



# VCU

Virginia Commonwealth University  
VCU Scholars Compass

---

Theses and Dissertations

Graduate School

---

2014

## A pollination network of *Cornus florida*

James H. Lee

Follow this and additional works at: <https://scholarscompass.vcu.edu/etd>



Part of the [Other Applied Mathematics Commons](#)

© The Author

---

Downloaded from

<https://scholarscompass.vcu.edu/etd/3615>

This Thesis is brought to you for free and open access by the Graduate School at VCU Scholars Compass. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of VCU Scholars Compass. For more information, please contact [libcompass@vcu.edu](mailto:libcompass@vcu.edu).

© James H. Lee 2014  
All Rights Reserved

A pollination network of *Cornus florida*

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

James H. Lee  
Master of Science

Director: David Chan, Associate Professor  
Department of Mathematics and Applied Mathematics

Virginia Commonwealth University  
Richmond, Virginia  
December 2014

## **Acknowledgment**

The research contained herein was supported by a generous grant from the Virginia Commonwealth University Inger and Walter Rice Center for Environmental Life Sciences.

Thank you to Dr. David Chan for all of your help and patience in guiding me through this process.

A special thank you to my wife, Nicole, for all of the support and love you gave me throughout my education.

For my daughters, Samantha and Elisabeth.

## Contents

Table of Variables		x
Abstract		xii
1 Introduction		1
2 Background		3
2.1 Field characteristics . . . . .		4
2.2 Tree characteristics . . . . .		4
2.3 Insect movement . . . . .		6
2.4 Pollination . . . . .		7
2.5 Model statistics . . . . .		8
2.5.1 Number of fathers . . . . .		8
2.5.2 Connectance . . . . .		9
2.5.3 Average weighted diversity of fathers . . . . .		9
2.5.4 Average pollination distance . . . . .		10
2.5.5 Average maximum pollination distance . . . . .		10
2.5.6 Clustering coefficient of fathers . . . . .		11
3 Results		12
3.1 Number of fathers . . . . .		13
3.2 Connectance . . . . .		16
3.3 Average weighted diversity of fathers . . . . .		18
3.4 Average pollination distance . . . . .		19
3.5 Average maximum pollination distance . . . . .		21
3.6 Clustering coefficient of fathers . . . . .		24
4 Discussion		29
Bibliography		32
Appendices		34

A	Data	34
A.1	Graphs . . . . .	34
A.1.1	Number of fathers per mother. Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing. Individual maximum pollen carryovers. . . . .	34
A.1.2	Number of fathers per mother. Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing. Individual maximum pollen carryovers. . . . .	39
A.1.3	Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing. . . . .	44
A.1.4	Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Pollination chance diminishing. . . . .	48
B	Original MATLAB Code	56
B.1	Master Files . . . . .	56
B.1.1	Pollination.m . . . . .	56
B.1.2	Rice.m . . . . .	70
B.2	Functions . . . . .	72
B.2.1	RandomTrees.m . . . . .	72
B.2.2	PlaceInsects.m . . . . .	72
B.2.3	MoveInsects.m . . . . .	73
B.2.4	InsectNearestTree.m . . . . .	74
B.2.5	TreeDistanceChart.m . . . . .	75
B.2.6	NetMaster.m . . . . .	76
B.2.7	BinaryB.m . . . . .	78
B.2.8	connectanceTT.m . . . . .	79
B.2.9	NumberParents.m . . . . .	80
B.2.10	ACCPBDN.m . . . . .	80
B.2.11	ACCPWDN.m . . . . .	81
B.2.12	AWDF.m . . . . .	82
B.2.13	runtime.m . . . . .	83
	Vita	85

## List of Tables

3.1	Fixed parameter values for all simulations . . . . .	12
3.2	Simulation parameter values . . . . .	13

## List of Figures

2.1	Fathering triangles. Arrows indicate direction of gene flow. . . . .	11
3.1	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	14
3.2	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	15
3.3	<i>Tree coordinates (scaled) at the VCU Rice Center.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ trees). . . . .	16
3.4	<i>Connectance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	17
3.5	<i>Connectance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	18
3.6	<i>Average weighted diversity of fathers.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	19
3.7	<i>Average weighted diversity of fathers.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	20
3.8	<i>Average pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	21
3.9	<i>Average pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	22



3.10	<i>Average pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance equal for all $\kappa \leq \kappa_{\max}$ . Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	23
3.11	<i>Average maximum pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance equal for all $\kappa \leq \kappa_{\max}$ . Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	24
3.12	<i>Average maximum pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	25
3.13	<i>Average maximum pollination distance.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	26
3.14	<i>Clustering coefficient of fathers.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	27
3.15	<i>Clustering coefficient of fathers.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	27
3.16	<i>Clustering coefficient of fathers.</i> Field Size $100 \times 100$ . Tree density $\omega = \{0.025, 0.050, 0.075, 0.100, 0.150\}$ ( $\tau = \{250, 500, 750, 1000, 1500\}$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \infty$ . . . . .	28
A.1	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 1$ . . . . .	34
A.2	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 3$ . . . . .	35
A.3	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 5$ . . . . .	36

A.4	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 7$ . . . . .	37
A.5	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \infty$ . . . . .	38
A.6	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 1$ . . . . .	39
A.7	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 3$ . . . . .	40
A.8	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 5$ . . . . .	41
A.9	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = 7$ . . . . .	42
A.10	<i>Number of fathers per mother.</i> Field Size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \infty$ . . . . .	43
A.11	<i>Number of fathers per mother.</i> Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 0^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	44
A.12	<i>Number of fathers per mother.</i> Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	45
A.13	<i>Number of fathers per mother.</i> Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 90^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	46

A.14	<i>Number of fathers per mother.</i> Field size $133.2794 \times 47.2927$ . Tree density $\omega = 0.071552$ ( $\tau = 451$ Rice Center trees). Maximum insect turning radius $\delta_{\max} = 180^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	47
A.15	<i>Number of fathers per mother.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 0^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	48
A.16	<i>Number of fathers per mother.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	49
A.17	<i>Number of fathers per mother.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 90^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	50
A.18	<i>Number of fathers per mother.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Maximum insect turning radius $\delta_{\max} = 180^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	51
A.19	<i>Average weighted diversity of fathers.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . .	52
A.20	<i>Average pollination distance.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . . . .	53
A.21	<i>Average maximum pollination distance.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . .	54
A.22	<i>Clustering coefficient of fathers.</i> Field Size $100 \times 100$ . Tree density $\omega = 0.050$ ( $\tau = 500$ randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ . . .	55

