Modelling collective foraging in endemic bark beetle populations

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Tree-killing bark beetles are widely studied at epidemic population densities because of their significant impacts on forests. At endemic levels, these species are restricted to poorly defended resources, such as wind-felled, lightning-struck, or suppressed trees. It is poorly understood how these scattered and unpredictable resources are discovered and exploited. In this prospect, the collective foraging shown by most bark beetles, in the form of independent searching by individual beetles combined with mutual attention to each other’s chemical signals, represents an efficient strategy to increase the probability to discover the resources.

In order to explore the role of host distribution and collective foraging on the discovery of and settlement on wind-felled trees by bark beetles at endemic population densities, we developed a spatially explicit foraging model for the major forest pest in Europe, \textit{Ips typographus}. The model is based on the diffusion of the beetles, the landing of pioneers on wind-felled trees realistically distributed based on field observations in southern Belgium, and the response of flying beetles to pheromones emitted by these pioneers.

The results show that social foraging effectively increases the proportion of beetles that landed on wind-felled resources compared to solitary foragers. Furthermore, the model highlights the parameters that influenced the foraging strategy of \textit{I. typographus} and that need narrower quantification in further experiments. Finally, in the frame of the tested parameters, the model highlights the existence of thresholds in the reproduction rate and in the size of the starting population under which populations collapse. If confirmed, this prediction would shed new light on the understanding of foraging at low, endemic population levels.

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1. Introduction

The biology and dynamics of tree-killing bark beetle populations have been intensively studied because of the high ecological and economic impacts of these insects during epidemics (Grégoire et al., 2015 and references therein). For example, bark beetles (mainly \textit{Ips typographus} (L.)) caused the loss of 124 million m\textsuperscript{3} of spruce (\textit{Picea abies} (L.) Karst.) in Europe between 1958 and 2001 (Seidl et al., 2011). Likewise, an outbreak of the mountain pine beetle, \textit{Dendroctonus ponderosae} Hopkins, affected over 18 million hectares in western Canada between 1999 and 2012. It resulted in the loss of more than 723 million m\textsuperscript{3} of \textit{Pinus contorta} merchantable wood (Natural Resources Canada, 2013). The carbon budget of conifer forests has even been significantly affected by bark-beetle activity (Kurz et al., 2008; Seidl et al., 2014). All these studies on bark beetles unveiled many questions pertaining to chemical ecology, symbiosis, sexual selection, population dynamics, disturbance ecology, and co-evolution (for a review, see Vega and Hofstetter, 2015).

However, these highly destructive species have been far less studied when they are at low, endemic levels, despite the fact that insects have to face critical issues influencing their population dynamics under these circumstances. One of the major limitations occurring at low densities is the beetles’ inability to attack healthy living trees. This leads to the highest constraint on foraging, that is, the location of scattered, poorly protected resources (Atkins, 1966; Kausrud et al., 2011) that typically consist of wind-felled, lightning-struck, or suppressed trees (Christiansen and Bakke, 1988; Coulson et al., 1983; Furniss and Carolin, 1977; Hodges and Pickard, 1971; Kausrud et al., 2011; Safranyik and Carroll, 2007; Wermeling, 2004). The discovery of these resources depends on their spatial distribution, and the collective foraging theory predicts that the encounter rate would increase with high dispersal capacities combined for collective foraging (Caraco et al., 1989; Giraldeau and

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Dubois, 2008; Stephens et al., 2007), i.e., in this case, independent searching by individual beetles combined with mutual attention to each other’s chemical signals.

