Math Industry Workshop Natural Resources Canada Ressources naturelles Canada

MODELLING MOUNTAIN PINE BEETLE INVASIONS BY LONG DISTANCE DISPERSAL

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Abstract. Dispersal models in mathematical biology typically represent dispersal using spatially invariant diffusion terms in partial differential equations or using dispersal kernels in integrodifference equations. In reality, dispersal is highly variable in space and time–this is especially true of long-distance dispersal. When insects disperse over long distances, they are subject to numerous meteorological variables that are dynamic in space and time. In this work, we address this challenge by abandoning the typical approaches to modelling dispersal mentioned above and instead we incorporate spatial variability using an atmospheric dispersion model driven by meteorological data. We overlay a mathematical model of beetle flight propensity and behaviour and simulate dynamics in response to changing temperature along flight trajectories driven by wind.

1. Introduction

Insect dispersal is often divided into two classes: local and long distance. Local dispersal is the most common dispersal mode. Local dispersal is well represented using dispersal kernels [6] that describe the population-level relocation patterns. Long distance dispersal is much more challenging to model because only a small proportion of insects are thought to disperse this way, and because the factors that govern whether and how far individuals disperse are meteorological [4], and therefore difficult to predict.

For example, most mountain pine beetles disperse between five and fifty meters from where they were born but approximately 0.2% traverse above tree canopies [7] where they can be pulled upwards by updrafts and then transported laterally by higher wind speeds in the lower atmosphere [4]. Long-distance dispersal is likely the dominant determinant of the speed of mountain pine beetle invasions, so describing this behaviour is of significant interest [5].

The goal of this project is pair an atmospheric dispersion model that represents the movement of air currents in three dimensional space with a stochastic differential equation model that will represent how long flying beetles remain within a

Received by the editors September 2021.

given air current. When paired, these two modelling approaches will enable realistic simulation of long-distance dispersal of the mountain pine beetle and visualization of dispersal patterns

2. Atmospheric Dispersion Model

To understand the role that meteorology plays in the long-distance dispersal of the mountain pine beetle, we used the Hysplit atmospheric dispersion model [8] developed by the American National Oceanic and Atmospheric Administration (NOAA). The Hysplit model is driven by meteorological data inputs and combines Lagrangian and Eulerian approaches to model dispersion of particles or chemicals in the atmosphere; this is the origin of the first two letters in the model name, which refer to a hybrid approach.

We capitalized on the Lagrangian aspect of Hysplit to understand how the air currents that carry mountain pine beetles may move through space and time. Trajectories of hypothetical infinitesimal volumes of air with uniform properties that are subject to meteorological conditions were modeled in Hysplit. In order to further analyze these trajectories, we utilized the Python module PySplit [9], developed by Mellissa Cross of the University of Minnesota. Pysplit introduces the HySplit model into the Python framework in order to make use of the flexible tools Python has to offer, such as analysis and plotting of trajectories.

