

GENE FLOW MODEL IN A FOREST FOR DOGWOOD

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ABSTRACT. The understanding of gene movement in plant species is critical to the management of both plant and animal species reliant on that plant. Pollen is the mechanism by which plants pass their genetic material from one generation to the next. Pollen dispersal studies have focused primarily on purely random diffusion processes, while this may be a good assumption for species pollinated mainly by abiotic means, such as wind, it is most likely an over simplification for species that are pollinated by biotic means, such as insects [?].

Correlated random walk (CRW) models are a model of animal movement [?] and have been successfully used to explore the movement of animals in varying ecological contexts [?]. An agent-based model (ABM) is developed to describe pollen movement via insects as a correlated random walk (CRW). This model is used to explore how insect path lengths and pollen distribution are affected by the varying turning angle and plant density.

1. Introduction

Pollen is the mechanism by which plants pass their genetic material from one plant to the another. Two modes of transporting pollen, from one plant to another, include abiotic (wind dispersal) and biotic (animal dispersal). Understanding the methods by which pollen spreads across the landscape is important for management of both plant and animal species. Understanding the pollination process may allow for optimization of the number of pollinators used for crop pollination, thereby reducing cost to farmers. Additionally, a better understanding of the pollination process can lead to the prevention of cross pollination of genetically modified plant species and non-genetically modified plant species.

Pollen dispersal studies, for both abiotic and biotic pollen dispersal, have focused primarily on purely random diffusion processes, while this may be a good assumption for species pollinated by wind, it is most likely an over simplification for species that are pollinated by animals [?]. A purely random diffusion process in two dimensions accurately predicts pollen dispersal at a particular time, but only for a purely random walk [?].

Pollen movement via biotic means may not be a purely random process and therefore would not diffuse in a purely random fashion. In fact, there are several examples of pollinating animals that exhibit *trap line* behavior [?]. That is, they follow a particular route as they collect pollen. Thus the movement of animals as they carry pollen may follow more direct paths and therefore would not result in a purely random diffusion process [?]. Such behaviors result in dispersal that does not mimic a purely random walk. The movement of animals can be described as a correlated random walk (CRW), where the correlation is based on the distribution and magnitude of random turning angles. In this way the previous direction of travel influences the direction of travel for the next step.

A purely random walk can be used to model a purely random diffusion process such as Brownian motion [?]. While a CRW can be used as a general model of animal movement [?] and have been successfully used to explore the movement of animals in varying ecological contexts [?]. CRW models have been used to model the dispersal of bark beetles, Coleoptera: Scolytidae [?], deterministic diffusion [?], and fractional Brownian motion [?].

An agent-based model (ABM) describing pollen movement via animals as a correlated random walk (CRW) is introduced. ABMs consist of agents that interact with each other and their environment. ABMs allow for simulations that consist of a large number of interacting parts that would not be easily constructed otherwise [?]. 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 [?]. ABMs have been used in modeling racial segregation, supply chain dynamics, and neural networks [?].

Consequences of the CRW and the interaction of animals with plants is examined using computer simulations. Two animal statistics (*average path distance* and *average maximum distance*) and three plant statistics (*average pollination distance*, *average maximum pollination distance*, and *average*

Received by the editors March 17, 2012.

Key words and phrases. linear operator, invariant subspace, transitive algebra.

This work was completed with the support of NSF..

weighted diversity of fathers) are presented. Turning angle and plant density are varied and their effects on animals paths and pollen distribution are examined.

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

An agent-based model simulates the pollination of trees in a forest. The model assumes continuous space and consists of two interacting agents; *animals* 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 gathered by animals. Animals transport the pollen across the environment to deliver the pollen to other plants. The animals movement is determined by a correlated random walk. At each step of their movement they search 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 animals. The plants do not move and the pollen is carried by the animals. At each step the movement of animals is conducted in two stages: *searching* and *movement*. First the animal checks the a neighborhood of radius r to see if there are any trees within the neighborhood. If there is one or more trees then the animal chooses the closest tree. If there are two or more trees equidistant from the animals current location then one of those trees are chosen randomly. The animal then moves to the location of the chosen tree.

If there are no trees within a distance r from the current location of the animal, the animal then moves according to a correlated random walk. At each step the animal chooses a direction based on a probability distribution in which the higher probabilities are centered around the current direction, see Figure 2.1. The animal then takes a step of length between 0 and 1 distributed uniformly. This length is denoted by $s_j^{(i)}$ which is the j^{th} -step taken by the i^{th} animal.

