Identification of Diffusion Coefficient in Nonhomogeneous Landscapes

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Abstract. Diffusion models have been found in various applications in the study of spatial population dynamics for modeling the species dispersal process in natural environments. Diffusion coefficient is a critical parameter in diffusion equations. In this paper, a new method for estimating the diffusion coefficient of insects is presented in terms of occupancy time and the method can produce any desired accuracy.

The study of modeling biological organism movement behaviors in a nonhomogeneous landscape is critical in investigating the interplay between environmental heterogeneity and organism movements. By constructing a set of eigenvalues, we can characterize the insect biased movement when insect crosses the intersection of two different type of landscape elements. Some numerical examples are provided to illustrate the theoretical outcomes obtained in the paper.

Keywords: Diffusion Equation, Probability Density, Edge Behavior, Nonhomogeneous Landscape.

1 Introduction

It is becoming more and more important to develop frameworks for understanding and predicting the effect of habitat alteration on biodiversity (e.g. see [9]). Landscape composition significantly affects the inter patch dispersal and movement patterns of insect (see [6]). It is well-known that the distribution of insects within a host-plant patch is strongly matrix dependent (e.g. see [7]). For instance, the planthopper *Prokelisia crocea* inhabits a complex landscape composed of patches of its host plant cordgrass (*Spartina pectinata*) embedded in a matrix of mudflat, other native grasses, and the introduced grass smooth brome (*Bromus inermis*). Dispersal (diffusion) rates also varied radically between cordgrass and brome vs. mudflat. Local and regional population dynamics of the planthopper are also strongly matrix dependent. Patches of cordgrass surrounded by brome typically have lower and more variable densities and populations that are very extinction prone, relative to patches in mudflat (see [4]).

Diffusion models have been found in various applications in the study of spatial population dynamics for modeling the species dispersal process in natural

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environments. The advantage of diffusion models is that they can be applied to any initial distribution of organisms and have been widely used in empirical insect movement modeling.

The quantity, diffusion coefficient, plays critical role in the diffusion model approach. On a homogeneous landscape, the linear diffusion model is in the form of

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) - c_0 u \tag{1}$$

where u is the density of the organisms which is subjected to boundary conditions and initial conditions, D is called the diffusion coefficient, the parameter c_0 is the disappearance rate of the organisms during experiments. Disappearance can include mortality as well as dispersal not captured by the experiment.

In order to use model (1) to describe insect dispersal dynamics, a key issue is how to estimate the diffusion rate D accurately. In current literature, the diffusion coefficient D is mainly estimated by two ways: (i) a static approach requiring the tedious location of large numbers of individuals at particular time, and then applying the method of maximum likelihood parameter estimation to determine the parameter that maximizes the probability (likelihood) of the sample data (see, e.g., [5], [11],[10], and references therein); (ii) extended observations of the movement patterns of individual organisms and then use the method of maximum likelihood or similar methods employed (e.g. [2] and [15]).

However, both methods mentioned above are required sample data to be covered almost the entire landscape, thus the implementation is mathematically and computationally intense even if this approach is applicable. Moreover measurement noise during data collection might be quite large due to the scale of the measurement.

Fagan proposes a complement of existing methods by measuring the cumulative proportion of initial number of insects across the boundaries at certain time instances, and then employs the maximum likelihood method to estimate D (see [13]). This approach reduces the overall required computational cost comparing to traditional methods, however, the complexity (including the size of samples as well as the computational cost) for applying the maximum likelihood method to the boundaries still remains.

Furthermore, when insect movements across different type of landscape elements are considered, the diffusion model becomes

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_1\left(\frac{\partial^2 u_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial y^2}\right) - c_0 u_1 \quad \text{on} \quad \Omega_1 \\ \frac{\partial u_2}{\partial t} &= D_2\left(\frac{\partial^2 u_2}{\partial x^2} + \frac{\partial^2 u_2}{\partial y^2}\right) - c_0 u_2 \quad \text{on} \quad \Omega_2 \end{aligned} \tag{2}$$

where u_i stands for the insect population density located in Ω_i, respectively. Here for simplicity, we assume the disappearance rates on both Ω_1 and Ω_2 are the same.