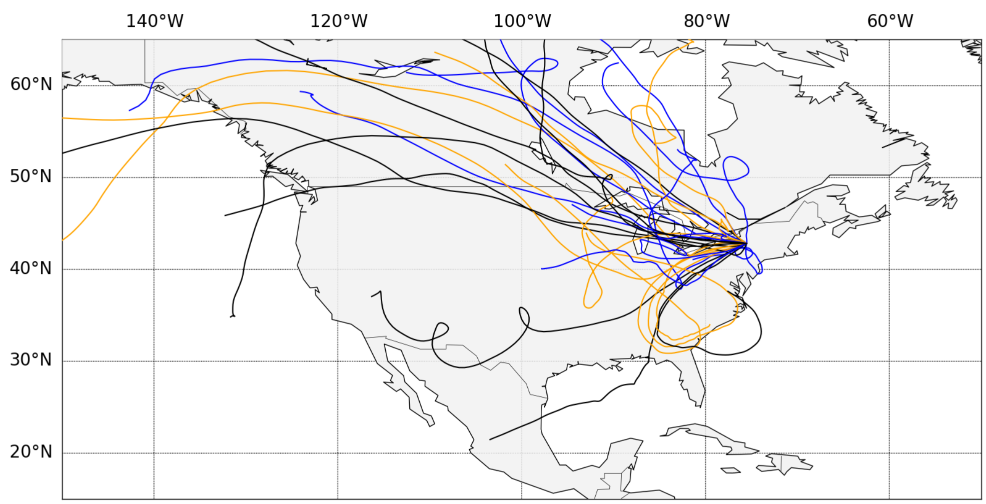

Figure 1. Example trajectories produced with PySplit, occuring during January 2007.

In Pysplit, most commonly, an initial Python script is executed in order to compute trajectories which occurred at a specific date, time, location, altitude, and with specified duration of flight. One can also choose to create various evenly spaced trajectories throughout surrounding days in Pysplit. This granted us flexibility in choosing desired meteorological conditions for air parcel trajectories. Once this step was complete, a second Python script was executed to generate trajectory plots.

For the sake of this project, we initially modeled a beetle in flight as an air parcel. Although this does not yet take into account beetle behaviour in the air, we can still obtain approximate trajectories for long-distance dispersal by estimating geographical location of beetle emergence as well as the time at which emergence likely occurred. Empirical data suggests that Mountain Pine Beetles emerged in late July and early August in 2005 [4]; in 2005, maximal emergence densities were observed on July 17, July 22 and July 26 [4]. During these periods of emergence, beetles were observed up to 800m above the forest canopy [4], where they were subject to higher wind speeds, and where they maintained flight for a maximum of 8 hours. To create the beetle trajectories that we used in combination with the stochastic differential equation model of beetle flight behaviour, we generated trajectories which occurred on July 17th, 22nd and 26th, starting at 12pm PT and progressing for 8 hours, with initial coordinates $(55.941, -121.405)$. We also considered trajectories with initial altitudes corresponding to the range in which the majority of airborne beetles were observed. These trajectories are included in Figure 2.

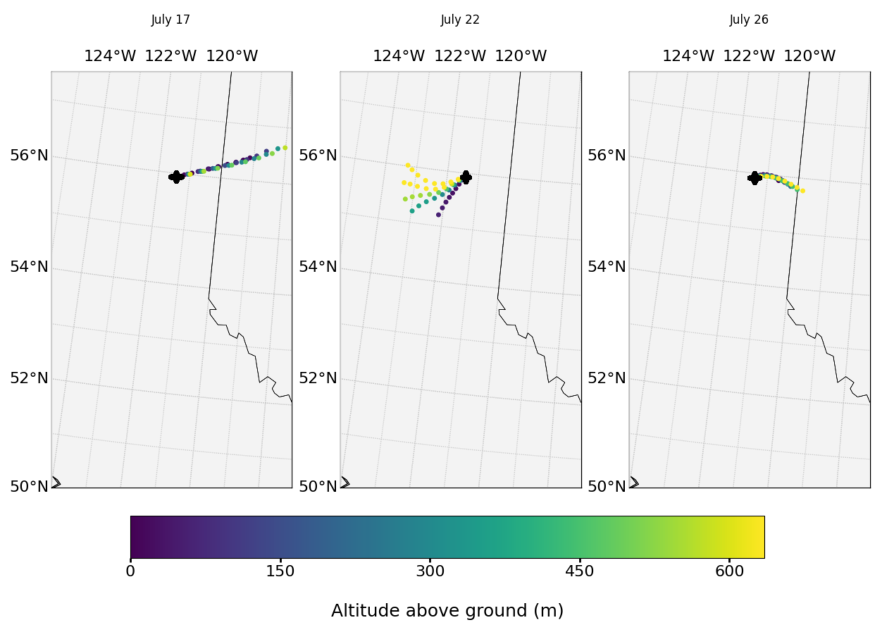

Figure 2. Approximate beetle trajectories in 2005, occurring on July 17th (left panel), July 22nd (middle panel) and July 26th (right panel). Trajectories are coloured according to altitude above ground (m), indicated by the colour bar. All trajectories begin at the black star at 12pm PT, and progress for 8 hours. Included are trajectories which have initial altitude 10m, 170m, 330m, 490m and 650m.