### Table of Variables

$A$	$\tau \times \tau$ adjacency matrix between father trees and mother trees
$a_{f,m}$	$a_{f,m} \in A$ , 1 if $f$ fathers seeds on $m$ , 0 otherwise
$B$	$\tau \times \tau$ interaction matrix between father trees and mother trees
$b_{f,m}$	$b_{f,m} \in B$ , number of seeds on tree $m$ fathered by tree $f$
$\beta$	Total number of insects
$C$	Clustering coefficient of fathers
$\bar{D}$	Global average pollination distance
$\bar{D}^{(i)}$	Average pollination distance for insect $i$
$\tilde{D}$	Global average maximum pollination distance
$\tilde{D}^{(i)}$	Maximum pollination distance for insect $i$
$\delta_n^{(i)}$	Turning angle of insect $i$ at time step $n$
$\delta_{\max}$	Maximum turning angle for all insects
$E$	Average weighted diversity of fathers
$\hat{F}_m$	Weighted diversity of fathers on tree $m$
$f$	Father tree
$f^{(i)}$	Tree from which insect $i$ delivers pollen
$\Phi_m$	Number of fathers per mother for all trees in the network
$\phi_m$	Set of trees that father seeds on tree $m$
$ \phi_m $	Number of trees that father seeds on tree $m$
$\phi_m^{(i)}$	Number of trees from which insect $i$ delivers pollen to tree $m$
$\gamma$	Number of grains of pollen
$i$	Insect
$k$	Number of flowers that will be visited by an insect
$\kappa$	Number of flowers previously visited by an insect
$\kappa_{\max}$	Maximum pollen carryover
$L$	Connectance of network
$m$	Mother tree
$m^{(i)}$	Tree pollinated by insect $i$
$\mu$	Number of mother trees in the network
$\mu^{(i)}$	Number of trees pollinated by insect $i$

$n$	Discrete time steps
$n_{\max}$	Stopping time
$P_{\kappa}$	Probability that an insect distributes pollen with carryover $\kappa$
$r_{\max}$	Maximum step size for all insects
$r_n^{(i)}$	Step size for insect $i$ at time step $n$
$\rho$	Probability of successful pollination when $\kappa = 1$
$T$	Tree, mother or father
$\tau$	Total number of trees
$\theta_n^{(i)}$	Heading of insect $i$ at time step $n$
$\mathbf{X}_n^{(i)}$	Coordinates of the $i$ th insect at time step $n$
$(x_{1,n}^{(i)}, x_{2,n}^{(i)})$	Coordinates of the $i$ th insect at time step $n$
$\mathbf{Y}^{(T)}$	Coordinates of tree $T$
$(y_1^{(T)}, y_2^{(T)})$	Coordinates of tree $T$
$(y_1^{(T^{(i)})}, y_2^{(T^{(i)})})$	Coordinates of tree $T$ which is mated with another tree by insect $i$
$(\bar{y}_1, \bar{y}_2)$	Coordinates of the center of the field
$\omega$	Tree density

## Abstract

### A POLLINATION NETWORK OF *CORNUS FLORIDA*

By James H. Lee, Master of Science.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2014.

Director: David Chan, Associate Professor, Dept. of Mathematics and Applied Mathematics.

From the agent-based, correlated random walk model presented, we observe the effects of varying the parameter values of maximum insect turning area,  $\delta_{\max}$ , density of trees,  $\omega$ , maximum pollen carryover,  $\kappa_{\max}$ , and probability of fertilization,  $P_{\kappa}$ , on the distribution of pollen within a population of *Cornus florida* (flowering dogwood). We see that varying  $\delta_{\max}$  and  $\kappa_{\max}$  changes the dispersal distance of pollen, which greatly affects many measures of connectivity. The clustering coefficient of fathers is maximized when  $\delta_{\max}$  is between  $60^\circ$  and  $90^\circ$ . Varying  $\omega$  does not have a major effect on the clustering coefficient of fathers, but it does have a greater effect on other measures of genetic diversity. Lastly, we compare our simulations with randomly-placed trees with that of actual tree placement of *C. florida* at the VCU Rice Center, concluding that in order to truly understand how pollen is distributed within a specific ecosystem, specificity in describing tree locations is necessary.

## Introduction

Understanding how distribution mechanisms of pollen dispersal influences genetic connectivity is critical to maintaining the long-term persistence of plant populations [15]. Movement patterns of animal pollinators greatly influence the genetic structure and connectivity within a local plant population [9, 18]. It is therefore an important research goal to understand the processes involved in gene flow. It is currently not feasible to conduct biological studies which track the movement of all insect pollinators in a forest environment, nor is it feasible to track the number of individual pollen grains each pollinator carries at any given time. In order to conceptualize the processes involved, a mathematical model is developed. An ideal model describing genetic structure is one flexible enough to account for varied characteristics of pollinators, trees and the intervening landscape, so that the interactions between the species can be better understood. Differentiation in pollinator species, weather patterns, and landscape alterations are known to influence the pollinator behavior of insects [18]. Recently, Dyer et al. collected, germinated, and genotyped *Cornus florida* (flowering dogwood) seeds from the the Virginia Commonwealth University Inger and Walter Rice Center for Environmental Life Sciences [9]. *C. florida* is pollinated by generalist insect pollinators [18], primarily by halictid and andrenid bees [14].

An *agent-based model* (ABM) was created to mimic the movement of insect pollinators. These pollinators are described as moving in a *correlated random walk* (CRW). In a CRW, the direction of movement is based on the previous heading. Any change in direction is done so randomly, but is limited within a maximum turning angle. The speed at which a

pollinator moves is also random up to a maximum rate. Parameters describing the CRW are varied in order to study how these changes affect the genetic landscape.

We use the ABM to conduct two experiments. The first experiment describes a network based on the random placement of trees. This is done in order to have a baseline for comparison to real world data. This is analyzed and compared with an experiment using the actual placement of trees present at the VCU Rice Center. By changing parameter values such as maximum pollen carryover, density of trees, maximum turning angle of insect pollinators, and probability of fertilization, this project describes how pollen is dispersed both within the Rice Center and in other ecosystems.

The pollinator parameters, carryover and maximum turning angle, greatly affect the genetic structure of a *C. florida* population. As the maximum pollen carryover of pollinators increases, greater pollen dispersal distance is observed in the network. As the maximum turning angle of insect pollinators increases, pollen dispersal distance decreases in the network.