In this paper, we develop new methodology for the estimation of the diffusion coefficients by using the mean occupancy time, which usually is not difficult to be measured in field experiments. The concept of occupancy time is first introduced by Ovaskainen (see [11]) in a formal mathematical terminology. It is quite often to observe in various experiments that in a given area, the shorter mean occupancy time the organisms have, the higher diffusion rate is expected. For a given homogeneous area Ω, the mathematical description of the mean occupancy time is given by

$$T_\Omega = \int_\Omega \int_0^\infty u(x, y; t) dt dA \tag{3}$$

where u is the density function of insects under observing. We establish a relationship between T_Ω and D appeared in (1). The first step is to define a homogeneous landscape through which the insects are dispersing and to select a (relatively small comparing with the entire landscape) rectangle located inside this landscape. We then specify that the four edges of the rectangle are absorbing boundaries, since insects away from the rectangle (resided in a large homogeneous landscape) are unlikely to return (see [5] and [13]). An explicit formula $D = f(T_\Omega)$ is obtained for the estimation of D in terms of T_Ω when Ω is set to be rectangular. For the other shapes of landscape, the proposed method is also applicable. The advantage of our proposed approach is essentially one-step method and thus the computational cost is greatly reduced since there is no need to rely on a large set of sample data such as the one used in maximum likelihood method.

This paper is organized as follows. In section 2, we present our main results which provides a formula to estimate the diffusion rate via the mean occupancy time. Technical details are given in section 3 to support the proposed approaches. A summary of experimental procedure, including numerical simulations, is provided in section 4. The paper ends with concluding remarks.

2 Main Results

Estimation of Diffusion Rate D. To model the dispersal of insects by the discrete two-dimensional random walks, it is often assumed in the literature that individuals take random steps towards a direction and each step is independent of the others. By taking the continuum limit of the Taylor expansion with infinitesimal small step length and frequency, the population dynamics can be described by the following two-dimensional diffusion equation:

$$\frac{\partial u}{\partial t} = D(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}) - c_0 u, \ (x, y) \in [0, l] \times [0, m], t > 0, \tag{4}$$

where $u(x, y, t)$ is the insects population density in the location (x, y) at time t, D is the diffusion coefficient, and c_0 denotes the disappearance rate of insects. The boundary of the rectangular domain is set to be absorbing, which implies that insects do not return after leaving the rectangle. This assumption is consistent with many field experiments when the observed area is relatively small comparing to the entire landscape (e.g., [5]). The initial distribution is given by $u(x, y; 0) = f(x, y)$, where f is a given integrable function over the rectangle $[0, l] \times [0, m]$.

Suppose that the mean occupancy time T_Ω is available. Then the diffusion coefficient D can be expressed as

$$D = \frac{4l^2m^2}{\pi^4 T_\Omega} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \frac{A_{i,j}}{ij(i^2m^2 + j^2l^2)}[1 - \cos(\pi i)][1 - \cos(\pi j)], \tag{5}$$

where $A_{i,j}$ is given by

$$A_{i,j} = \int_\Omega f(x, y) \sin(\frac{\pi i x}{l}) \sin(\frac{\pi j y}{m}) dA. \tag{6}$$

If an individual is released at $(x_0, y_0) \in (0, l) \times (0, m)$, then the diffusion coefficient D is given by

$$D = \frac{4l^2m^2}{\pi^4 T_\Omega} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \frac{1}{ij(i^2m^2 + j^2l^2)} \sin(\frac{\pi i}{l}x_0) \sin(\frac{\pi j}{m}y_0)[1-\cos(\pi i)][1-\cos(\pi j)]. \tag{7}$$

The summation of the first 25 terms is given

$$D \approx \frac{4l^2m^2}{\pi^4 T_\Omega} \sum_{i=1}^{5}\sum_{j=1}^{5} \frac{1}{ij(i^2m^2 + j^2l^2)} \sin(\frac{\pi i}{l}x_0) \sin(\frac{\pi j}{m}y_0)[1-\cos(\pi i)][1-\cos(\pi j)], \tag{8}$$

which offers a quite accurate approximation according to our numerical simulations.

Table 1. Estimations of diffusion rate D by using formula (8) for different releasing points and mean occupancy times

Released point	(40,55)	(40,55)	(55,55)	(55,55)	(40,70)	(40,70)
Mean occupancy time T_Ω	0.2540	0.7200	0.2540	0.7200	0.2540	0.7200
Diffusion rate D	0.3898	0.1375	0.4640	0.1637	0.3553	0.1253