Bark beetles are known for their high dispersal flight potential, up to tens of kilometres (Amslie and Jackson, 2011; Jackson et al., 2008; Nilsson, 1984), and many species rely on chemical communication to aggregate on the resource located by “pioneer” beetles (Pitman et al., 1969; Raffa et al., 2015; Schlyter et al., 1987a,b; Wood, 1982). This mode of foraging, however, raises many questions, with the following being a central one: how do bark beetles locate these scattered and unpredictable resources quickly enough to bypass inter-specific competition (Louis et al., 2014; Raffa et al., 2015)? Answering this question is difficult, as the dispersion and foraging strategies of these species are hard to characterise at the endemic level due to their small size and the long-range dispersal abilities that can be at work. Trapping networks (e.g., Botterweg, 1982; Franklin and Grégoire, 1999; Piel et al., 2005) and modelling have been used to understand their spread, together with theoretical studies that mostly focused on the path followed by individual insects (Byers, 1996; Gries et al., 1989). Models addressing spatial patterns, host selection and the influence of landscape feature on D. ponderosae were developed by Logan et al. (1998), Chubaty et al. (2009) and de la Giroday et al. (2011). Pérez and Dragičevič (2011) implemented an agent-based model of beetle outbreaks based on a swarm intelligence algorithm and integrated into GIS on real datasets to simulate D. ponderosae aggregation and mass attack. Similarly, I. typographus elicited an exceptionally rich modelling activity. Grégoire et al. (2015) recorded 24 published models centred on L. typographus, and four of these models specifically addressed spatially explicit dispersal and population changes (Gilbert et al., 2005; Kautz et al., 2011; Lausch et al., 2013; Wichmann and Raven, 2001). One additional study (Okland et al., 2016) used empirical data and simulation models to explain the spatial patterns of infestation spots. Most of these models can be considered as inductive, as they attempted to derive a set of general rules from particular observations. Another recent model (Kautz et al., 2014) used a deductive approach in an attempt to predict particular outcomes from general rules, linking individual (beetle and tree) behaviour to system-specific traits (dispersal and infestation patterns). However, few studies considered diffusion-based models (Holland et al., 1989), despite their frequent and successful use in ecology, especially when the considered individuals were difficult to follow (Shigesada and Kawasaki, 1997; Turchin, 1998).

No study specifically addressed foraging in endemic populations. Typographus, the European spruce bark beetle, is a species of choice for studying the importance of dispersion and aggregation in a foraging strategy. Its biology is well documented because it is the major forest pest in Eurasia (Grégoire et al., 2015; Grégoire and Evans, 2004). At endemic levels, this species mostly settles on wind-felled spruce (Picea spp.). Upon emergence, only approximately 1% of the emerging insects land on local trees in a one-hectare area surrounding their point of emergence (Franklin and Grégoire, 1999). A larger but still limited proportion (2% to 30%) of the emerging population is able to respond immediately to pheromones (Duelli et al., 1997; Franklin et al., 2000; Weslien, 1992). However, the majority of naive emerging beetles probably need to reach a certain fatigue level before responding to pheromones (Jactel, 1991). Hence, most individuals fly, sometimes over long distances (8 km: Botterweg, 1982; 18 km: Forsee and Sölbreck, 1985; 43 km: Nilsson, 1984).

Once a pioneer male discovers a resource, it initiates the boring of a gallery in the phloem and emits aggregation pheromones that attract both females and other males (Bakke et al., 1977; Schlyter et al., 1987a,b), eliciting mass colonisation of the resource, with ca 1200 to 5000 attacks per tree in the case of wind-felled trees (Gonzalez et al., 1996; Grégoire et al., 1997; Louis et al., 2014). A male mates, on average, with 2 females, and females do not emit pheromones (Birgersson et al., 1984). Each female lays 60–80 eggs, from which 13–33 adults will survive and emerge at endemic levels, with a globally balanced sex-ratio (Annila, 1971; Faccoli and Buffo, 2004; Louis et al., 2014).

The patterns of colonisation of identified host trees, egg laying and brood development until emergence are well known (Byers, 1984; Anderbrant et al., 1985; De Jong and Grijpma, 1986; Wermelinger and Seifert, 1998). On the contrary, insect dispersal and localisation of suitable hosts still require focus to fill major gaps in our knowledge of the entire life cycle of I. typographus. More specifically, the constraints governing the foraging strategy in endemic conditions are still largely unknown. The discovery of, and settlement on, wind-felled trees depends on the entangled effects of the scattered distribution and density of the hosts, as well as the dispersal capacities and local density of the insects.

In order to account for these factors and their interactions, we developed a spatially explicit deterministic foraging model for I. typographus, based on a set of non-differential equations describing the diffusion of the beetles (no direct cues to the potential hosts), landing and gallery initiation by the “pioneers” (defined as the insects that were first to discover a host) and social landing of the following individuals in response to pheromones. The stochastic component of the simulations lies in the random distribution of the wind-felled trees within the environment, based upon realistic spatio-temporal observed distribution of the hosts in southern Belgium.

2. Model

2.1. Model area

Our model is based on a series of assumptions regarding the known behaviour of I. typographus, which was spatially, explicitly modelled in a simulated environment consisting of a grid containing i = 100 columns and j = 100 rows of 500 m wide square cells (n = 1 x j = 10,000 cells = 250,000 ha). Source and target trees, i.e., infested and uninfested wind-felled trees, respectively, were distributed within the grid (see Section 2.3). Each simulation consisted of 250 steps, with a step duration of 1 h.