Although Hysplit has been used previously to model the trajectories of mountain pine beetles dispersing over long distances [1], trajectories simulated using Hysplit alone have limited utility because mountain pine beetles are not inert particles. Rather, beetles need to fly to maintain aloft: When fat reserves are depleted by the effort of flight, beetles will cease flying [2]. In addition, there are numerous behavioural responses to environmental conditions that likely result in movement patterns that differ significantly from those of inert particles. Thus, modelling long-distance dispersal of mountain pine beetles requires the addition of a level of realism by supplementing the Hysplit model simulation with a second stochastic differential equation model that represents beetle behaviour. This model is described in the following section.

3. Mathematical Model of Beetle Flight

To model the long-distance dispersal of the beetles within a moving parcel of air, we consider the mean beetle density in that parcel of air U_t as a function of time t. The mean beetle density during a flight is primarily affected by fatigue [2] and temperature. The beetles fold their wings and drop when they get tired. This process has been modeled previously as an exponential loss process such that the density of beetles decays over time like a negative exponential function [3]. Mountain pine beetles also require ideal flying conditions. When the temperature drops below their ideal flying temperature they also tend to fold their wings and drop [4]. As the process of beetle dispersal is very close to a drift-diffusion process, we use a Stochastic Differential Equation to model the mean beetle density. Considering all the factors affecting the mean beetle density U_t, we arrive at the following SDE for our model:

$$dU_t = \underbrace{-aU_t dt}_{\text{settling: fatigue}} - \underbrace{b_t U_t dt}_{\text{settling: temperature}} + \underbrace{\sigma_t U_t dW_t}_{\text{volatility}} \tag{3.1}$$

where a and b_t are the settling parameters for fatigue and temperature, σ is the percentage volatility, and W_t is a Wiener process or Brownian motion defined as follows:

Definition 1. *A standard (one-dimensional) Wiener process (also called Brownian motion) is a stochastic process $\{W_t\}_{t\geq 0}$ with the following properties:*

1. $W_0 = 0$.
2. *With probability* 1*, the function $t \mapsto W_t$ is continuous in t.*
3. *The process $\{W_t\}_{t\geq 0}$ has stationary, independent increments.*
4. *The increment $W_{t+s} - W_s$ has the $NORMAL(0, t)$ distribution.*

The fatigue parameter b_t due to temperature is dependent on time as temperatures along a trajectory changes over time.

We do not have enough beetle flight data to estimate b_t numerically. We instead try to write a function that roughly describes the settling due to temperature. First we look at the temperatures at which beetles fold their wings and which temperature is ideal for their flight at which settling rate will be very close to 0. Based on some recent research, the ideal flying temperature for beetles is more or less between $10°C$ and $35°C$. Based on these observations we take the map b_t to be

$$b_t = \begin{cases} c/e & \text{if } T_t \leq 10 \\ ce^{-\frac{1}{1-S_t^2}} & \text{if } 10 < T_t < 35 \\ 0 & \text{if } T_t \geq 35 \end{cases} \tag{3.2}$$

where $S_t = \frac{T_t - 10}{25}$ and T_t is the temperature at time t. The constant c is to be determined. The ideal scenario would be to have some flight data and be able to estimate c. For the purpose of this project we assume c to be 1. The plot of the function b_t with respect to the temperature T_t is shown in Figure 3. Notice that

