

Gene Flow Modelling by Correlated Random Walk

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Abstract

Correlated random walk (CRW) models are a model of animal movement [10] and have been successfully used to explore the movement of animals in varying ecological contexts [1]. An agent-based model (ABM) is developed to describe pollen-mediated gene flow under a correlated random walk (CRW). This model is used to explore how insect dispersal processes influence the movement of pollen pollen distribution are affected by the varying turning angle and plant density.

1 Introduction

Pollination is a critical component of every ecosystem, is essential to creating and maintaining diversity and reproduction, and is required for world crop production [12]. There are two main vectors for pollen movement; passive pollination where individual grains are dispersed through the aid of wind and/or water and active pollination where an animal (most commonly an insect). Given the size of individual pollen grains, direct monitoring of how pollen is dispersed across the landscape is impractical. Several indirect approaches have been developed including the use of pollen traps and the application of genetic paternity approaches applied to successfully pollinated seeds [2, 15]. While these approaches are able to quantify the end result of the dispersal process, they provide no information on the specifics of the precise transport mechanism, which is critical because different features of the landscape have variable permeability to pollen movement [6, 5]. In this study, a model is created to simulate animal-mediated dispersion of pollen between plants. These models are used to examine the consequences of movement assumptions and their interactions with variation in plant density.

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Pollen dispersal studies, for both abiotic and biotic pollen dispersal, have assumed that the dispersal process is one of random diffusion. While this may be a good assumption for passively pollinated species, there is little evidence that animals randomly diffuse across the landscape during pollination [13]. In fact, there are several examples of animal pollinators exhibiting via *trap line* behavior [14, e.g., repeated sequential visits to individual plants]. Even for pollinator species that do not trapline, their movement patterns do not resemble pure diffusion [4]. One approach being applied to describe animal movement is through the use of correlated random walk (CRW). In these models, directionality is not random but directionality and distance are based on the distribution derived from the movement at the previous time step. Models based upon CRW can have been applied to a wide range of animal movement processes across varying ecological contexts [1, 3], using deterministic diffusion [11], and fractional Brownian motion [7] approaches.

In this paper, an agent-based model (ABM) describing pollen movement via animals as a correlated random walk (CRW) is introduced. This model consist of agents that interact with each other using pre-defined rule sets as they explore their environment. Agent based models allow for simulations that consist of a large number of interacting parts that would not be easily constructed otherwise [8]. Agents can represent things such as people, animals, organizations, etc. that interact with each other and their environment. The environment in an ABM can represent things such as a spatial domain, or a network in which the agents are connected to each other [9]. Using ABMs, the efficacy of CRW apporaches was examined in a system approximating plant-pollinator interactions using computer simulations. Two statistics describing pollinator movement (*average path distance* and *average maximum distance*) were collected and parameters relevant to the plant reproduction (*average pollination distance*, *average maximum pollination distance*, and *average weighted diversity of fathers*) are collected and analyzed to describe how assumptions about agant movement infleunce plant pollination dynamics.

It is shown that bias can be introduced by describing animal movement as a purely random walk. That is, there is a significant difference between the model outcomes for a purely random walk as compared to a CRW. Thus, modeling animal mediated pollen dispersal by way of a purely random diffusion process is likely to result in errors in the approximation of the extent of pollen dispersal.

2 Methods

In this study, an agent-based model simulates the pollination of plants in a forest. The model assumes continuous space and consists of two interacting agents; *pollinators* and *plants*. We consider different plant densities to determine what effect density has on the distribution of pollen. The plants have a limited supply of pollen that can be gathered by pollinators. Pollinators in turn transport pollen across the landscape using particular movement rules during normal foraging. In this model, movement is determined by a corrolated random walk.

At each step, pollinators examine the local neighborhood for plants where they will collect additional pollen and deposit pollen.

2.1 Movement

Movement in the model is centered on the pollinators. Pollen is carried from one plant to another. At each step the movement of a pollinator is conducted in two stages: *searching* and *movement*. First, the pollinator checks a neighborhood of radius r to see if there are any plants within the neighborhood. If there are one or more plants, the pollinator chooses the closest. If there are two or more that are equidistant from the pollinator, one is randomly chosen.