The border condition depicts the situation of a study area located in a larger territory with homogeneous insect density; some individuals exit the region when reaching its border, while new individuals come from the outside. Such a system is constructed by simulating a periodic grid system (i.e., a torus) whose opposite ends are linked. Individuals that reach one side of the grid are relocated to the opposite side. We also investigated the scenario of a finite region where the beetles that crossed the grid sides were removed from the model, and none entered the area. This second border condition is further described in Supplementary material: Appendix D.

2.2. Behaviour

2.2.1. Emergence and diffusion

During the 60 first steps of the simulation, we assumed a constant rate of beetle emergence from source trees equal to \( \Phi = \Phi/60 \) (with \( \Phi \) the total number of emerging male beetles per tree). We focused on the behaviour of males because the females do not participate in the pioneering and on the amplification of the dynamics (aggregative pheromones). We also assumed a balanced sex-ratio and considered (an obvious simplification) that every male landing is joined by two females and thereafter started a successful brood system leading to the production of \( \rho \) offspring/attack (Table 1).

The males’ behaviour was translated in a series of equations. \( N_B(t) \) is the number of emerging flying “naïve” beetles (i.e., bee-
The number in each cell of coordinates \((i;j)\) were calculated at time \(t\) by Eqs. (1a) and (1b) for naive and experienced beetles, respectively.

\[
\frac{dN_{ij}}{dt} = W_{ij}^\phi \phi(t) - \gamma N_{ij} - \text{Landing}_{ij}(N_{ij}) - 4DN_{ij} \quad (1a)
\]

\[
\frac{dE_{ij}}{dt} = -\gamma E_{ij} + \Pi_{ij} - D(4F_{ij} - \Omega_{ij}) - \text{Landing}_{ij}(E_{ij}) \quad (1b)
\]

\[
\Pi_{ij} = \sum_{l=1,l \neq 0}^{1} (N_{i+l,j} + N_{i,j+l})
\]

\[
\Omega_{ij} = \sum_{l=1,l \neq 0}^{1} (E_{i+l,j} + E_{i,j+l})
\]

In Eq. (1a), \(N_{ij}\) stands for the number of naïve beetles, \(\phi\) is the total number of emerging beetles from source trees, \(D\) is the diffusion coefficient of the mean residence time in a cell, and \(\gamma\) is the mortality rate of naïve beetles due to predation. 

The parameter values used in the model are based on the cited literature and are shown in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Range</th>
<th>Default value</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>emergence</td>
<td>reproduction rate: number of living adults produced/attack</td>
<td>13–45</td>
<td>20</td>
<td>Anderbrant, 1990; Faccoli and Bernardelli, 2010; Louis et al., 2014; Sallé et al., 2005; Weslien, 1994</td>
</tr>
<tr>
<td>(\Phi)</td>
<td>number of emerging male beetles per tree</td>
<td>2500–22,500 males/tree</td>
<td>3,000</td>
<td>Gonzalez et al., 1996; Louis et al., 2014</td>
</tr>
<tr>
<td>diffusion</td>
<td>diffusion coefficient: inverse of the mean residence time in a cell</td>
<td>0–0.25 beetles h(^{-1})</td>
<td>0.12</td>
<td>Gries et al., 1989; Helland et al., 1984; Zolubas and Byers, 1995</td>
</tr>
<tr>
<td>(\gamma)</td>
<td>mortality rate: inverse of the mean lifespan</td>
<td>0–0.66 beetles h(^{-1})</td>
<td>0.022</td>
<td>Byers and Löfqvist, 1989</td>
</tr>
<tr>
<td>landing</td>
<td>intrinsic landing rate on a tree</td>
<td>0–0.001,5 beetles h(^{-1})</td>
<td>0.000,5</td>
<td>Franklin and Grégoire, 2001 (Supplementary material: Appendix B)</td>
</tr>
<tr>
<td>(\beta^\prime)</td>
<td>landing rate of experienced beetles in response to the number of landed conspecifics</td>
<td>0–0.001,5 beetles h(^{-1})</td>
<td>0.000,022,5 (&lt;0 in non-social scenario)</td>
<td>Franklin and Grégoire, 2001</td>
</tr>
<tr>
<td>(\beta^{\prime\prime})</td>
<td>landing rate of emerging naïve beetles in response to the number of landed conspecifics</td>
<td>0–0.000,15 beetles h(^{-1})</td>
<td>0.000,012,5 (&lt;0 in non-social scenario)</td>
<td>Franklin and Grégoire, 2001</td>
</tr>
<tr>
<td>(K)</td>
<td>carrying capacity of a tree (maximal number of attacks)</td>
<td>0–15,000 attacks</td>
<td>2,500</td>
<td>Gonzalez et al., 1996; Louis et al., 2014</td>
</tr>
<tr>
<td>(K^\prime)</td>
<td>measure of the saturation in the response to pheromones</td>
<td>2,500 attacks</td>
<td>2,500 (&lt;0 in non-social scenario)</td>
<td>Franklin and Grégoire, 2001</td>
</tr>
<tr>
<td>trees distribution</td>
<td>number of source ((W^\prime)) and target ((W)) trees distributed in the model area</td>
<td>5,000–25,000</td>
<td>17,000</td>
<td>Louis et al., in prep.</td>
</tr>
<tr>
<td>distribution of target trees</td>
<td>distribution of uninfested wind-felled trees</td>
<td>random vs observed distribution</td>
<td>observed distribution</td>
<td>Louis et al., in prep. (Supplementary material: Appendix A)</td>
</tr>
<tr>
<td>distribution of source trees</td>
<td>distribution of infested wind-felled trees</td>
<td>random vs observed distribution</td>
<td>observed distribution</td>
<td>Louis et al., in prep. (Supplementary material: Appendix A)</td>
</tr>
<tr>
<td>inter-annual clustering</td>
<td>spatio-temporal clustering of wind-felled trees</td>
<td>clustered vs independent</td>
<td>independent</td>
<td>Louis et al., in prep. (Supplementary material: Appendix A)</td>
</tr>
</tbody>
</table>