Alternatively, if the animal is already at a plant then the animal picks a random direction uniformly and then takes a step of size $r + 0.1$. This will ensure that the animal will not immediately return to the same plant on the very next step.

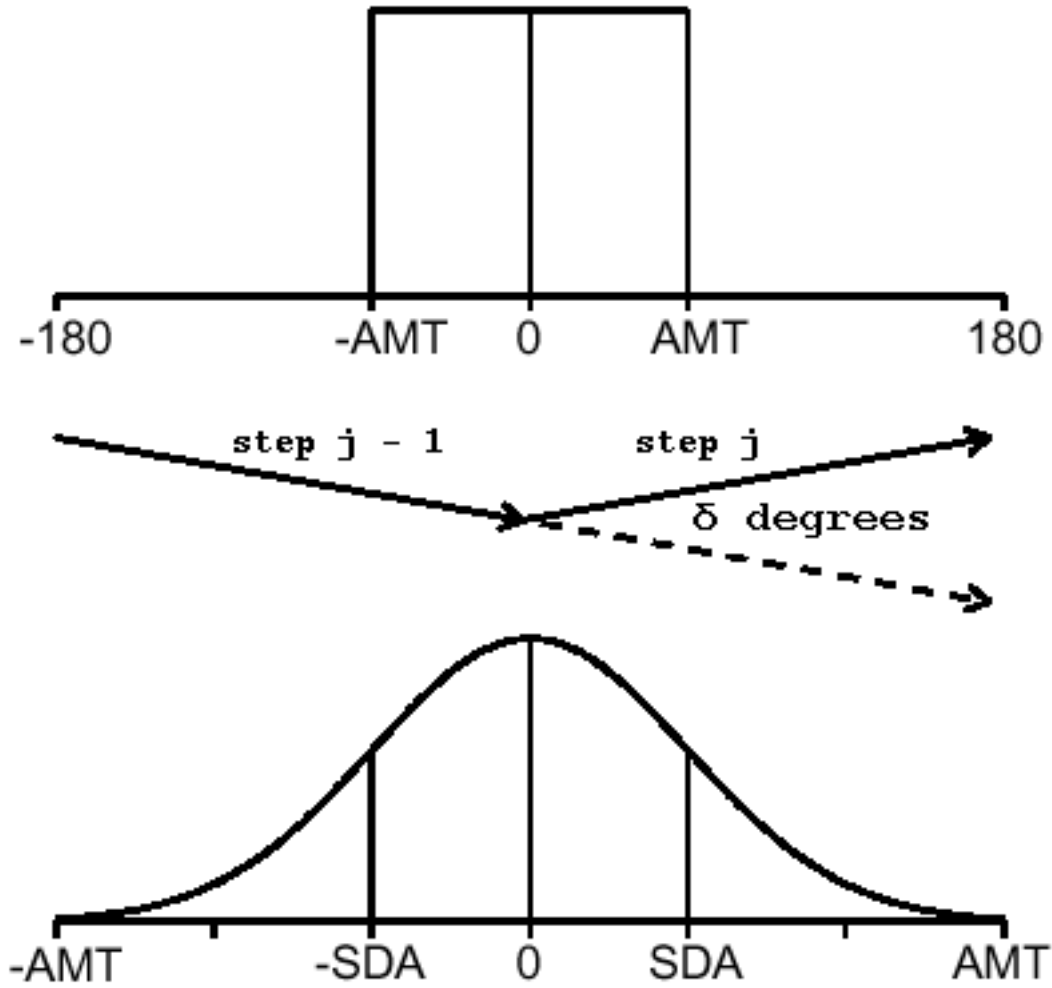


FIGURE 1. Turning Angle for (a) uniform distribution and (b) depiction of what a path may look like.

2.2. **Pollination.** When an animal is on a plant, it collects pollen, distributes pollen, and consumes food. Each plant contains a number of flowers, ϕ , from which an animal may obtain pollen. When an animal visits a plant it picks up pollen from one or more flowers. The number of flowers from which an animal 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 animal, 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

$$(2.2.1) \quad f_{j,k} = \phi \cdot a \cdot \eta^k.$$

It is assumed that the amount of food eaten and the amount of pollen collected is proportional to the number of visited flowers. An animal 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 (2.2.1). Let $f_{j,k}^{(i)}$ be the number of flowers visited by the i^{th} animal during the k^{th} visit to the j^{th} plant then the amount of pollen/nectar in the i^{th} animal's stomach after m plant visits is given by

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

where β is the proportionality constant for the amount of pollen collected at a plant. Each animal 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.

