1), 21-25.
546 <https://doi.org/10.1111/j.1439-0418.2006.01111.x>
- 547 Naves P, Camacho S, Sousa EM, Quartau J (2007) (b). Transmission of the pine wood
548 nematode Bursaphelenchus xylophilus through oviposition activity of Monochamus
549 galloprovincialis (Coleoptera: Cerambycidae). *Entomologica Fennica*, 18(4), 193-198.
550 <https://doi.org/10.33338/ef.84398>
- 551 Naves P, Mota M, Pires J, Penas AC, Sousa E, Bonifácio L, Bravo MA (2001).
552 Bursaphelenchus xylophilus (Nematoda; aphelenchoididae) associated with Monochamus
553 galloprovincialis (Coleoptera; Cerambycidae) in Portugal. *Nematology*, 3(1), 89-91.
554 <https://doi.org/10.1163/156854101300106937>
- 555 Naves P, Bonifácio L, de Sousa E (2016). The pine wood nematode and its local vectors in the
556 Mediterranean Basin. In *Insects and diseases of Mediterranean forest systems* (pp. 329-
557 378). Springer, Cham. https://doi.org/10.1007/978-3-319-24744-1_12
- 558 O'Reilly-Nugent A, Palit R, Lopez-Aldana A, Medina-Romero M, Wandrag E, Duncan RP
559 (2016). Landscape effects on the spread of invasive species. *Current Landscape Ecology*
560 Reports, 1(3), 107-114. <https://doi.org/10.1007/s40823-016-0012-y>
- 561 Pierce IH (1994). Using pheromones for location and suppression of phycitid moths and
562 cigarette beetles in Hawaii—a five-year summary. In Proc. 6th Intl. Working Conf. Stored-
563 Prod. Prot, CAB International, Wallingford, United Kingdom (pp. 439-443).

- 564 Pimentel D, Zuniga R, Morrison D (2005). Update on the environmental and economic costs
565 associated with alien-invasive species in the United States. *Ecological Economics*, 52(3
566 SPEC. ISS.), 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- 567 Ranius T (2006). Measuring the dispersal of saproxylic insects: a key characteristic for their
568 conservation. *Population ecology*, 48(3), 177-188. [https://doi.org/10.1007/s10144-006-0262-3](https://doi.org/10.1007/s10144-006-
569 0262-3)
- 570 Rigot T, Van Halder I, Jactel H (2014). Landscape diversity slows the spread of an invasive
571 forest pest species. *Ecography*, 37(7), 648-658. [https://doi.org/10.1111/j.1600-0587.2013.00447.x](https://doi.org/10.1111/j.1600-
572 0587.2013.00447.x)
- 573 Robinet C, Roques A, Pan H, Fang G, Ye J, Zhang Y, Sun J (2009). Role of human-mediated
574 dispersal in the spread of the pinewood nematode in China. *PLoS One*, 4(2), e4646.
575 <https://doi.org/10.1371/journal.pone.0004646>
- 576 Robinet C, David G, Jactel H. (2019). Modeling the distances traveled by flying insects based
577 on the combination of flight mill and mark-release-recapture experiments. *Ecological
578 Modelling*, 402, 85-92. <https://doi.org/10.1016/j.ecolmodel.2019.04.006>
- 579 Robinet C, Castagnone-Sereno P, Mota M, Roux G, Sarniguet C, Tassus X, Jactel H (2020).
580 Effectiveness of clear-cuttings in non-fragmented pine forests in relation to EU regulations
581 for the eradication of the pine wood nematode. *Journal of Applied Ecology*, 57(3), 460-466.
582 <https://doi.org/10.1111/1365-2664.13564>
- 583 Sanchez-Husillos E, Etxebeste I, Pajares J (2015). Effectiveness of mass trapping in the
584 reduction of *Monochamus galloprovincialis* Olivier (Col.: Cerambycidae) populations.
585 *Journal of Applied Entomology*, 139(10), 747-758. <https://doi.org/10.1111/jen.12219>
- 586 Schroeder LM (2013). Monitoring of *Ips typographus* and *Pityogenes chalcographus*: influence
587 of trapping site and surrounding landscape on catches. *Agricultural and Forest
588 Entomology*, 15(2), 113-119. <https://doi.org/10.1111/afe.12002>
- 589 Schroeder M (2019). Trapping strategy for *Monochamus sutor* and *Monochamus
590 galloprovincialis*: potential vectors of the pine wood nematode in Scandinavia. *Agricultural
591 and Forest Entomology*, 21(4), 372-378. <https://doi.org/10.1111/afe.12339>
- 592 Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Essl F. (2017). No
593 saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 1–9.