2.2.2. Landing

A general scenario of landing in a cell \((i;j)\) is described as follows:

\[
\frac{dL_{ij}}{dt} = (W_{ij}\beta + \beta^{\prime\prime}K^\prime L_{ij})/(K + L_{ij}) \times (1 - L_{ij}/W_{ij}K)E_{ij} + (W_{ij}\beta^N + \beta^{\prime\prime\prime}K^\prime L_{ij})/(K + L_{ij}) \times (1 - L_{ij}/W_{ij}K)N_{ij}\]

where \(L_{ij}\) is the number of landed beetles, \(W_{ij}\) is the number of target trees in the cell, and \(\beta\) is the intrinsic landing rate (see Supplementary material: Appendix B). The social component of the landing response to landed individuals, i.e., mediated by aggregation pheromones, is parameterised with \(K\) a measure of the saturation term in the response to pheromones and \(\beta^\prime\) and \(\beta^{\prime\prime}\), the social landing rate for the experienced and naïve beetles, respectively (naïve beetles can be attracted on the target in their cell of origin).
origin). Finally, \( K \) represents the carrying capacity of each tree in the cell, i.e., the maximum number of male attacks on a target tree due to physical constraints (size of the tree) and inhibitory processes (anti-aggregation pheromones). The carrying capacity constrains the total number of males landed, but the total number of emerging adults from an infested tree is only bound by the number of landed beetles and the reproduction rate \( \rho \) (Figure A3 in the Supplementary material: Appendix C shows how the landing rate varies with the number of landed conspecifics).

Using Eq. (2), two landing scenarios were tested:

- the first (hypothetical) scenario corresponds to a non-social landing, i.e., landing without inter-individual communication that is totally independent of any other landed beetle, where the social landing rates \( \beta = \beta^N = 0 \) and the saturation term in the response to pheromones \( k^* \) = 0,
- the second (more realistic) scenario corresponds to a social landing, i.e., landing with inter-individual communication that is dependent of the number of landed conspecifics, where the social landing rates \( \beta^N \) and \( \beta^N \) and the saturation to pheromones \( K^* \) differ from zero (see Table 1).

Here, the first scenario (landing without inter-individual communication) is used as a reference to quantify the potential benefits of the social foraging depicted in the second scenario (landing without inter-individual communication (pioneers) plus landing mediated by inter-individual communication).

2.3. Spatial distribution of the trees

The spatial distribution of the trees was the stochastic component of the simulations. We tested the impact of different spatial distributions of both source and target trees.

The first distribution followed a Poisson distribution and was achieved by the random selection of cells within the whole simulated area to establish wind-felled trees. Multiple selection of the same cell was allowed, and the filling ended when a value of \( W \) wind-felled trees was reached (Table 1). The hypothetical random tree distribution used here served as a baseline to investigate the influence of a realistic field-based tree distribution on the efficiency of social foraging.