If there are no plants within a distance r from the current location of the pollinator, the pollinators movement is defined using a correlated random walk. For the correlated random walk, the pollinator chooses a direction based on a probability distribution in which the higher probabilities are centered about the their current direction, see Figure 1. The pollinator then takes a step of length between 0 and 1 distributed uniformly in the new chosen direction. This length is denoted by $s_j^{(i)}$, which is the j^{th} -step taken by the i^{th} pollinator.

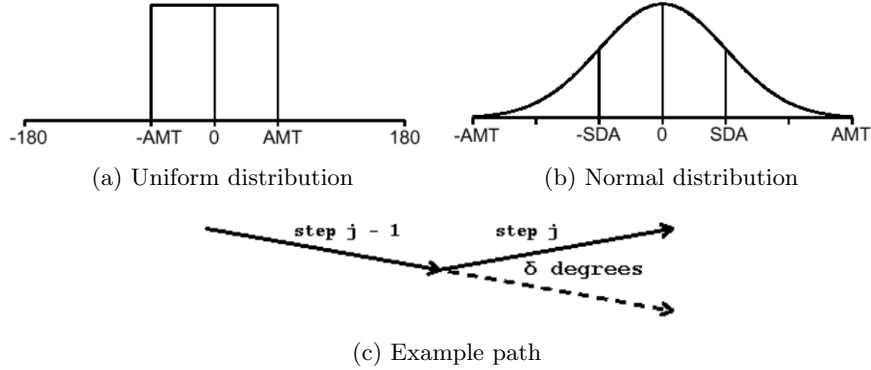


Figure 1: Turning Angle for 1a uniform distribution, 1b normal distribution, and 1c depiction of what a path may look like.

Alternatively, if the pollinator is already at a plant, the pollinator picks a random direction uniformly and takes a step of size $r + 1.0$. This will ensure that the pollinator will not immediately return to the same plant on the very next step.

2.2 Pollination

When an pollinator is on a plant, it collects pollen, distributes pollen, and consumes food. Each simulated plant contains a number of flowers, ϕ , from which an pollinator may obtain pollen. When an pollinator visits a plant it

picks up pollen from one or more flowers. The number of flowers from which an pollinator can obtain pollen is determined by the total number of flowers on a plant, the fraction of flowers in bloom at any one time (a), the number of times (j) the plant has previously been visited by an pollinator, and the maximum fraction of flowers available for pollination (η). The formula for the number of total flowers available for visitation during a k^{th} visit to the j^{th} plant ($f_{j,k}$) is given by

$$f_{j,k} = \phi \cdot a \cdot \eta^k. \quad (1)$$

It is assumed that the amount of food eaten and the amount of pollen collected is proportional to the number of visited flowers. An pollinator collects pollen and eats from every flower that it visits, and so the amount of pollen collected and the amount of food eaten is proportional to the equation (1). Let $f_{j,k}^{(i)}$ be the number of flowers visited by the i^{th} pollinator during the k^{th} visit to the j^{th} plant then the amount of pollen/nectar in the i^{th} pollinator's stomach after m plant visits is given by

$$c_m^{(i)} = \sum_{j=0}^m \beta f_{j,k}^{(i)}, \quad (2)$$

where β is the proportionality constant for the amount of pollen collected at a plant. Each pollinator has a maximum amount of food they will ingest, c_{max} , at which time they will stop search for food and return to their lair.

The fraction, α , of all flowers are pollinated, and the associated probability that a flower is pollinated, ρ , are related by the equation,

$$\alpha = \rho \cdot \hat{f}_k. \quad (3)$$

Using equation (2) and (3) we can determine the probability that a flower is pollinated, ρ , by the formula

$$\rho = \frac{\alpha}{\phi} \cdot \frac{1 - \eta}{a \cdot \eta}.$$

When a flower is pollinated it must determined which previous plant donated the pollen. Each flower visited is recorded and is available to pollinate the current flower, except those flowers that are on the same plant. Self-pollination, is not considered, because the likelihood of self-pollination is low due to mechanisms that impedes self-pollination. Each flower considered has an equal likelihood of pollinating the current flower.