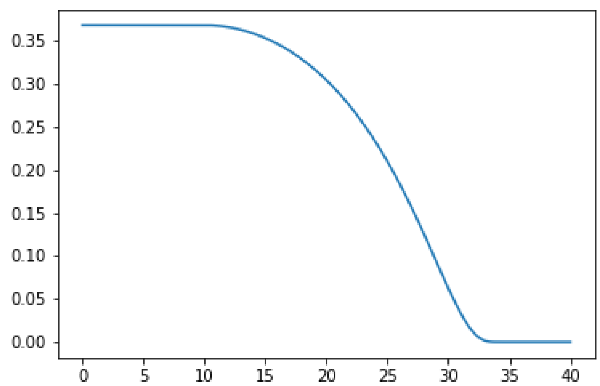

Figure 3. Plot of b_t (/hr) with respect to T_t ($°C$)

we have assumed that beetles don't fold their wings at temperatures above $35°C$. In the context of atmospheric dispersal, it might be a fair assumption because the warmest temperatures are going to be at ground level and beetles can disperse at temperatures of $35°C$. The parameters a and b_t are indicating deterministic trends and the parameter σ is responsible for a set of unpredictable events occurring during the beetle flight.

4. Estimation of Parameters

This section calculates the best value of parameter a representing settling rate due to fatigue. For this purpose, we first assume that beetles settle at a constant rate a. To prove this fact, we use a dataset that contains information about beetles that were flown on flight mills 2 days after they emerged and the total duration and velocity of their flight were measured [2]. To calculate the value of settling rates, we are interested to apply a negative exponential function as:

$$f(t) = \exp(-a * t), \tag{4.1}$$

where t denotes the time. Thus, a simple least squares fit allows us to obtain an estimation of the slope, that is, a. In fact, we are interested minimizing the following equation to obtain the best value for parameter a:

$$\min_a Z = \sum_{i=1}^{n} (e^{(-at_i)} - y_i)^2 \tag{4.2}$$

By taking natural log function, we have:

$$-at_i = \log(e^{(-at_i)}).$$

So, the equation (4.3) can be rewritten as:

$$\min_a Z = \sum_{i=1}^{n} (-at_i - \log(y_i))^2 \tag{4.3}$$

As we know that, the best value for parameter a can be obtained by taking the first derivative of function Z. So we have:

$$Z' = 0 \Rightarrow a = \frac{\sum_{i=1}^{n} t_i \log(t_i)}{\sum_{i=1}^{n} t_i^2} \tag{4.4}$$

Considering (4.4), we can compute settling rate due to fatigue. We used this strategy and obtained the value of parameter a for the dataset and plotted results in Figure 4.

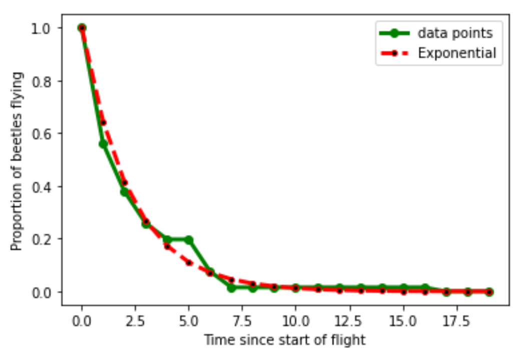

FIGURE 4. The behavior of fitting negative exponential curves

5. Solution of the SDE

We want to find a solution of the Stochastic Differential Equation 3.1 which describes our model for the mean beetle density along a trajectory. The key step towards our solution requires an good understanding of the Itô's lemma. Let us start by stating Itô's lemma.