The second distribution of the trees was based on a power-law like distribution similar to that of real wind-felled trees observed in the field (see Supplementary material: Appendix A). Distribution data were obtained from the forest department of the Walloon region/Belgium. It consisted of a yearly census of wind-felling events in 18,777 stands, collected over a 22-year period (1993–2014) and corresponded to a total of 413,094 records. \( W \) wind-felled trees were scattered within the simulated area following the distribution observed in the field, as described in Appendix A of the Supplementary material (see Supplementary material: Appendix A).

Finally, we tested the effect of inter-annual clustering on the random and observed spatial distributions, i.e., a spatio-temporal autocorrelation of the wind-felled trees, as observed under natural conditions. In the random distribution, we truncated the random selection of cells available for target trees so that 20% of the cells contained source trees and obligatorily contained target trees. In the observed spatial distribution, we used the power-law like distribution of trees but truncated the cumulated frequencies of wind-felled densities to fill the cell with at least 1 target tree if the cell already contained at least 1 source tree (see Supplementary material: Appendix A for the computation method for the observed spatial distribution).

2.4. Analyses

Our analyses were based on the following elements:

a) Effects of social foraging and tree distribution—we investigated a model that included social interaction with clustered source and target trees according to the observed host distribution and characterised by a periodic grid system regarding beetle entry and exit. This model is referred to, hereafter, as the complete model;

b) Sensitivity of landing rates—we investigated the sensitivity to the main parameters (diffusion coefficient \( D \), landing rate \( \beta \), target tree's carrying capacity \( k^* \) and mortality rate \( \gamma^* \)) analysed by varying one parameter while the others were kept at their default values;

c) Temporal evolution and stationary state—by simulating the evolution of the landed proportion with various population densities, we calculated population changes from generation to generation and estimated the stationary states of the system; and

d) Sensitivity of population thresholds—we tested the main parameters (diffusion coefficient \( D \), landing rate \( \beta \), target tree's carrying capacity \( k^* \) and mortality rate \( \gamma^* \)), on the evolution of the thresholds highlighted by the analyses of the stationary states.

The investigated range of the parameters values is listed in Table 1 with 15 repetitions for each set of parameters.

Simulations, graphics and statistical analyses were performed in R, version 3.1.2 (R Development Core Team; http://www.r-project.org/). All the statistical models were used under their conditions of applicability, with statistical significance set to \( \alpha = 0.05 \).

3. Results

3.1. Effects of social foraging and tree distribution

The addition of a social response in the landing rate (Eq. (2)) greatly increases the proportion of the population that landed at the end of the simulation, regardless of the spatial distribution of the hosts (Fig. 1).

Moreover, while the spatial distribution pattern of the source and target trees only leads to slight differences in the landing proportions under the non-social scenario, it exerts a much stronger influence under the social landing scenario. At its maximum value, a random host distribution leads to a two-fold higher landing proportion compared to a power-law-like observed tree distribution (Fig. 1). The inter-annual clustering of the resources attenuates this effect and increases the landed proportion (Anova: \( F_{7,152} = 1201; P < 0.0001 \); Fig. 1). An example of the spatial distribution of the landed beetles under the complete model is shown in Fig. 2.

3.2. Sensitivity of landing rates

The increase of the diffusion coefficient increases the landed proportion in an asymptotic way (Fig. 3A). In the same way, the landed proportion increases in an asymptotic way with the landing rate and carrying capacity (Fig. 3B and C). Inversely, the model is sensitive to the mortality rate, and the landed proportion quickly tends to 0 with increasing mortality (Fig. 3D).

3.3. Temporal evolution and stationary state

By varying the number of emerging insects per tree, the number of trees remained constant, and we simulated the evolution of the landed proportion with various population densities. When
social interactions were withdrawn from the model and all the other parameters were set at the default values, the landed proportion decreased because of the constant effect of overcrowding with increasing beetle densities (Fig. 4A). However, under the conditions of the complete model and with all the other parameters being the same, the landed proportion increased rapidly to a maximum value before declining (Fig. 4B), which corresponded first to the combined effect of social response and the attraction of flying beetles to resources discovered by pioneers (ascending phase), and later to intra-specific competition (declining phase).

The evolution allowed us to calculate population changes from generation to generation and estimate the stationary states of the system with Eq. (3):

\[ S_g = \rho L (S_{g-1}) S_{g-1} \]

where \( S_g \) is the size of the population at generation \( g \), \( L \) is the landed proportion at generation \( g - 1 \), which varies with the population size at \( g - 1 \) (Fig. 4), and \( \rho \) is the reproduction rate per attack.