594 <https://doi.org/10.1038/ncomms14435>
- 595 Simberloff D (1997). The biology of invasions. *Strangers in Paradise: Impact and Management
596 of Nonindigenous species in Florida*, 3-17.
- 597 Sylla S, Brévault T, Bal AB, Chailleur A, Diatte M, Desneux N, Diarra K. (2017). Rapid spread
598 of the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), an invasive pest in Sub-
599 Saharan Africa. *Entomologia Generalis*, 36(3), 269-283.
600 <https://doi.org/10.1127/entomologia/2017/0453>

- 601 Tischendorf L, Fahrig L. (2000). On the usage and measurement of landscape
602 connectivity. *Oikos*, 90(1), 7-19. <https://doi.org/10.1034/j.1600-0706.2000.900102.x>
- 603 Tokushige Y, Kiyohara T. (1969). Bursaphelenchus sp. in the wood of dead pine trees. *Journal*
604 *of the Japanese Forestry Society*, 51(7), 193-195.
605 https://doi.org/10.11519/jjfs1953.51.7_193
- 606 Torres-Vila LM, Zugasti C, De-Juan JM, Oliva MJ, Montero C, Mendiola FJ, Conejo Y, Sánchez
607 A, Fernández F, Ponce F, Espárrago, G. (2015). Mark-recapture of Monochamus
608 galloprovincialis with semiochemical-baited traps: population density, attraction distance,
609 flight behaviour and mass trapping efficiency. *Forestry: An International Journal of Forest*
610 *Research*, 88(2), 224-236. <https://doi.org/10.1093/forestry/cpu049>
- 611 Liou JY, Shih JY, Tzean SS (1999). Esteya, a new nematophagous genus from Taiwan,
612 attacking the pinewood nematode (Bursaphelenchus xylophilus). *Mycological*
613 *Research*, 103(2), 242-248. <https://doi.org/10.1017/S0953756298006984>
- 614 Walther GR, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, ... Settele, J. (2009). Alien
615 species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*,
616 24(12), 686–693. <https://doi.org/10.1016/j.tree.2009.06.008>
- 617 Wang IJ, Savage WK, Bradley Shaffer H (2009). Landscape genetics and least-cost path
618 analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma*
619 *californiense*). *Molecular ecology*, 18(7), 1365-1374. <https://doi.org/10.1111/j.1365-294X.2009.04122.x>
- 621 Wilson BE, Beuzelin JM, Reagan TE. (2017). Population distribution and range expansion of
622 the invasive Mexican rice borer (Lepidoptera: Crambidae) in Louisiana. *Environmental*
623 *Entomology*, 46(2), 175-182. <https://doi.org/10.1093/ee/nvx036>
- 624 Yi C, Byun B, Park J, Yang S, Chang K (1989). First finding of the pine wood nematode,
625 Bursaphelenchus xylophilus (Steiner et Buhrer) Nickle and its insect vector in Korea.
626 *Research Reports of the Forestry Research Institute Seoul*, 38, 141–149
- 627 Zeller KA, McGarigal K, Whiteley AR (2012). Estimating landscape resistance to movement: a
628 review. *Landscape ecology*, 27(6), 777-797. <https://doi.org/10.1007/s10980-012-9737-0>
- 629 Zhao BG, Futai K, Sutherland JR, Takeuchi Y (2008). Pine wilt disease. Springer, Tokyo,
630 Japan.
- 631 Zhang ZY, Zha YP, Cai SS, Hong CH, Liang P, Chen JY (2020). Application of harmonic radar
632 to analyze dispersal behavior of the Japanese pine sawyer beetle, Monochamus alternatus
633 (Coleoptera: Cerambycidae). *Entomological Research*, 50(1), 50-58.
634 <https://doi.org/10.1111/1748-5967.12411>
- 635 Zhang QH, Schlyter F (2004). Olfactory recognition and behavioural avoidance of angiosperm
636 nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology*,
637 6(1), 1-20. <https://doi.org/10.1111/j.1461-9555.2004.00202.x>