If we set the rectangular area to be $[0, 110] \times [0, 110]$ and the releasing point at the center $(55, 55)$, then the estimation formula (8) gives

$$D \approx \frac{8.9789 \times 10^2}{T_\Omega}.$$

Notice $l = m = 110$, the error is given by

$$\frac{4l^2m^2}{\pi^4 T_\Omega} \sum_{i=6}^{\infty}\sum_{j=6}^{\infty} \frac{1}{ij(i^2m^2 + j^2l^2)} \sin(\frac{\pi i}{l}x_0) \sin(\frac{\pi j}{m}y_0)[1 - \cos(\pi i)][1 - \cos(\pi j)].$$

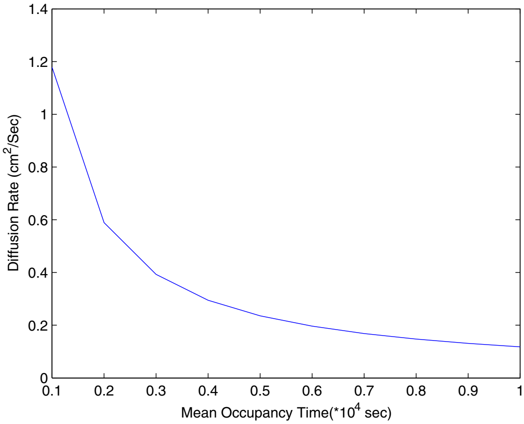

Fig. 1. Diffusion Rates Estimation with Centered Point Release at $(55, 55)$

Clearly the mean occupancy time is negatively associated with the diffusion rate (see Fig. 1), which is consistent with the intuition. We also calculated a few diffusion rates D for different releasing points and mean occupancy times T_Ω (see Table 1). The mean occupancy time T_Ω in the Table 1 is the total seconds of an individual remained inside of $[0, 110] \times [0, 110]$. For convenience, $T_\Omega = 0.7200$ in Table 1 stands for 0.7200×10^4 seconds, which approximately equals to 120 minutes. Without further specification, all time appeared in this paper use the same scale.

3 Technical Approach

When insects can be followed during field experiments, mark-recapture study provides a wealth of information about their movements. For example, an individual can be tracked (or observed) in a given area and then the duration time before leaving the area can be recorded. This quantity can be characterized as occupancy time, which is an important quantity for insect's duration in the domain Ω. As expected, short mean occupancy time T_Ω implies high diffusion rate, while long mean occupancy time yields low diffusion dynamics (see Fig. 1).

We consider the diffusion equation (4) on a rectangular homogeneous landscape subject to Dirichlet boundary condition:

$$\begin{aligned}
\frac{\partial u}{\partial t} &= D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) - c_0 u, \ (x, y) \in \Omega = [0, l] \times [0, m], t > 0, \\
u(0, y, t) &= u(l, y, t) = u(x, 0, t) = u(x, m, t) = 0, \\
u(x, y, 0) &= f(x, y), \quad (x_0, y_0) \in \Omega = [0, l] \times [0, m],
\end{aligned} \tag{9}$$

where $f = f(x, y)$ is a given integrable function on Ω. By using method of separation of variables, one can obtain the general solution to the diffusion equation in terms of a double Fourier series

$$u(x,y,t) = \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} A_{i,j} \sin(\frac{\pi i x}{l}) \sin(\frac{\pi j y}{m}) e^{\{-D[(\frac{\pi i}{l})^2+(\frac{\pi j}{m})^2+\frac{c_0}{D}]t\}}, \tag{10}$$

where the numbers $A_{i,j}$ are constants to be determined. Applying the initial condition in (9), we have

$$u(x,y,0) = \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} A_{i,j} \sin(\frac{\pi i x}{l}) \sin(\frac{\pi j y}{m}) = f(x,y), \tag{11}$$

and thus the coefficient $A_{i,j}$ is given by

$$A_{i,j} = \int_{\Omega} f(x,y) \sin(\frac{\pi i x}{l}) \sin(\frac{\pi j y}{m}) dA. \tag{12}$$

Thus, the occupancy time T_Ω can be obtained by

$$T_\Omega = \int_0^m \int_0^l \int_0^\infty u(x,y,t) dtdxdy \tag{13}$$

$$= \frac{4l^2m^2}{D\pi^2} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \frac{A_{i,j}}{D\pi^2 ij(i^2m^2+j^2l^2)+c_0l^2m^2}[1-\cos(i\pi)][1-\cos(j\pi)]. \tag{14}$$