In the field it is observed that a fraction of all flowers are pollinated (α), then there is an associated probability that a flower is pollinated (ρ), where

$$(2.2.2) \quad \alpha = \rho \cdot \hat{f}_k.$$

Using equation (??) and (2.2.2) we can determine the probability that a flower is pollinated, ρ , by the formula

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

If it has been determined that a flower should be pollinated we must determine which previous plant should pollinate that flower. 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 impeded self-pollination. Each flower considered has an equal likelihood of pollinating the current flower.

2.3. Time and Stopping Criteria. Let the velocity an animal travels (v) be fixed, and the time spent at a plant (t_{plant}) be fixed then the travel time for an animal will be 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} animal. 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 animal is removed from the simulation. t_{max} is based on the optimal searching time during the day. When there are no animals left the simulation terminates.

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. \downarrow ADD \downarrow

In order to quantify these differences we measure statistics that are properties of the animal: *Average Path Distance*, *Average Maximum Distance*, and properties of the plant: *Average Pollination Distance*, *Average Maximum Pollination Distance*, *Average Weighted Diversity of Fathers*. The calculations of these statistics are given in the Table 2.4.

In these equations it is assumed that b is the total number of animals, n is the total number of plants, $(x_{1,0}^{(i)}, x_{2,0}^{(i)})$ is the starting location of the i^{th} animal, $(x_{1,j}^{(i)}, x_{2,j}^{(i)})$ is the location of the i^{th} animal 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.

3. Results

The following results are based on simulations of the model with parameter values given in Table 3. These parameters are based on field data estimates from the VCU Rice Center (unpublished). 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% of average, so will not be shown due to the small size.

Determining how far animals will travel during a foraging trip is important 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 directly affects 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 to

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	$E = \frac{1}{n} \sum_{i=1}^n 1 / \frac{1}{(\tau^{(i)})^2} \sum_{j=1}^{\Delta \tau^{(i)}} F_{j,i}^2$

TABLE 1. Equations

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

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 the continually 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 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 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 farther the animal is likely to travel from its initial position allow for longer pollination distances.

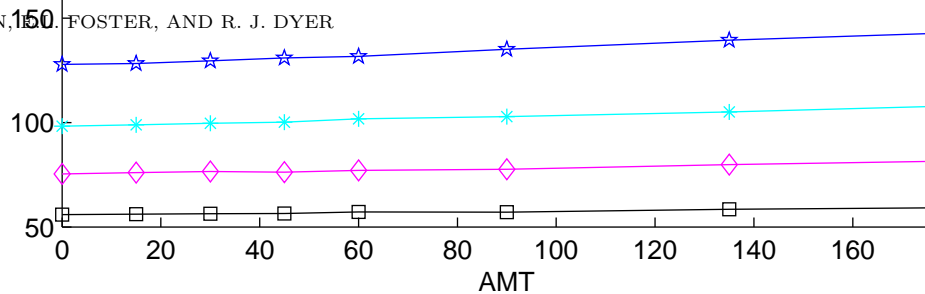


FIGURE 2. Average Path Distance vs. Turning Angle for Various Plant Densities

For a plant density of 0.01 and $\text{AMT} = 0^\circ$ the average maximum pollination distance is approximately triple of that for the same plant density and $\text{AMT} = 180^\circ$. Additionally, for plant density of 0.15 and $\text{AMT} = 0^\circ$ the average pollination distance is approximately double of the average pollination distance for the same density and $\text{AMT} = 180^\circ$. 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 despite the plant densities simulated.

The average maximum pollination distance is clearly affected by the turning angle, as can be seen in Figure 5. However, the effect of plant density on the average maximum pollination distance is unclear, due to strange behavior observed for low plant densities. The average maximum pollination distance for both plant densities 0.01 and 0.03, unexpectedly, have varying behavior across the different turning angles. However, as a general trend, excluding the 0.01 and 0.03 plant densities, the average maximum pollination distance decreases as the density increases. This behavior is what would be expected, since plants are closer together for high densities.