The clustering coefficient of fathers is maximized with a maximum turning angle of pollinators,  $\delta_{\max}$ , between  $60^\circ$  and  $90^\circ$ . When  $\delta_{\max}$  is not at an extreme value, the displacement of the insects is high enough so that the insect can visit many trees, but low enough so that all of the trees that it visits are within a close proximity to one another.

Furthermore, many differences in the genetic structure of *C. florida* populations can be observed when comparing random models with models incorporating actual tree placement at the VCU Rice Center. Although much can be inferred from random models, in order to truly understand how pollen is distributed within a specific ecosystem, specificity in describing tree locations is necessary.



## Background

In this ABM, we consider two types of agents, trees and insects. Trees are randomly placed on a rectangular field. The density of the trees is varied to determine its effect on the pollination network. Trees are static agents where insects are mobile. If an insect is within one 'unit' distance of a tree, it is assumed that it visits flowers on the tree and a pollination event is possible. An insect can only visit one tree at a time, so if an insect is within 1 unit of more than one tree, it chooses the closest one. It is assumed that, when an insect visits a tree, there will always be a flower available from which the insect will be able to both gather pollen and deposit pollen from other trees.

CRW models are widely used to describe the paths that animals take as they forage for food [1, 3–5, 16]. For each experiment, we have 1000 insects start at a random location and move in a CRW throughout the field containing trees. At each time step, each insect will choose a random heading based upon its previous heading, move up to 1 distance unit forward, and if it is on a tree, visit a flower. This process continued for 600 time steps and is described in detail below.

We use the mathematical modeling software MATLAB to produce an ABM to describe the movement of insect pollinators and to analyze the resulting pollination network. Insect statistics studied are *average pollination distance* and *average maximum pollination distance*. Tree statistics studied are *number of fathers per mother*, *connectance*, *average weighted diversity of fathers*, and the *clustering coefficient of fathers*.

## 2.1 Field characteristics

The field size is set at 100 units  $\times$  100 units. The distances are measured in 'units' so that it can be scaled to a field of any size. The density of the trees can easily be determined as the number of trees per unit area. For our simulations,

$$\omega = \frac{\tau}{100 \times 100} = \frac{\tau}{10\,000} = 0.0001 \tau$$

where  $\tau$  is the number of trees in the network.

The edge of the field is considered to be an impermeable barrier. Insects cannot leave the field nor new insects enter the field. When an insect comes into contact with the edge of the field, its subsequent heading is set such that it 'bounces' off of the barrier at the opposite angle from which it approached.

## 2.2 Tree characteristics

For tracking purposes, each tree,  $T$ , is numbered such that  $1 \leq T \leq \tau$  where  $\tau$  is the number of trees in the network. Let  $\mathbf{Y}^{(T)} = (y_1^{(T)}, y_2^{(T)})$  be the location of tree  $T$ ,  $1 \leq T \leq \tau$ , which is static. Unless exact coordinates were provided, trees are randomly placed using a uniform random distribution within the allotted field size. Since *C. florida* is self-incompatible [18], it is assumed that all pollination distances are greater than zero. Data was collected to determine the number of seeds on each tree that are germinated, which trees are fathers to those seeds, and the number of times each tree fathers seeds on other trees.

Coordinates of the trees considered at the VCU Rice Center were provided by the Dyer Lab [7]. The provided coordinates are rotated  $25^\circ$  in order to minimize the open space along

the edges of the borders of the field. This is done using the rotation

$$\mathbf{Y}_{\text{rotated}}^{(T)} = \begin{bmatrix} y_{1,\text{rotated}}^{(T)} \\ y_{2,\text{rotated}}^{(T)} \end{bmatrix} = \begin{bmatrix} \sin\left(\frac{5\pi}{36}\right) & \cos\left(\frac{5\pi}{36}\right) \\ -\cos\left(\frac{5\pi}{36}\right) & \sin\left(\frac{5\pi}{36}\right) \end{bmatrix} \begin{bmatrix} y_1^{(T)} \\ y_2^{(T)} \end{bmatrix}.$$

A linear translation is used to place the origin at the average of the extreme values of  $y_1^{(T)}$  and  $y_2^{(T)}$  such that

$$\mathbf{Y}_{\text{translated}}^{(T)} = \begin{bmatrix} y_{1,\text{translated}}^{(T)} \\ y_{2,\text{translated}}^{(T)} \end{bmatrix} = \begin{bmatrix} y_1^{(T)} - \bar{y}_1 \\ y_2^{(T)} - \bar{y}_2 \end{bmatrix} = \begin{bmatrix} y_1^{(T)} - 2062 \\ y_2^{(T)} - 3201 \end{bmatrix}$$

where  $\bar{y}_1$  and  $\bar{y}_2$  are the average of the extrema of  $y_1^{(T)}$  and  $y_2^{(T)}$  respectively. A  $6200 \times 2200$  rectangular field is assumed so that all of the trees to be studied fit just inside the borders, further minimizing the open areas of the field. In order to have better comparisons across all runs, the field is scaled by the ratio of the lengths of the field diagonals. That is,

$$\mathbf{Y}_{\text{scaled}}^{(T)} = \begin{bmatrix} y_{1,\text{scaled}}^{(T)} \\ y_{2,\text{scaled}}^{(T)} \end{bmatrix} = \frac{\sqrt{100^2 + 100^2}}{\sqrt{6200^2 + 2200^2}} \begin{bmatrix} y_1^{(T)} \\ y_2^{(T)} \end{bmatrix} = \frac{1}{2\sqrt{541}} \begin{bmatrix} y_1^{(T)} \\ y_2^{(T)} \end{bmatrix}.$$

Combining the equations above, we find total linear transformation to be

$$\mathbf{Y}^{(T)} = \frac{1}{2\sqrt{541}} \left( \begin{bmatrix} \sin\left(\frac{5\pi}{36}\right) & \cos\left(\frac{5\pi}{36}\right) \\ -\cos\left(\frac{5\pi}{36}\right) & \sin\left(\frac{5\pi}{36}\right) \end{bmatrix} \begin{bmatrix} y_1^{(T)} \\ y_2^{(T)} \end{bmatrix} - \begin{bmatrix} 2062 \\ 3201 \end{bmatrix} \right)$$

or equivalently,

$$\begin{cases} y_1^{(T)} \approx 0.009085 y_1^{(T)} + 0.019483 y_2^{(T)} - 44.326152 \\ y_2^{(T)} \approx -0.019483 y_1^{(T)} + 0.009085 y_2^{(T)} - 68.810870 \end{cases} .$$