Lemma 1 (Itô). *For an Itô's drift-diffusion process*

$$dX_t = \mu_t dt + \sigma_t dW_t$$

and any twice differentiable scalar function $f(t,x)$ of two real variables t and x, one has

$$df(t,X_t) = \Big(\frac{\partial f}{\partial t} + \mu_t \frac{\partial f}{\partial X} + \frac{\sigma_t^2}{2}\frac{\partial^2 f}{\partial X^2}\Big)dt + \sigma_t \frac{\partial f}{\partial X} dW_t$$

The SDE we want to solve is very similar to a Geometric Brownian motion. So, we take a similar approach and define

$$Y(t) := \phi(t,U) = \ln(U_t).$$

Then by Itô's lemma

$$dY_t = \Big(\frac{\partial \phi}{\partial t} + \frac{\partial \phi}{\partial U}(-a-b_t)U_t + \frac{1}{2}\frac{\partial^2 \phi}{\partial U^2}\sigma^2 U_t^2\Big)dt + \Big(\frac{\partial \phi}{\partial U}\sigma U_t\Big)dW_t \tag{5.1}$$

which simplifies to

$$dY_t = -(a + b_t + \frac{1}{2}\sigma^2)dt + \sigma dW_t$$

As the right hand side of (5) has no Y_t term, we can compute the stochastic integral:

$$\begin{aligned} Y_t &= Y_0 - \int_0^t (a + \frac{1}{2}\sigma^2)ds - \int_0^t b_s ds + \int_0^t \sigma dW_t \\ &= Y_0 - (a + \frac{1}{2}\sigma^2)t - \int_0^t b_s ds + \sigma W_s \end{aligned}$$

Substituting $Y_t = \ln(U_t)$ we have

$$\ln(U_t) = \ln(U_0) - (a + \frac{1}{2}\sigma^2)t - \int_0^t b_s ds + \sigma W_t$$

$$U_t = U_0 \cdot \exp\Big(-(a + \frac{1}{2}\sigma^2)t - \int_0^t b_s ds + \sigma W_t\Big). \tag{5.2}$$

5.2 describes the mean beetle density over time along a flight trajectory. Although, we have the integral $\int_0^t b_s ds$ in the solution, for our simulation purposes the integral will be interpreted as a Riemann sum as the temperature data along a Hysplit trajectory is discrete, not continuous.

6. Results and Discussion

We simulate the beetle flights along some of the Hysplit trajectories from section 2 using the solution 5.2 of the SDE. We have different Hysplit trajectories on different heights above the ground level. We will run our simulations along the Hysplit trajectories with height 330 meters and 170 meters from ground level. We also have Hysplit data for three different dates on which the average temperature along the beetle flight are different.

Based on preliminary examination of the beetle flight data and prior analyses, a good estimate of the parameter σ is 0.68/hr. In section 4 from our estimates for the parameter a, we see that the ideal value of a lies between 0.2/hr and 0.3/hr. For our first simulation we choose a to be 0.24/hr and run the simulation along the three Hysplit trajectories at 330 meters above the ground level on three different dates. The plots of the mean beetle density with respect to time for our first simulation is described is Figure 5. The key observation from this simulation is that the number of beetles drop faster when the mean air temperature is lower.

We assumed the initial beetle number in an arbitrary parcel of air to be 100. This number is somewhat random. As we are dealing with beetle density we can normalize the y-values to be between 0 and 1. In that way the y-axis can be interpreted as beetle density.