The average maximum pollination distance decreases as AMT increases from 0° to 180° across all densities. This is due to animals covering a shorter 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.

Testing...

In general as the turning angle increases the average weighted diversity of fathers decreases. For a plant density of 0.01 and $\text{AMT} = 180^\circ$ the average weighted diversity of fathers is approximately three-quarters of the average weighted diversity of fathers for the same plant density and $\text{AMT} = 0^\circ$. This is likely due to the animal returning to the same plants multiple times for the larger values of AMT.

The averages weighted diversity of fathers tends to increase, across all values of turning angle, as density increases. This is due to the availability of more plants in a shorter distance. Thus, the average weighted diversity of fathers for wind dispersal will be less than that for animals that travels straighter paths.

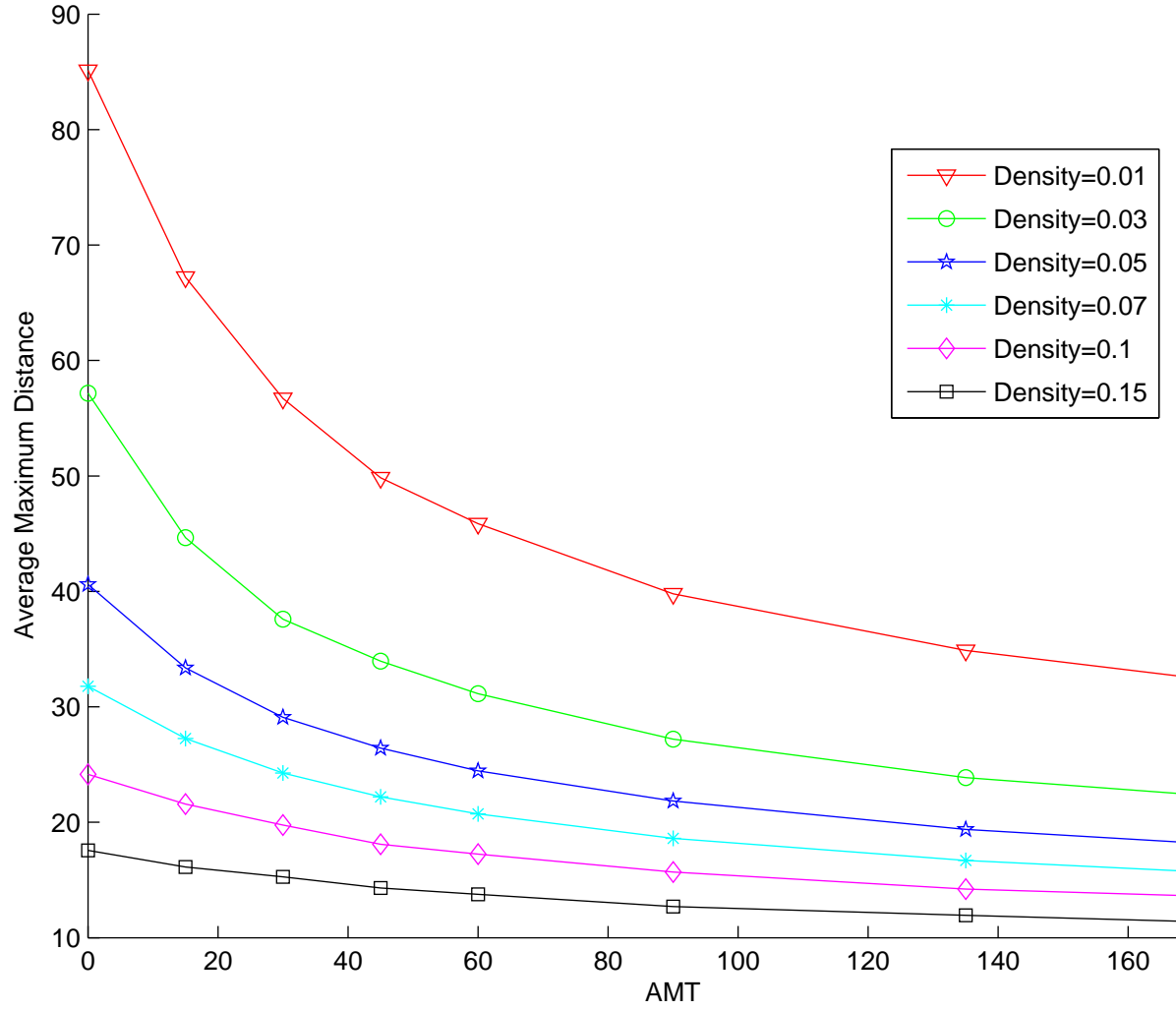


FIGURE 3. Average Maximum Distance vs. Turning Angle for Various Plant Densities

4. Discussion

The majority of models studying pollination have assumed a purely random diffusion process. However, if the magnitude of an animal's turning angle is smaller than $AMT = 180^\circ$, the results show that significant bias can be introduced into the analysis of pollination. From the agent based correlated random walk model presented we can see that significant issues are introduced when treating animal dispersal as a purely random process when the animals pollinating may move along straighter paths.

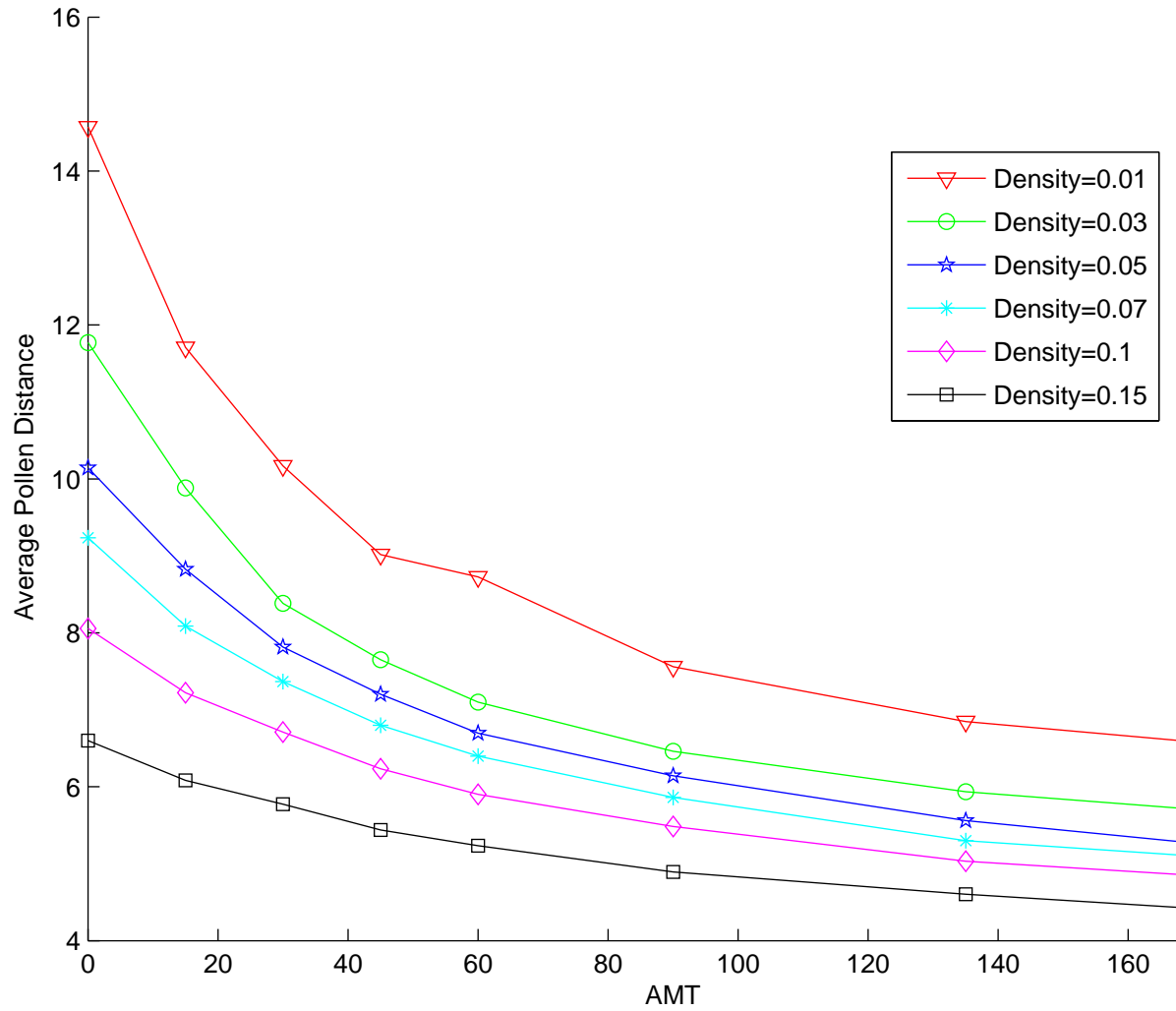


FIGURE 4. Average Pollination Distance vs. Turning Angle for Various Plant Densities