2.3 Time and Stopping Criteria

The velocity an pollinator travels (v) is assumed to be constant, as well as the time spent on a plant (t_{plant}). The travel time for an pollinator is then given by the formula

$$t^{(i)} = \frac{s^{(i)}}{v} + T^{(i)} \cdot t_{plant},$$

where $T^{(i)}$ is the number of plants visited by the i^{th} pollinator. If we let the maximum allowable travel time be t_{max} , then once $t^{(i)} \geq t_{max}$ or $c_m^{(i)} \geq c_{max}$ the pollinator is removed from the simulation. t_{max} is based on the optimal searching time during the day. When the pollinator leaves the simulation, it is terminated.

2.4 Model Statistics

To best explore the inherent differences between biotic and abiotic pollination this study focuses on the effects of movement as well as the effects of plant density.

Measure	Equation
Average Path Distance	$\bar{s} = \frac{1}{b} \sum_{i=1}^b \sum_{j=1}^n s_j^{(i)}$
Average Maximum Distance	$\bar{M} = \frac{1}{b} \sum_{i=1}^b \max_j \sqrt{(x_{1,0}^{(i)} - x_{1,j}^{(i)})^2 + (x_{2,0}^{(i)} - x_{2,j}^{(i)})^2}$
Average Pollination Distance	$\bar{p} = \frac{1}{n} \sum_{i=1}^n \left(\frac{1}{\tau^{(i)}} \sum_{j=1}^{\tau^{(i)}} \sqrt{(x_1^{(i)} - x_1^{(j)})^2 + (x_2^{(i)} - x_2^{(j)})^2} \right)$
Average Maximum Pollination Distance	$\bar{P} = \frac{1}{n} \sum_{i=1}^n \max_j \sqrt{(x_1^{(i)} - x_1^{(j)})^2 + (x_2^{(i)} - x_2^{(j)})^2}$
Average Weighted Diversity of Fathers	$E = \frac{1}{n} \sum_{i=1}^n 1 / \left(\frac{1}{\tau^{(i)}} \sum_{j=1}^{\tau^{(i)}} F_{j,i}^2 \right)$

Table 1: Equations

In order to quantify these way in which the parameters influence the pollination in this system, we recorded *Average Path Distance* and *Average Maximum Distance* based upon pollinators directly and *Average Pollination Distance*, *Average Maximum Pollination Distance*, and *Average Weighted Diversity of Fathers* based upon the set of pollen that was deposited at individual plants. The calculations of these statistics are given in the Table 1.

In these equations it is assumed that b is the number of pollinators, n is the total number of plants, $(x_{1,0}^{(i)}, x_{2,0}^{(i)})$ is the starting location of the i^{th} pollinator, $(x_{1,j}^{(i)}, x_{2,j}^{(i)})$ is the location of the i^{th} pollinator after j steps, $\tau^{(i)}$ is the total number of seeds for the i^{th} plant, $\Delta\tau^{(i)}$ is the number of different fathers contributing pollen to the i^{th} plant, and $F_{j,i}$ is the number of times the j^{th} father contributed pollen to the i^{th} plant.

Parameter Description	Symbol	Value	
Total number of animals	b	1,000	fixed
Maximum time	t_{max}	1,200 seconds	fixed
Fraction of blooms at one time	a	0.2	fixed
Maximum fraction of available flowers	η	0.75	fixed
Search radius	r	1.0	fixed
Number of flowers per plant	ϕ	100	fixed
Probability of pollination	ρ	0.4286	calculated
Number of plants	n	1000	fixed
Time spent at each plant	t_{plant}	100 seconds	fixed

Table 2: Parameter Values

3 Results

The following results are based on simulations of the model with parameter values given in Table 2. The grid size was 101 patches by 101 patches.

The standard error was calculated by dividing the sample standard deviation by the square root of the total number of samples. The standard errors were all less than 1% on average, so will not be shown due to the small size.