There are 541 tree coordinates in the data provided by the Dyer lab[7], so the density of the trees on these simulations is

$$\omega_{\text{Rice}} = \frac{451}{\left(\left(\frac{1}{(2\sqrt{541})}\right) 6200 \times \left(\frac{1}{(2\sqrt{541})}\right) 2200\right)} = \frac{22181}{310\,000} \approx 0.071552 .$$

### 2.3 Insect movement

Let  $\beta$  be the total number of insects in a simulation, and let  $\mathbf{X}_n^{(i)} = (x_{1,n}^{(i)}, x_{2,n}^{(i)})$  be the location of the  $i$ th insect,  $1 \leq i \leq \beta$ , at time step  $n$ ,  $0 \leq n \leq n_{\max}$ . The initial position of each insect,  $\mathbf{X}_0^{(i)}$  is distributed randomly throughout the field. Since the insect is not yet moving at  $n = 0$ , the  $i$ th insect's initial heading  $\theta_1^{(i)}$  is at time  $n = 1$  and is chosen from a uniform random distribution between  $0^\circ$  and  $360^\circ$ . At each subsequent time step, the insect's new heading  $\theta_{n+1}^{(i)}$  is dependent upon its current heading  $\theta_n^{(i)}$  and a random number  $\delta_{n+1}^{(i)}$ . That is

$$\theta_{n+1}^{(i)} = \theta_n^{(i)} + \delta_{n+1}^{(i)}$$

where  $\delta_{n+1}^{(i)}$  is in the open interval  $(-\delta_{\max}, \delta_{\max})$  for each  $n = 1, 2, \dots, n_{\max}$ . Similarly, the initial step size of each insect,  $r_1^{(i)}$  is at time  $n = 1$ . Each subsequent step size,  $r_{n+1}^{(i)}$ , for each insect is determined so that  $r_{n+1}^{(i)}$  is in the open interval  $(0, r_{\max})$  for each  $n = 1, 2, \dots, n_{\max}$ . In Cartesian coordinates, the position of the  $i$ th insect at each subsequent time step will be

$$\mathbf{X}_{n+1}^{(i)} \left( \mathbf{X}_n^{(i)}; r_{n+1}^{(i)}, \theta_{n+1}^{(i)} \right) = \left( x_{1,n}^{(i)} + r_{n+1}^{(i)} \cos \left( \theta_{n+1}^{(i)} \right), x_{2,n}^{(i)} + r_{n+1}^{(i)} \sin \left( \theta_{n+1}^{(i)} \right) \right)$$

for each  $n = 0, 1, \dots, n_{\max}$ . For all simulations, we assume insects move throughout the field for 600 time steps, i.e.,  $n_{\max} = 600$ .

## 2.4 Pollination

If an insect is within 1 unit of the center of a tree, it will visit a flower on that tree in order to collect nectar for food. When it visits the flower, it will pick up and drop off pollen with a probability of  $P_{\kappa}$ , where  $\kappa$  is the number of previously visited flowers and  $P_{\kappa} = 0$  if  $\kappa > \kappa_{\max}$  so that  $\kappa_{\max}$  is the maximum pollen carryover. This probability factor includes the fact that the insect will likely visit more than one flower on the tree and that some of the flowers may not be available for pollination, i.e., the flower has already been pollinated.

As an insect continues along its path, it picks up pollen from flowers on various trees. After visiting flowers on many trees, if it visits a flower on a tree it has not yet visited, pollen may be dispersed from any flower it has visited up to that point in time, up to the maximum pollen carryover,  $\kappa_{\max}$ . As an insect visits multiple flowers, the chances that it deposits pollen from a previous flower diminishes with each successive flower visited [12]. It was shown by [6] that from a given flower, an insect will deposit  $\gamma(1 - \gamma)^{k-1}$  pollen grains onto the  $k$ th flower visited after that flower, where  $\gamma$  depends upon the type of pollen as well as the type of pollinator. We assume that the chance of pollination is proportional to the amount of pollen that a flower receives so that the probability that an insect distributes pollen to tree  $m$  from tree  $f$ , which it visited  $\kappa$  time steps ago, is given by

$$P_{\kappa} = \begin{cases} \rho(1 - \rho)^{\kappa-1} & \text{if } \kappa \leq \kappa_{\max} \\ 0 & \text{otherwise} \end{cases}$$

where  $\rho$  is the chance of pollination when  $\kappa = 1$ , and  $\kappa_{\max}$  is the maximum pollination carryover, which is varied as a parameter.

For comparison purposes, this model also shows the results of our simulations when there is no diminishment of pollination chance with successive flowers visited. That is,  $P_\kappa = \rho$  for all  $\kappa \leq \kappa_{max}$ . In any case, since *C. florida* is self-incompatible, the probability that any tree will self-pollinate is fixed at zero.

## 2.5 Model statistics

This study examines the effects of tree density  $\omega$ , pollination carryover  $\kappa$ , probability of fertilization  $P_\kappa$ , and insect maximum turning angle  $\delta_{max}$  on the *number of fathers per mother*, *connectance*, *average weighted diversity of fathers*, the *clustering coefficient of fathers*, *average pollination distance*, and *average maximum pollination distance*.

### 2.5.1 Number of fathers

Each tree has the ability to contribute pollen to seeds on other trees and to accept pollen from other trees. When applicable, we will refer to a tree as a father tree,  $f$ , if the tree contributes pollen to another tree. We will refer to a tree as a mother tree,  $m$ , if the tree is accepts pollen from another tree. For tracking purposes, each tree,  $T$ , is numbered such that  $1 \leq T \leq \tau$  where  $\tau$  is the number of trees in the network, and if  $T = f = m$ , then  $T$ ,  $f$ , and  $m$  all refer to the same tree. Let  $\phi_m$  be the set of trees which father seeds on tree  $m$ . Then the number of fathers for each  $m$  in the network is  $|\phi_m|$ ,  $m = 1, 2, \dots, \tau$ , where  $|\cdot|$  denotes cardinality. The set containing the *number of fathers per mother* for all trees in the network is

$$\Phi_m = \{|\phi_1|, |\phi_2|, \dots, |\phi_\tau|\} .$$

Furthermore, there is an edge between  $m$  and  $f$  where  $f \in \phi_m$  and  $b_{f,m}$  is the weight of that edge, which is equal to the number of times  $f$  fathers seeds on  $m$ .