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

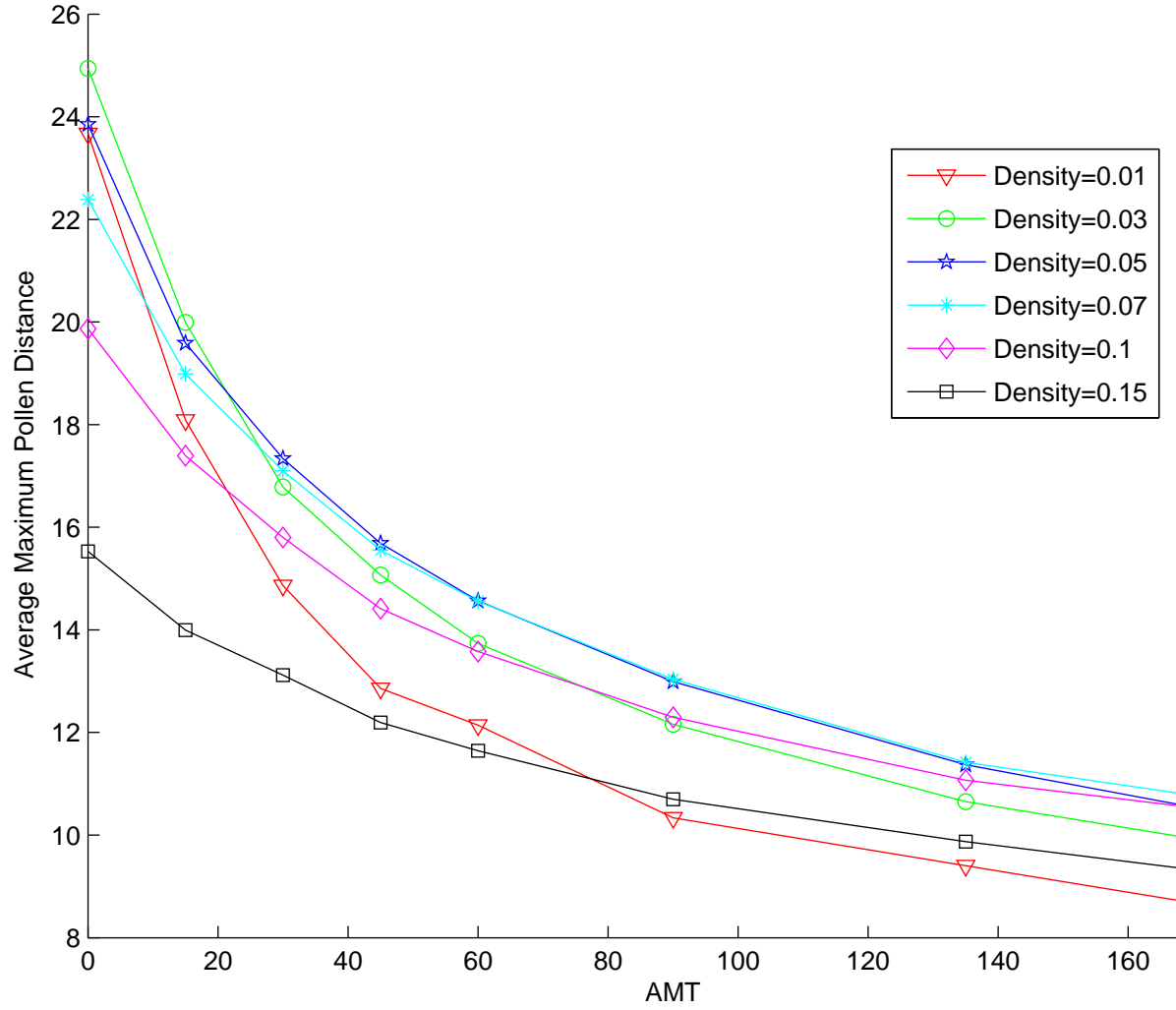


FIGURE 5. Average Maximum Pollination Distance vs. Turning Angle for Various Plant Densities