Determining the distance animals travel during a foraging trip is important factor for their survivability. In order for an animal to survive it must find enough food foraging without losing too much energy. In this study the density of plants is varied, which can directly affect the amount of foraging the animals will be able to achieve in a set amount of time. The higher the density the greater the potential for the animal to forage. The maximum angle is also varied. The relationship of this angle with respect to foraging is a more complicated one. In terms of foraging, a very small maximum turning angle may not result in successful foraging due to the paths are too linear. On the other hand, a maximum turning angle which is too large can result in searching patterns that repetitively cover the same area over and over again.

In Figure 2 the average distance traveled for each animal decreases with increasing density due to higher foraging success. In this situation the animals will spend more time on plants since they can find plants more readily. The maximum turning angle does not have a large effect on the distance. There is a modest effect of maximum turning angle on low plant density where the larger the angle increases the average distance due to less success of foraging.

The average maximum distance traveled by animals, see Figure 3, is affected by both the turning angle and plant density. As with the average path distance, the maximum distance decreases with higher density which decreases the overall travel time for the animals. Though in this case due to the movement patterns the angle has a large effect on maximum distance especially at lower densities. As the maximum angle decreases the animals are more likely to travel directly away from their starting points increasing the maximum distance traveled.

For a plant density of 0.01 and $AMT = 0^\circ$ the average maximum distance

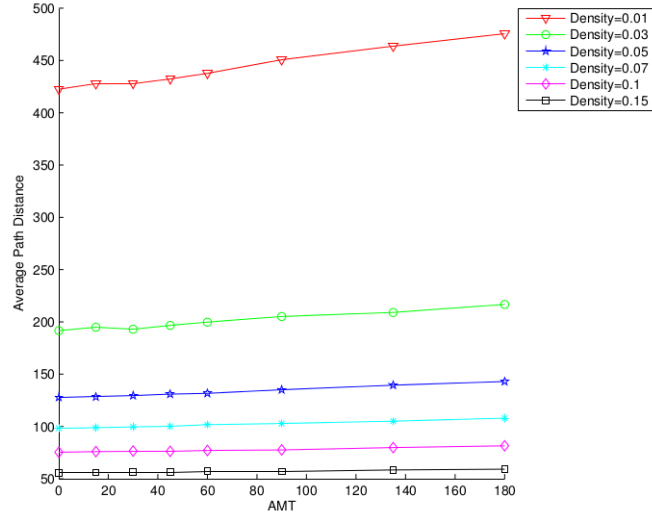


Figure 2: Average Path Distance vs. Turning Angle for Various Plant Densities

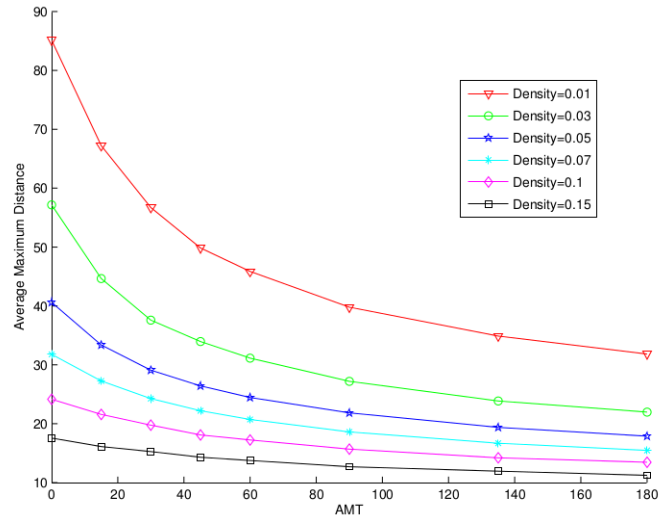


Figure 3: Average Maximum Distance vs. Turning Angle for Various Plant Densities

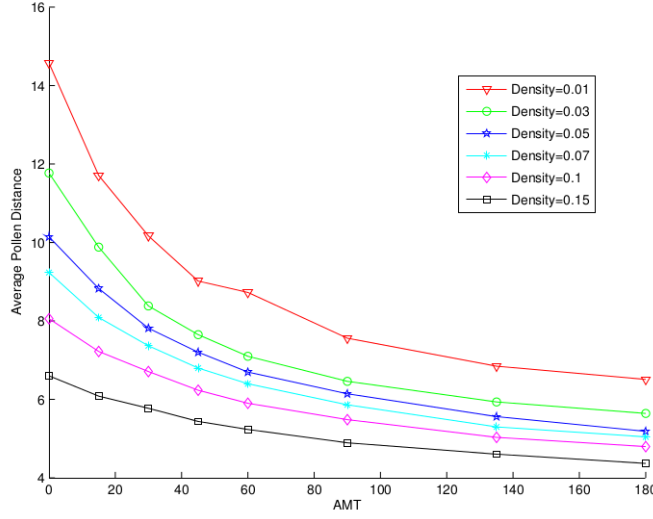


Figure 4: Average Pollination Distance vs. Turning Angle for Various Plant Densities