## 2.5.2 Connectance

The *connectance*,  $L$ , of a network is the proportion of realized pollination events to the number of possible pollination events [13]. Let  $A$  be a  $\tau \times \tau$  adjacency matrix, such that  $a_{f,m} = 1$  if tree  $f$  fathers at least one seed on tree  $m$ , and 0 otherwise. Then  $A$  is a binary representation of the connectance of the network. Since we are assuming that the trees do not self-pollinate, the number of possible interactions on this matrix is  $\tau(\tau - 1)$ . Then the connectance of the network is given by

$$L = \frac{\sum_{f=1}^{\tau} \sum_{m=1}^{\tau} a_{f,m}}{\tau(\tau - 1)} .$$

## 2.5.3 Average weighted diversity of fathers

Let  $B$  be a  $\tau \times \tau$  matrix such that  $b_{f,m}$  is the number of seeds that tree  $f$  fathers on tree  $m$ . The weighted diversity of fathers for a mother tree  $m$  is a weighted measurement of the number of fathers that contribute pollen to seeds on  $m$ , accounting for the various number of seeds fathered by each father tree. The weighted diversity of fathers,  $\hat{F}_m$ , is computed for each  $m$  in the network by the formula

$$\hat{F}_m = \frac{\left( \sum_{f=1}^{|\phi_m|} b_{f,m} \right)^2}{\sum_{f=1}^{|\phi_m|} (b_{f,m})^2}$$

The *average weighted diversity of fathers* is the mean average of the weighted densities of fathers over all mother trees and is given by the formula

$$E = \frac{1}{\mu} \sum_{m=1}^{\mu} \hat{F}_m$$

where  $\mu$  is the total number of mother trees in the network.

### 2.5.4 Average pollination distance

The average pollination distance for an insect  $i$  is the average of the distances between any two trees mated by  $i$ . Let  $\mathbf{Y}^{(f^{(i)})} = \left( y_1^{(f^{(i)})}, y_2^{(f^{(i)})} \right)$  be the location of father tree  $f^{(i)}$  and  $\mathbf{Y}^{(m^{(i)})} = \left( y_1^{(m^{(i)})}, y_2^{(m^{(i)})} \right)$  be the location of mother tree  $m^{(i)}$  such that insect  $i$  delivers pollen from  $f^{(i)}$  to  $m^{(i)}$ . Then the average pollination distance,  $\bar{D}^{(i)}$ , achieved by  $i$  for all such pairings is

$$\bar{D}^{(i)} = \frac{1}{\mu^{(i)}} \sum_{m=1}^{\mu^{(i)}} \sum_{f=1}^{\phi_m^{(i)}} \frac{1}{\phi_m^{(i)}} \sqrt{\left( y_1^{(m^{(i)})} - y_1^{(f^{(i)})} \right)^2 + \left( y_2^{(m^{(i)})} - y_2^{(f^{(i)})} \right)^2} .$$

The average pollination distance,  $\bar{D}^{(i)}$ , for each insect is averaged over all of the insects to obtain the *average pollination distance*,  $\bar{D}$ , for the network. That is,

$$\bar{D} = \frac{1}{\beta} \sum_{i=1}^{\beta} \bar{D}^{(i)}$$

where  $\beta$  is the total number of insects in the network.

### 2.5.5 Average maximum pollination distance

The *maximum pollination distance* for an insect  $i$  is

$$\tilde{D}^{(i)} = \max_{m^{(i)} \leq \mu^{(i)}, f^{(i)} \leq \phi_m^{(i)}} \left( \sqrt{\left( y_1^{(m^{(i)})} - y_1^{(f^{(i)})} \right)^2 + \left( y_2^{(m^{(i)})} - y_2^{(f^{(i)})} \right)^2} \right) .$$

The maximum pollination distance for each insect is averaged over all of the insects to obtain the *average maximum pollination distance* for the network,

$$\tilde{D} = \frac{1}{\beta} \sum_{i=1}^{\beta} \tilde{D}^{(i)} .$$



### 2.5.6 Clustering coefficient of fathers

Define a fathering triplet as the relationship between three trees such that tree  $f$  is a father to seeds on both  $m_1$  and  $m_2$ . Define a fathering triangle as a subset of fathering triplets such that  $m_1$  also fathers seeds on  $m_2$  (Figure 2.1(a)),  $m_2$  fathers seeds on  $m_1$  (Figure 2.1(b)), or both (Figure 2.1(c)). The *clustering coefficient of fathers*,  $C$  is the number of fathering triangles in the pollination network over the total number of fathering triplets. That is,

$$C = \frac{\text{number of fathering triangles}}{\text{number of fathering triplets}} .$$

Thus,  $C$  is a measurement of the tendency of parent trees to be clustered together in densely connected groups.

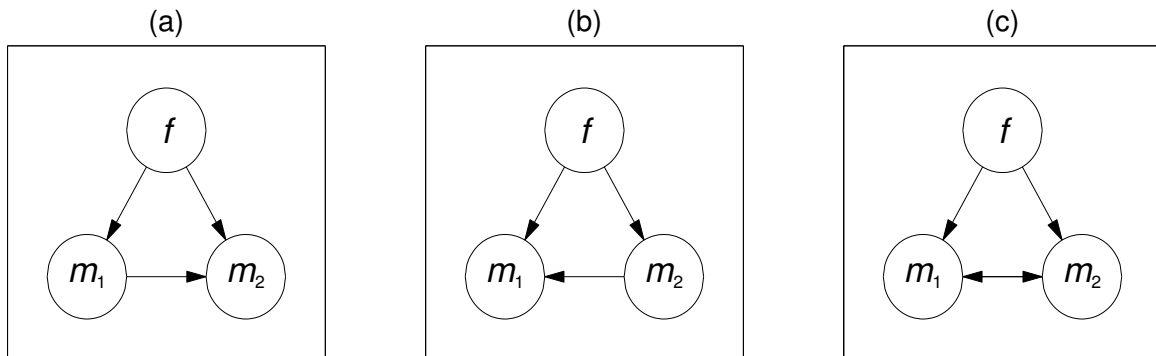


Figure 2.1: Fathering triangles. Arrows indicate direction of gene flow.