By assuming that \( S_g = S_{g-1} \) at steady state, we can construct a bifurcation diagram showing the stability regions of the model (Eq. (3)) (Fig. 5A and B).

For the non-social model, the outcomes are trivial, and the stability of the population depends solely on the reproduction rate if all the other parameters are constant. Under the critical value of 31 offspring/attack, the population will always tend to 0 (Fig. 5A). However, the social interactions introduce a threshold (which corresponds to an unstable steady state), as highlighted by Fig. 5B. The evolution of the population from generation to generation will tend to two stable states, depending on the reproduction rate and on the size of the population at the starting point. The population will always tend to 0 if the reproduction rate is lower than the minimum of the reproduction rate on Fig. 5B (\( \rho = 14.73 \) offspring/attack). Conversely, the population will grow independently of the size of the initial population if the reproduction rate is higher than the value at the intersection of the dashed line with the X-axis (\( \rho = 30.38 \) offspring/attack).

In the range delimited by the upper and lower reproduction critical values, the outcome of the population growth will depend on the size of the initial population, represented by the dashed line, below which the population will always tend to 0, if all the other parameters were constant. We therefore note the existence of a population threshold (Fig. 5B). For example, with a realistic intermediate reproduction rate of \( \rho = 20 \) offspring/attack and all the other parameters set as default values, the population will always decrease and reach 0 if there is less than the equivalent of 865 emerging beetles per trees (Fig. 6).

3.4. Sensitivity of population thresholds

The reproduction rate and population thresholds depend on the parameters of the model because they influenced the landed proportion (equation in Fig. 4B). We tested the effect of some of the parameters on the evolution of the thresholds (Fig. 7). An increase of the diffusion coefficient tends to decrease the population threshold at the same reproduction rate (Fig. 7A). The intrinsic landing rate and the carrying capacity have similar effects on the population thresholds (Fig. 7B and C). The model is more sensitive to variations of the mortality rate (Fig. 7D).

4. Discussion

This is to our knowledge, the first study addressing the collective foraging of bark-beetles per tree, and not as a byproduct of a mass attack. It is a deductive study testing simple assumptions and, in this respect, it could be compared with the work of Kautz et al. (2014, 2016). However, our own approach differs from
that of Kautz et al. (2014, 2016) in several aspects: (i) it explicitly focuses on testing a limited, robust set of simple hypotheses based only on foraging for wind-felled trees with no resistance to bark beetles (each single landing beetle can start an attack by itself; the social interactions only increase host discovery rates and not the overcoming of tree defences); (ii) the hosts’ spatial distribution in the model follows the distribution observed in the field (spatial distribution and patchiness); (iii) apart from a distinction between “naïve” and “experienced” beetles, we do not consider insect variability (as, e.g. energy level; consumption efficiency; movement angle: see Kautz et al., 2014, 2016); (iv) we operate at the landscape scale (250,000 ha), our 500 × 500 m (25 ha) units each corresponded to one forest compartment. In contrast, Kautz et al. (2014, 2016) considered several beetle- and tree-related parameters at the stand scale (approx. 500 ha) with a much finer grid cell resolution (5 × 5m).

Although the results presented here are only valid in the frame of the tested parameters and under our explicit assumptions, they have the merit to support our hypothesis concerning the dispersal behaviour of *I. typographus* with a limited number of parameters and to predict some trends in its population dynamics.

First of all, in the range of the tested parameters, our model confirms our hypotheses, according to which a collective foraging component is necessary and sufficient for the beetles to locate scattered resources on which they will reproduce. As predicted by the collective foraging theory (Caraco et al., 1989), the addition of a social response directed to already landed conspecifics greatly improves the finding of realistically distributed hosts. The effect of wind on the flight of *I. typographus* is not clear, with evidence of flight upwind and downwind depending on wind speed (Franklin et al., 2000; Schlyter et al., 1987a,b). Our hypothesis of homogenous diffusion is therefore a simplistic but parsimonious assumption. Also parsimonious is the fact that we did not consider primary attraction to the hosts in our approach, a choice largely supported by the literature. Although the response of *I. typographus* to pheromones seems to increase in the presence of host monoterpenes (Austarål et al., 1986; Erbilgin et al., 2007), the general consensus is that primary attraction is weak in this species (see e.g., Byers et al., 1989) as in other aggressive bark-beetle species (Hynum and Berryman, 1980; Moecck et al., 1981; Raffa and Berryman, 1983; Wood, 1972), although Lindelöv et al. (1992) reported a response in the field to logs stored over the winter. Saint-Germain et al. (2007) reported interesting results, showing that primary attraction could play a role at long range, but it was replaced by random landings at closer range. However, this study centred on secondary species Dryocoetes spp. and Hylurgops pinifex (Fitch) and might not be transposable to *I. typographus*. Visual cues seem to be weak or even absent (Byers, 1993; Niemeyer,