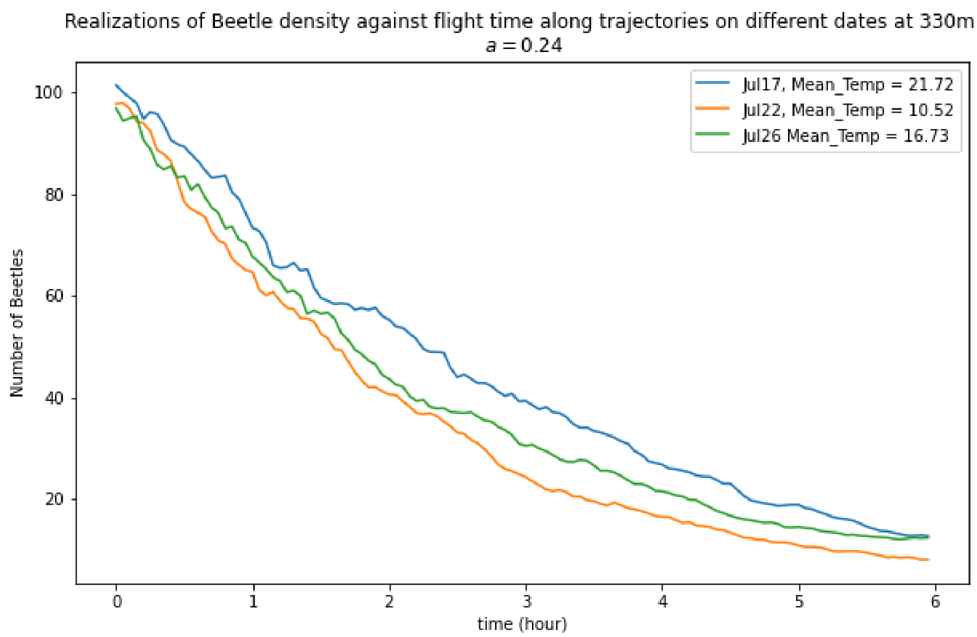

FIGURE 5. Beetle numbers along trajectories on three different dates

For our second simulation we take three different values for a, namely 0.2/hr, 0.24/hr, 0.28/hr and run the simulation along the Hysplit trajectory on Jul 17 at 170 meters above the sea level. We see that the number of beetles drop faster when the value of the settling parameter a is higher, which is expected (see Figure 6).

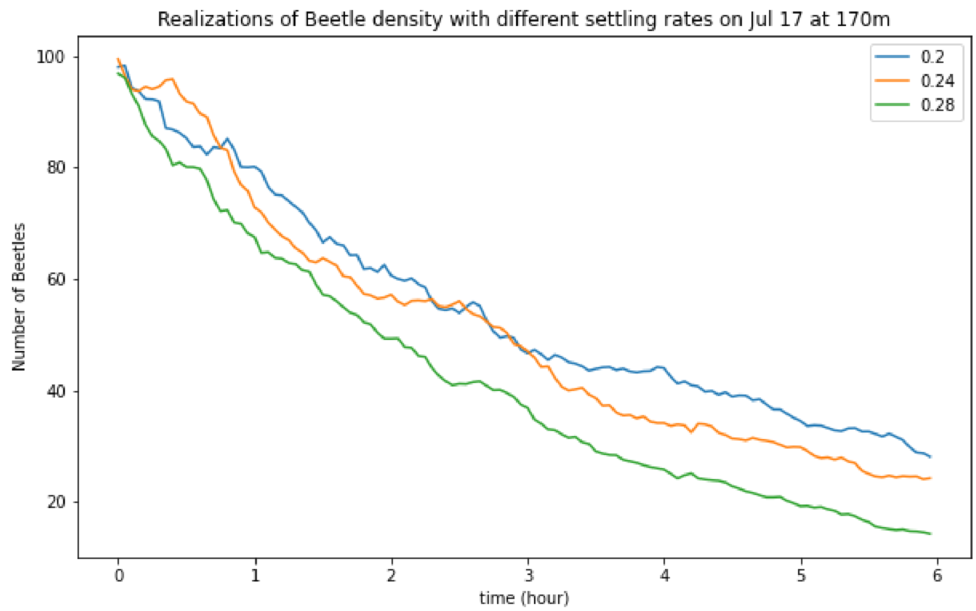

FIGURE 6. Beetle numbers along a trajectory with three different a-values

Acknowledgements

The team would like to thank our industry mentor Devin Goodsman and our academic mentor Julien Arino for their guidance, support, and feedback during the advancement of this project. We are also incredibly thankful to Allen Herman, Kristine Bauer, Ian Allison, and the rest of the PIMS organizing committee and instructors of the M2PI 2021 workshop for providing us this great experience.

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