## Results

We vary the parameters: tree density,  $\omega \in \{0.0250, 0.0500, 0.0750, 0.1000, 0.1500\}$ , pollination carryover,  $\kappa_{\max} \in \{1, 3, 5, 7, \infty\}$ , probability of fertilization,  $P_{\kappa} = 0.30$  or  $P_{\kappa} = 0.30(1 - 0.30)^{\kappa_{\eta} - 1}$  for all  $\kappa \leq \kappa_{\max}$ , and insect maximum turning angle,  $\delta_{\max} \in \{0, 15, 30, 45, 60, 75, 90, 120, 150, 180\}$ . The effect of varying these parameters are measured by the network indicators: the number of fathers per mother,  $\Phi_m$ , connectance,  $L$ , the average weighted diversity of fathers,  $E$ , the clustering coefficient of fathers,  $C$ , the average pollination distance,  $\bar{D}$ , and the average maximum pollination distance,  $\tilde{D}$ .

Simulations were run for two field sizes. A  $100 \times 100$  field size was used with randomly-placed trees for general analysis purposes, and a field size of  $\frac{3100}{\sqrt{541}} \times \frac{1100}{\sqrt{541}} \approx 133.2794 \times 47.2927$  was used for trees at the VCU Rice Center. All of the results are based on an average of the 10 runs per data point.

Parameter description	Symbol	Value
Total number of insects	$\beta$	1000
Stopping time	$n_{\max}$	600
Maximum step size for all insects	$r_{\max}$	1
Probability of successful pollination when $\kappa = 1$	$\rho$	0.30

Table 3.1: Fixed parameter values for all simulations

Parameters that were held constant for the simulations were the total number of insects,  $\beta$ , stopping time,  $n_{\max}$ , the maximum step size,  $r_{\max}$ , and probability of successful fertilization when  $\kappa = 1$ ,  $\rho$ . These parameter values are shown in Table 3.1. The total number of

insects,  $\beta$ , is fixed at 1000 to ensure statistical reliability. The maximum step size,  $r_{\max}$ , and stopping time,  $n_{\max}$ , are fixed at 1 and 600 respectively based on a field report by [11]. The probability of successful fertilization,  $\rho$ , is based on data by [10].

Chance of pollination for $\kappa \leq \kappa_{\max}$ , $P_{\kappa}$	Maximum pollen carryover, $\kappa_{\max}$	Maximum turning angle in degrees, $\delta_{\max}$	Tree density (Number of trees), $\omega(\tau)$
$P_{\kappa} = 0.30$	1	0	0.0250 (250)
$P_{\kappa} = 0.30(1 - 0.30)^{\kappa-1}$	3	15	0.0500 (500)
	5	30	0.0750 (750)
	7	45	0.1000 (1000)
	$\infty$	60	0.1500 (1500)
		75	
		90	0.071552 (541) <sup>a</sup>
		120	0.071552 (541) <sup>b</sup>
		150	
		180 <sup>c</sup>	

Table 3.2: Simulation parameter values

<sup>a</sup>133.2794 × 47.2927 field with randomly-placed trees.

<sup>b</sup>133.2794 × 47.2927 field with tree placement at the VCU Rice Center.

<sup>c</sup>Brownian motion. Near representation of wind dispersal of pollen.

### 3.1 Number of fathers

One way to analyze the genetic structure and connectivity within a local plant population is to examine the number of different father trees per mother tree,  $\Phi_m$ , in the pollination network. As can be seen in Figure 3.1, the number of different fathers per mother in a randomized placement of trees is distributed in a Gaussian-like distribution. For clarity, the distributions are shown individually in Figures A.1, A.2, A.3, A.4, and A.5 for each  $\kappa_{\max} \in \{1, 3, 5, 7, \infty\}$ . This is an expected outcome as we would expect that gene flow would be directly proportional to the distance traveled by an insect. It was shown by [2] that the

distribution range resulting from a CRW would necessarily result in Gaussian-like behavior for large  $n$ .

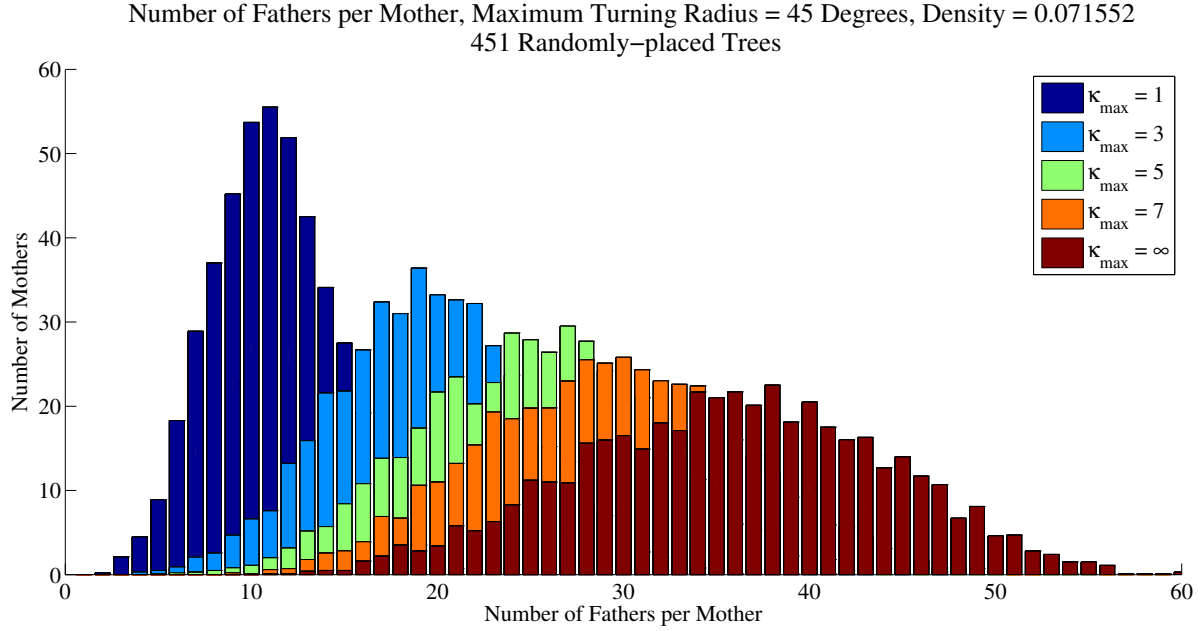


Figure 3.1: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

As pollen carryover increases, the mean number of fathers also increases. This is to be expected as each insect would have greater ability to pollinate a greater number of flowers on a greater number of trees. The variance in the distribution also increases as pollen carryover increases. This is due to the insects having the ability to pollinate more flowers on each individual tree as carryover increases. This results in increased randomness in the number of flowers pollinated per tree per visit and in which trees are the father to those seeds.