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

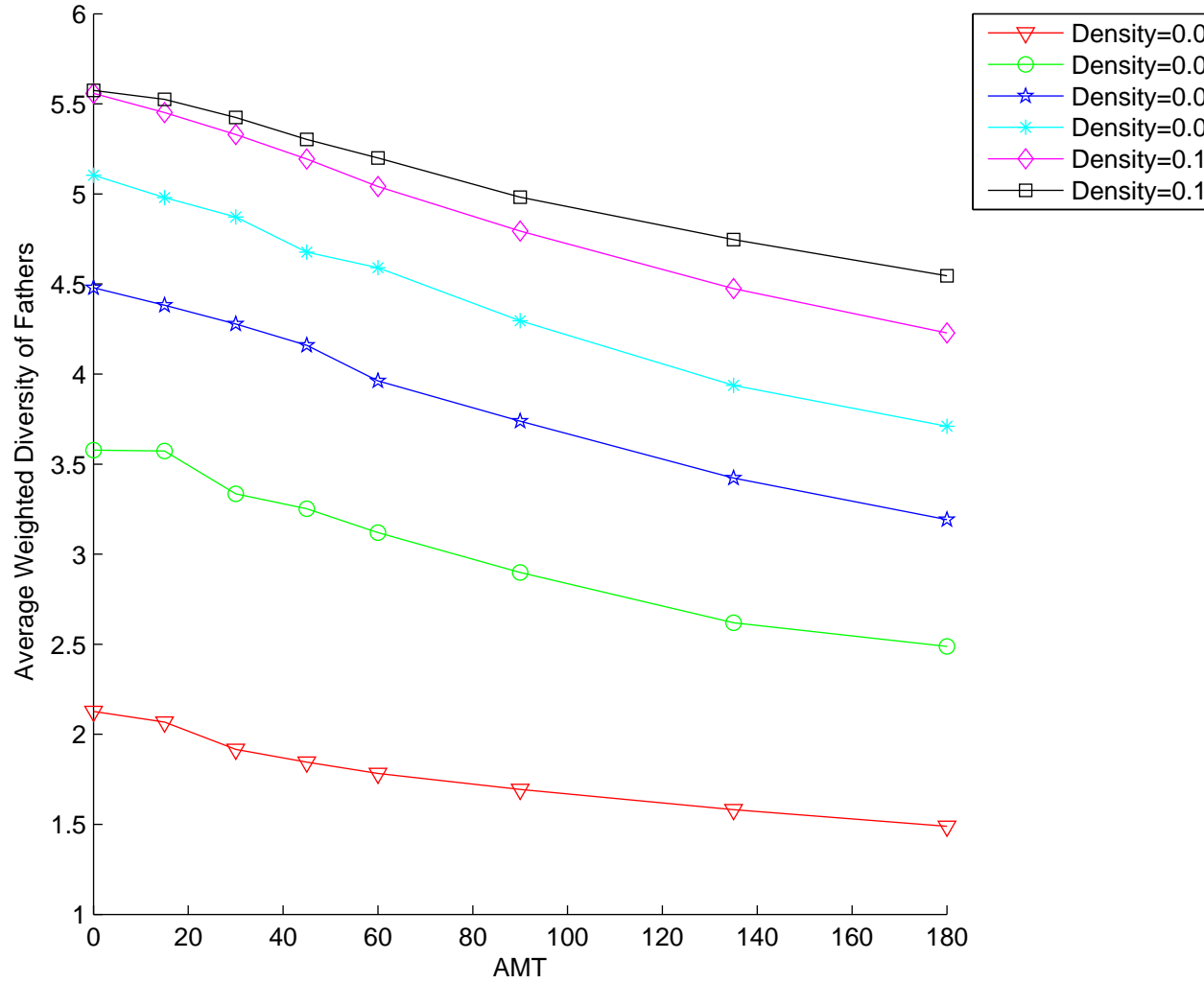


FIGURE 6. Average Weighted Diversity of Fathers vs. Turning Angle for Various Plant Densities

of a purely random walk may lead 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 affected by turning angle for high plant densities the average weighted diversity of fathers had 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.

Acknowledgment.

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