is quadruple of the average maximum distance for a plant density of 0.01 and $AMT = 180^\circ$. For a higher plant density of 0.15 the average maximum distance is 50% larger. Thus, a purely random diffusion process results in shorter average maximum distances as compared to smaller turning angles, and as was seen with the average pollination distance the effect of turning angle is more pronounced for smaller plant densities. Again, this is expected since for higher plant densities the animal direction is reset more often and therefore the animal path becomes more and more like a purely random walk.

The average pollination distance, see Figure 4, decreases with increasing density due to the greater likelihood of pollinating nearby trees. As with the average maximum distance, as the maximum angle decreases the animal is likely to travel farther from its initial position which allows for longer pollination distances.

For a plant density of 0.01 and $AMT = 0^\circ$ the average maximum pollination distance is approximately triple of that for the same plant density and $AMT = 180^\circ$. Additionally, for plant density of 0.15 and $AMT = 0^\circ$ the average pollination distance is approximately double of the average pollination distance for the same density and $AMT = 180^\circ$. Clearly, the average pollination distance for wind dispersal is less than that of an average pollination distance for an animal that follows a straighter path for any of the simulated plant densities.

The average maximum pollination distance has a much more complicated relationship with density and maximum turning angle, see Figure 5. The average maximum pollination distance decreases as maximum turning angle increases from 0° to 180° across all densities. This is due to animals covering a shorter

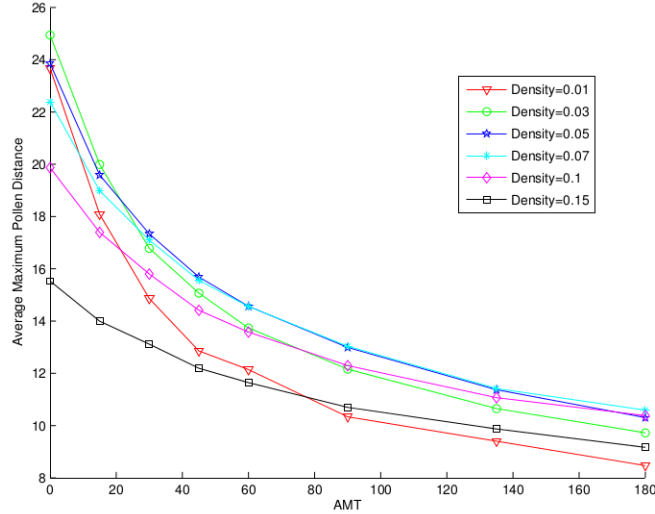


Figure 5: Average Maximum Pollination Distance vs. Turning Angle for Various Plant Densities

distance for higher turning angles, and therefore the plants that are visited will be closer together on average.

Additionally, we see that the resultant average maximum pollination distance for a purely random diffusion process is marketably lower than those for correlated random walks resulting in straighter animal paths. Thus, wind dispersal will result in an average maximum pollination distance that is less than the average maximum pollination distance for a correlated random walk. Thus, one might expect that wind dispersal of pollen results in a smaller areal extent of gene flow as compared to animal mediated gene flow.

The density affects the maximum pollination distance in a more complex fashion. The higher the density the more gradual the decrease is in the maximum pollination distance as the maximum turning angle increases. Whereas for lower densities this decrease is much larger. This is likely due to the fact that at lower densities pollination occurs less frequently with a larger variability of maximum pollination distances.