![Fig. 2. Maps of source and target tree locations and their colonisation through time (complete model = social landing, observed tree distribution, no inter-annual clustering). The number on the top left corner of each map indicates the depicted time step: for the time step 0, the initial distribution and number of sources and target trees (logarithmic colour scale) is shown, while for the time steps 50–250 the fraction of cell carrying capacity filled by beetles is visualised.](image-url)
In addition, a theoretical simulation (Byers, 1996) indicated that beetles could find their resources without any primary attraction. Moreover, our model allows us to highlight the parameters that influenced the foraging strategy of *I. typographus* and would need narrower quantification in further experiments. The majority of the parameters tested in the model were estimated from the literature, but others were hardly measurable, such as the diffusion coefficient of the beetles. This coefficient depends not only on flight velocity or on the maximum distances covered but also on the trajectories of the insects. We avoided these complications by assuming that the diffusion coefficient is equivalent to the inverse of the mean residence time in a certain area. We chose a default residence time of 8 h in each cell, partly based on the flying speed of *ips* spp. on flight mills (1–10 m/sec; Jactel, 1991; J. Jacquemin, pers. comm.; see also Byers, 1996) but also on the fact that most recaptures occurred in a maximum radius of 700 m within the first 8 h of mark-release experiments (Gries et al., 1989; Helland et al., 1984; Zolubas and Byers, 1995). The study of the sensitivity of the model to the diffusion coefficient showed that diffusion coefficients higher than this default value have little effect on the landed proportion while lower values are rather unlikely considering the dispersal range of *I. typographus* and the results of mark-release experiments. Diffusion is important because it effectively increases the finding rate (Fig. 3A). However, high diffusion values can also be a disadvantage because of the associated costs (e.g., increased mortality linked to

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**Fig. 3.** Evolution of the mean landed proportion in the complete model with increasing values of different parameters. (A) the diffusion coefficient. (B) the landing rate. (C) the carrying capacity of the target trees. (D) the mortality rate. The error bars represent the standard deviation of 15 replicates. The red dashed lines indicate the default values of the tested parameters.
higher energy consumption and a higher probability to meet predation), as these costs could decrease the population densities and thus decrease the mating probabilities. In addition, high dispersal could lead the insects to unsuitable environments (Gandon et al., 1998). We partly tested the potential cost of high diffusion values by comparing our results in a periodic system to those obtained in an open system (see Supplementary material: Appendix D). These results showed that even if insects could exit small forests (open system), it has limited impact on the landed proportion.

Our results show that random distribution of target trees led to higher proportion of landed beetles. The distribution observed on the field leads to an intense clustering of the target trees that become much more concentrated and rare than when randomly distributed (fraction of non-empty cells: 6.7 ± 0.9% in observed distribution; 81.7 ± 0.3% in random distribution; see Supplementary material: Appendix A). The extreme patchiness of the observed distribution hence increases the time to find a target, what subsequently raises the amount of insects that die before they find a cell with a suitable host.

When target trees followed the observed distribution, the interannual clustering increased the landed proportion, partly because of the stratified dispersion implemented in the model (Shigesada and Kawasaki, 1997). A few naïve emerging beetles landed in the vicinity of the tree from which they emerged (Franklin and Grégoire...
and attracted conspecifics, among which some were from their trees of emergence, and a majority came from other, further cells (Franklin et al., 2000; Weslien and Lindelow, 1989), resulting in a local inoculum close to the former infestation focus (Wichmann and Ravn, 2001). The increased success allowed by this behaviour could be counterbalanced by other negative effects, such as a higher density of local natural enemies (Hougardy and Grégoire, 2001).

We could not measure nor document in the literature the value of the landing rate (B) and the response to landed conspecifics for the naïve and mature beetles (B' and B^N respectively). We calibrated the magnitude of these two parameters by comparing the results of a simplified model with the results of two mark-release experiments, as described in Appendix B of the Supplementary material (Supplementary material: Appendix B) (Franklin and Grégoire, 1999, 2001). The results of the model are sensitive to these parameters, which deserve closer attention in further experiments.