However, with the tree placement at the Rice Center as in Figure 3.2, we see a bimodal distribution of the number of fathers per mother. For clarity, the distributions are shown individually in Figures A.6, A.7, A.8, A.9, and A.10 for each  $\kappa_{\max} \in \{1, 3, 5, 7, \infty\}$ . This

distribution can be attributed to the influence of intervening landscape in a natural environment. These results are consistent with the real world data from Dyer et al. who suggested that spatial heterogeneity and intervening landscape influence the genetic structure and connectivity in *C. floria* populations [9].

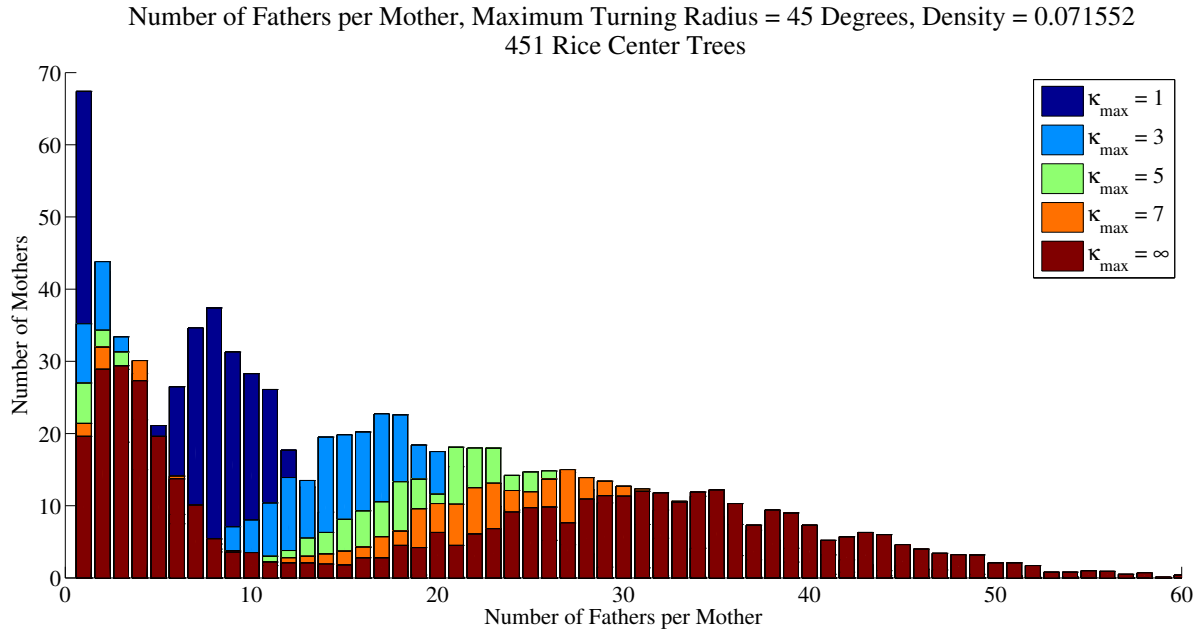


Figure 3.2: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

The spatial heterogeneity is evident in Figure 3.3. The explanation of the bimodal distribution of the number of fathers per mother can be inferred from the different densities of tree distribution. As an insect forages for food in a CRW, it will come into close proximity of a larger number of trees if it is in an area of greater tree density. The second peak in the bimodal distribution of the number of fathers per mother as shown in Figure 3.2 can be attributed to spatial neighborhoods where *C. florida* populations are greater. When  $\kappa_{\max} = \infty$ ,

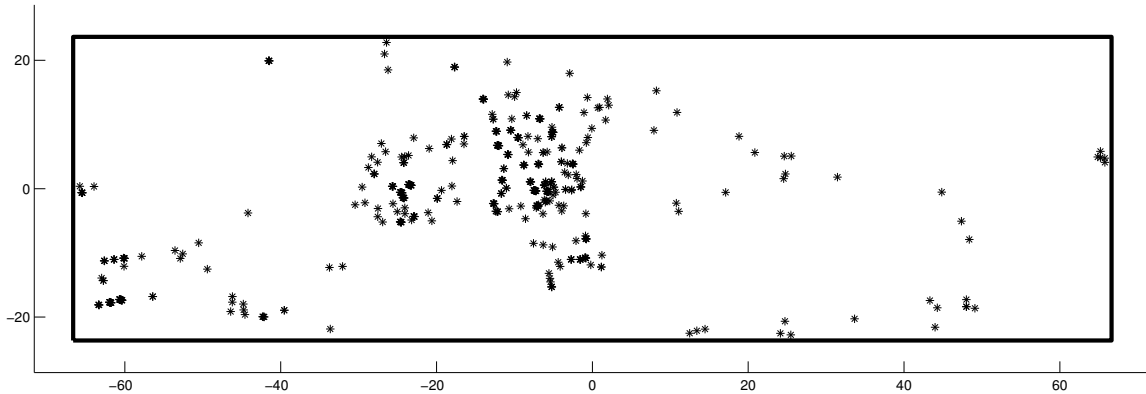


Figure 3.3: *Tree coordinates (scaled) at the VCU Rice Center.* Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  trees).

the first peak is close to 3 fathers per mother on 29 mother trees, and the second peak is close to 32 fathers per mother on 12 mother trees.

As can be seen in Figures A.11, A.12, A.13, and A.14 this bimodality is present whether an insect is restricted to moving in a straight line, i.e.,  $\delta_{\max} = 0$ , or with random dispersal by wind, i.e.,  $\delta_{\max} = 0$ . The differences that are apparent with the differing maximum turning angles are quantitative and do not affect the qualitative nature of the data.

### 3.2 Connectance

As shown in Figure 3.4, if the maximum pollen carryover is limited, the connectance of the pollination network is also limited. Connectance is also greatly influenced by the maximum turning angle  $\delta_{\max}$  for an insect. Clearly, if an insect travels in a straight line, it will cover a greater spatial distance as it visits various trees than it would if it just spun around in circles. This increases the potential for mating to occur between trees a greater distance apart. In Figure 3.4, network connectance is three to five times greater with small  $\delta_{\max}$  than it is with large  $\delta_{\max}$ .