In general there is a small decrease in the average weighted diversity of fathers as the maximum turning angle increases, see Figure 6. With higher maximum turning angles the search patterns tend to be more circular lowering the overall diversity that a plant will see. On the other hand, by increasing the density, plants will see an increase in diversity due to the larger amount of plants near by. This increase is lessens at higher densities due to the limited foraging time of the pollinators.

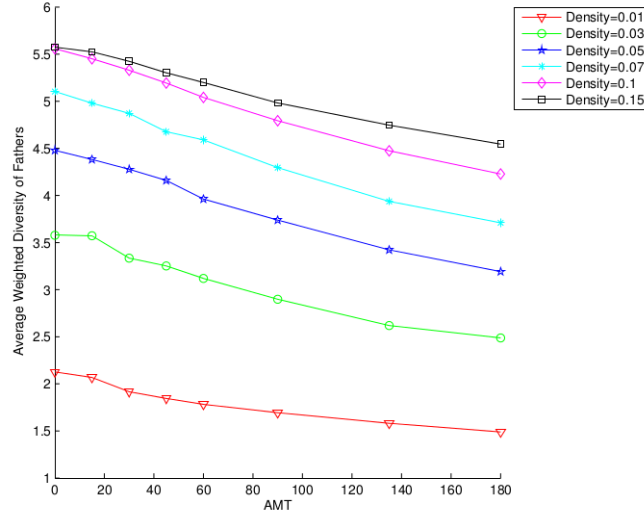


Figure 6: Average Weighted Diversity of Fathers vs. Turning Angle for Various Plant Densities

4 Discussion

I'm not quite sure how math discussion sections work typically. In Biology we tend to bloat a lot here putting things into context and figuring out why this is a valuable thing to be added to the literature. However, I think that may not be the approach you are trying to do. As a consequence, I just minimally edited this section after reworking the first paragraph a bit.

Each factor that influences the behavior of pollinators may thus have large effects on the spatial distribution of pollination. Because plants rely upon pollinators for reproduction, the way in which these animals move across the landscape may have significant impacts on plant population structure and diversity. Reductions in the distance of pollination events or the size of the potential population contributing pollen can have significant impacts including inbreeding, loss of genetic diversity, and local extinction. As such, understanding which parameters are most influential in models that accurately describe pollination becomes a critical tool for both conservation and management policies. Adopting a simulation approach, as presented here, provides a powerful method for studying pollination given the logistical difficulties associated with direct field monitoring. By far, the most striking result of these model is the extent to which deviations from random diffusion impact pollination distances and the consequences for paternity in the plant populations.

The majority of models studying pollination have assumed a purely random diffusion process. There is clear evidence that there are differences in statistics

seen between plants pollinated through wind dispersal from those pollinated through animal dispersal [13]. It is demonstrated here through an agent based correlated random walk that if an animal is not moving in a purely random fashion, then important pollination statistics can be dramatically affected.

As can be seen in the results section the magnitude of turning angle had varying degrees of effects over different plant densities and therefore pollination patterns predicted by a model assuming a purely random walk could be vastly different from a model assuming a correlated random walk. For high plant densities, the effects of correlated random walk was less pronounced than that of low plant densities, except for the *average weighted diversity of fathers*. In the case of *average weighted diversity of fathers* the affect of turning angle magnitudes were more pronounced for high densities. Therefore, although diffusion models for densely populated plant species may not vary greatly from models that assume a correlated random walk for *average pollination distance* or *average maximum pollination distance* they will vary significantly for *average weighted diversity of fathers*. This has the affect of under estimating the diversity of pollination for high plant densities and animal dispersal as compared to similar plant densities and wind dispersal.

The variation between correlated random walk and that of a purely random walk is significant at low plant densities for the statistics such as *average maximum distance*, *average pollination distance*, and *average maximum pollination distance* and so for the case of low plant densities the assumption of a purely random walk may lend to bias in the analysis of pollination. Most studies to date have been conducted on small herbaceous plant species whose densities tend to be high. Even though most of the animals statistics presented were not greatly influenced by turning angle for high plant densities the average weighted diversity of fathers was still greatly affected by the turning angle at these densities, and therefore an assumption of a purely random walk would be an inappropriate assumption and at any of the densities examined in this study. Therefore a correlated random walk may be a better approximation to animal movement.

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