If the initial distribution is a point release, i.e., $f(x,y) = M\delta(x-x_0, y-y_0)$ (where M represents the amount of insects and (x_0, y_0) is the release location), then the solution of (9) is given by

$$u(x,y,t) = \frac{4M}{lm} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \sin(\frac{\pi i x_0}{l}) \sin(\frac{\pi j y_0}{m}) \sin(\frac{\pi i x}{l}) \sin(\frac{\pi j y}{m}) e^{\{-D[(\frac{\pi i}{l})^2+(\frac{\pi j}{m})^2+\frac{c_0}{D}]t\}}, \tag{15}$$

and the occupancy time is

$$\begin{aligned} T_\Omega &= \int_0^m \int_0^l \int_0^\infty u(x,y,t) dtdxdy \\ &= \frac{4l^2m^2M}{D\pi^4} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \frac{(1-\cos(i\pi))(1-\cos(j\pi))}{D\pi^2 ij(i^2m^2+j^2l^2)+c_0l^2m^2} \sin(\frac{\pi i x_0}{l}) \sin(\frac{\pi j y_0}{m}). \end{aligned}$$

Hence the diffusion rate D can be expressed as

$$D = \frac{4l^2m^2M}{\pi^4 T_\Omega} \sum_{i=1}^{\infty}\sum_{j=1}^{\infty} \frac{(1-\cos(i\pi))(1-\cos(j\pi))}{ij(i^2m^2+j^2l^2)} \sin(\frac{\pi i x_0}{l}) \sin(\frac{\pi j y_0}{m}). \tag{16}$$

when the disappearance rate c_0 is assumed to be zero.

It is worthy to making a comment here. Although the technical approach is straightforward, the result contains two important implications: (i) the idea based on occupancy time is a natural approach in field studies and the calculation for D is simple; (ii) this method leads to the possibility for estimating the returning probabilities across different type of landscape elements, as shown below.

4 Summary and Illustration of Simulations

In this paper we consider a homogeneous rectangular area resided in the same type of landscape, denoted as $\Omega = [0, \ell] \times [0, s]$. Then we measure the occupancy time for a set of insects in Ω, provided that the initial distribution $f = f(x, y)$ is known. The diffusion coefficient D then can be estimated by

$$D = \frac{4\ell^2 s^2}{\pi^4 T_\Omega} \sum_{i=1}^{\infty} \sum_{j=1}^{\infty} \frac{A_{i,j}}{ij(i^2 s^2 + j^2 \ell^2)} [1 - \cos(\pi i)][1 - \cos(\pi j)], \tag{17}$$

where $A_{i,j}$ is given by

$$A_{i,j} = \int_\Omega f(x, y) \sin(\frac{\pi i x}{\ell}) \sin(\frac{\pi j y}{s}) dA. \tag{18}$$

If the first N^2 summation is used, then

$$D \approx \frac{4\ell^2 s^2}{\pi^4 T_\Omega} \sum_{i=1}^{N} \sum_{j=1}^{N} \frac{A_{i,j}}{ij(i^2 s^2 + j^2 \ell^2)} [1 - \cos(\pi i)][1 - \cos(\pi j)], \tag{19}$$

and the error is given by

$$\text{Error} = \frac{4\ell^2 s^2}{\pi^4 T_\Omega} \sum_{i=N+1}^{\infty} \sum_{j=N+1}^{\infty} \frac{A_{i,j}}{ij(i^2 s^2 + j^2 \ell^2)} [1 - \cos(\pi i)][1 - \cos(\pi j)]. \tag{20}$$

Obviously, the error approaches to zero as $N \to \infty$.

If M individuals are released at $(x_0, y_0) \in (0, \ell) \times (0, s)$, then the diffusion coefficient D is given by

$$D = \frac{4\ell^2 s^2 M}{\pi^4 T_\Omega} \sum_{i=1}^{\infty} \sum_{j=1}^{\infty} \frac{1}{ij(i^2 s^2 + j^2 \ell^2)} \sin(\frac{\pi i}{\ell} x_0) \sin(\frac{\pi j}{s} y_0)[1 - \cos(\pi i)][1 - \cos(\pi j)]. \tag{21}$$

5 Concluding Remarks

The estimation of diffusion coefficient in the nonhomogeneous landscapes is critical in describing the dynamical behaviors of biological organism. Different from current literature, in this paper, we provide a simple, new method to estimate the diffusion coefficient by the insect occupancy time without making use of the maximum likelihood method. This method can achieve any desired accuracy. The proposed approaches in this paper are readily implemented once the occupancy time is available in the field studies. Furthermore, a methodology for estimating the returning probability by the occupancy time was developed by constructing a set of eigenvalues which can capture the biased movement along the intersection of two different type of habitats in the nonhomogeneous landscapes. However, the method is not included here.

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