The cross attraction of beetles to the landed conspecifics is implicitly limited by the model by the size of the cells, i.e., 500 m wide squares. It is in agreement with the values estimated in the literature, which ranged from 12 m to 100 m (Franklin and Grégoire, 2001; Louis, unpublished data; Schlyter, 1992). The fact that we chose not to take into account other beetle characteristics such as energy level, consumption efficiency and angular movements probably had little influence on our model’s outcome. Kautz et al. (2016) suggest that individual variability does not impact dispersal success when, as in the present conditions, the susceptible hosts have a scattered distribution.

Based on the literature, we imposed a 1:1 sex-ratio upon emergence, and we considered that males after landing reproduced with 2 females (Ammila, 1971; Faccoli and Buffo, 2004; Louis et al., 2014). The difference in the sex ratio might seem surprising but might be explained in two ways. First, males that are the pioneer individuals in I. typographus face greater risks of predation (Gara, 1963) and exposure to trees’ remaining defences (Jakšič, 1998; Louis et al., 2016), and they might suffer higher mortality (Faccoli and Buffo, 2004). Second, the difference might arise from a differential response to the pheromones emitted by settled males. Arriving males may be more prone to avoid high concentrations of pheromones, contrary to the females (Botterweg, 1982; Zumr, 1982).

Finally, the social landing implemented in the model, along with the spatial distribution of the source and target trees, resulted in one of the most appealing results from our simulations, which was the existence of thresholds in the reproduction rate and in the size of the starting population.

First, the reproduction rates tested in this study were extracted from the literature in endemic conditions, when beetles attacked wind-felled or weakened trees (Anderbrant, 1990; Faccoli and Bernardinelli, 2010; Louis et al., 2014; Sallé et al., 2005; Weslien, 1994). These rates were included between the lower and upper critical values for population steady states. However, most publications give lower reproduction rates under epidemic conditions, when the attack densities were higher (Faccoli and Bernardinelli, 2010; Kärnemo and Schroeder, 2010; Sallé et al., 2005) and natural enemy pressure was higher (Hougardy and Grégoire, 2001; Mills, 1985; Weslien and Regnander, 1992). If the reproduction rates are lower than the critical value, our model predicts a decrease in the population. This could also explain why epidemic conditions returned to a steady state characterised by the reproduction on weakened resources with higher reproduction rates because beetles showed reproduction rates below the critical values when attacking living trees. This fit with the behaviour of I. typographus outbreaks in Europe, where a return to the endemic state was observed after a variable period of several years (Anderbrant and Schlyter, 1989; Marina et al., 2013; Meier et al., 2015). In our model, the only limiting factors regulating the population at the endemic level are the resource availability and intra-specific competition (Komonen et al., 2011) via the limited carrying capacity offered by the wind-felled trees, which only allowed the reproduction of a fraction of the emerging population. In light of our results and the importance of the reproduction rate, intra-specific competition appeared to be an important potential regulating population driver that should be investigated further.

Second, the population threshold value predicted in our model is high (865 males/tree, which in our model corresponds to a mean territorial density of 5882 males/km² and is higher than the flying densities observed in other studies (up to 4500 males/km² in Byers et al., 1989), assuming a 1:1 sex ratio). The existence of a threshold would have strong impacts on the ecology of the bark beetle, especially in terms of invasive capacities. High values of population density thresholds coupled with high dispersal has been shown detrimental to the establishment of species in new habitats (Liebold and Tobin, 2008). The existence and the size of a population density threshold in I. typographus should be experimentally confirmed. It would bring new insights on the invasive capacities of this pest, which has never established in any country separated from the Eurasian mainland by geographical barriers, even though it has been regularly intercepted (Brockerhoff et al., 2006; EPPO Reporting Service, 1997; Haack, 2006).

The model presented in this paper could be refined with narrower estimations of the key parameters, i.e., the diffusion rates, the landing probabilities and the mortality rates, which deserve focused experiments. The impact of other model hypotheses, such as the function governing the carrying capacity on the tree, could also be tested. The hypotheses tested regarding the foraging strategy and importance of social response could easily be transposed and tested not only to other bark-beetle species but also to any species that reproduces on scattered resources and rely on a collective foraging strategy.

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Fig. 7. Variations of the bifurcation diagrams (as shown in Fig. 5B) with different values of parameters of complete model. (A) The diffusion coefficient $D$. (B) Landing rate $\beta$. (C) The carrying capacity of the target trees $K$. (D) The mortality rate $\gamma$. Values below the dashed line will always lead to the collapse of the population. The red lines indicate the default values of the tested parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.07.008.

References