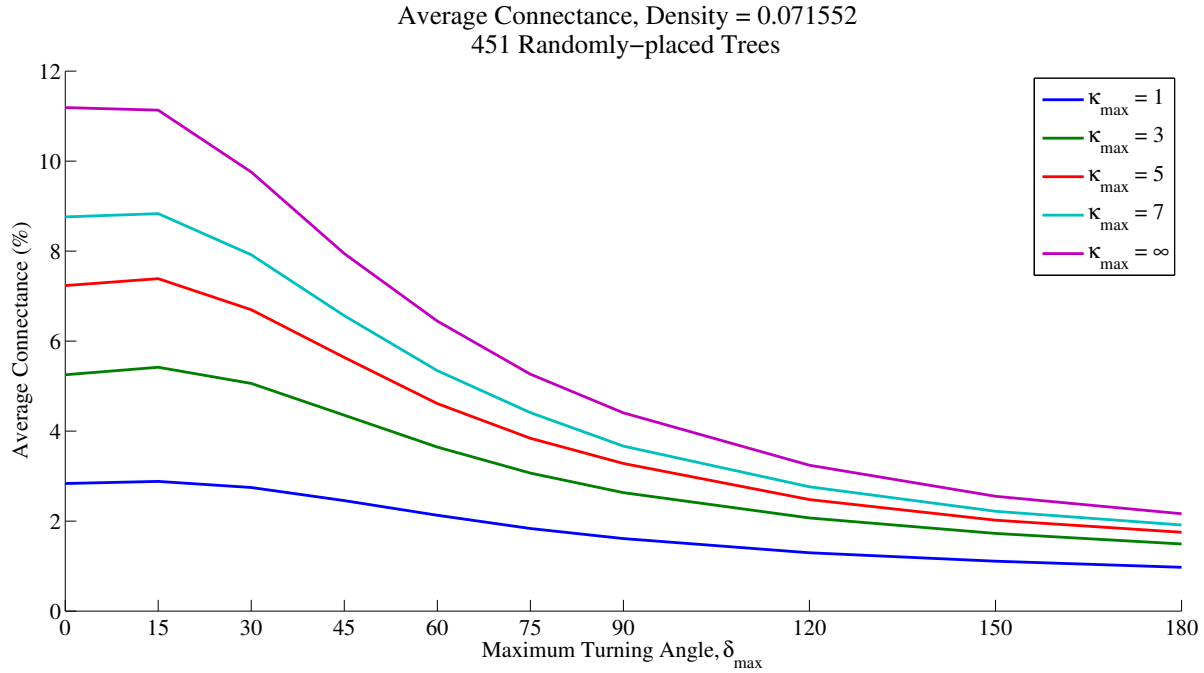


Figure 3.4: *Connectance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

If an insect does not venture very far from its starting location, as would be the case when  $\delta_{\max}$  is close to  $180^\circ$ , the effect of maximum pollen carryover on the connectance of the network is lessened. When  $\delta_{\max} = 0$ , the connectance of the network is 3.9473 times greater if the maximum pollen carryover is unlimited versus the case when pollen carryover is limited to only one flower. However, when  $\delta_{\max} = 180$ , the connectance of the network is only 2.2232 times greater if the maximum pollen carryover is unlimited.

When considering the actual tree locations at the Rice Center, the connectance of the network is close to half of the connectance value with randomly-placed trees. The differences between the networks is greatest when  $\delta_{\max}$  is close to  $0^\circ$ . Connectance values for simulations run with the Rice Center data are shown in Figure 3.5.

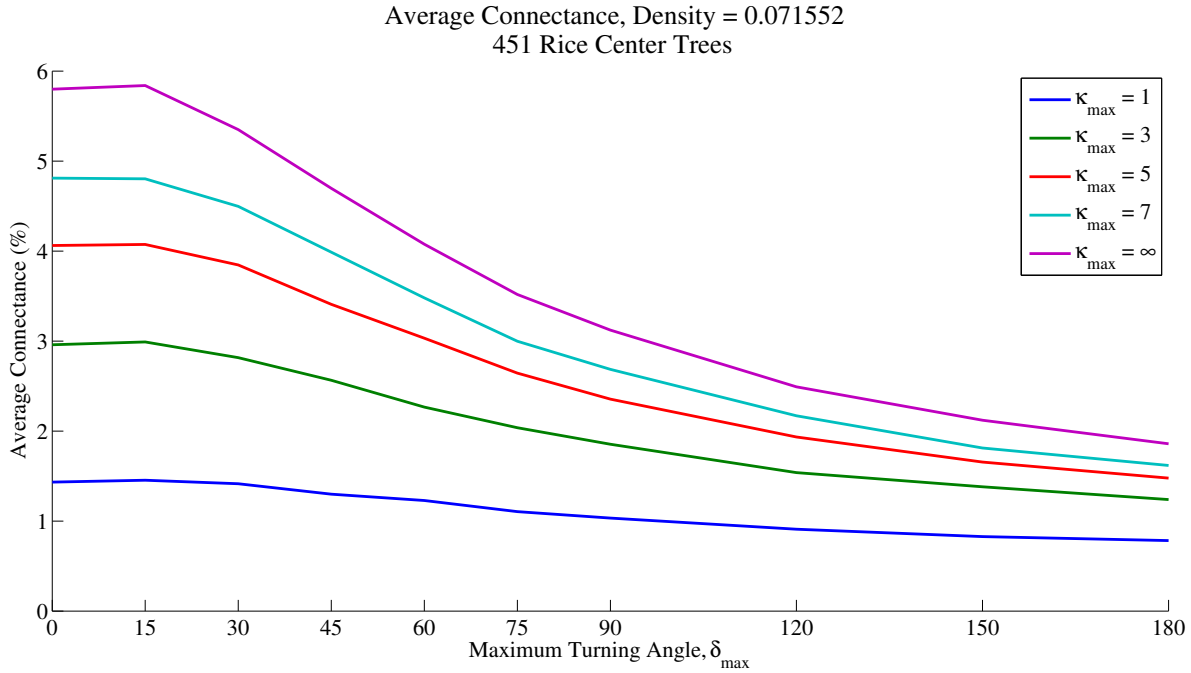


Figure 3.5: *Connectance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

### 3.3 Average weighted diversity of fathers

In Figure 3.6, the average weighted diversity of fathers is clearly affected by both the maximum turning angle of insects and in pollen carryover. As the maximum turning angle increases, the average weighted diversity of fathers tends to decrease. The greatest change occurs between  $15^\circ$  and  $90^\circ$  and tends to even out at the extremes.

The differences in average weighted diversity of fathers as pollen carryover increases are exactly as one would expect. As described earlier, with greater potential for more and more fathers, the average number of fathers contributing to seeds on mother trees increases as the maximum turning angle of insects decreases. This adds more randomness to the system and greater genetic diversity to the tree population. That is, insects which travel in straighter paths not only distribute pollen greater distances, but also with greater diversity.



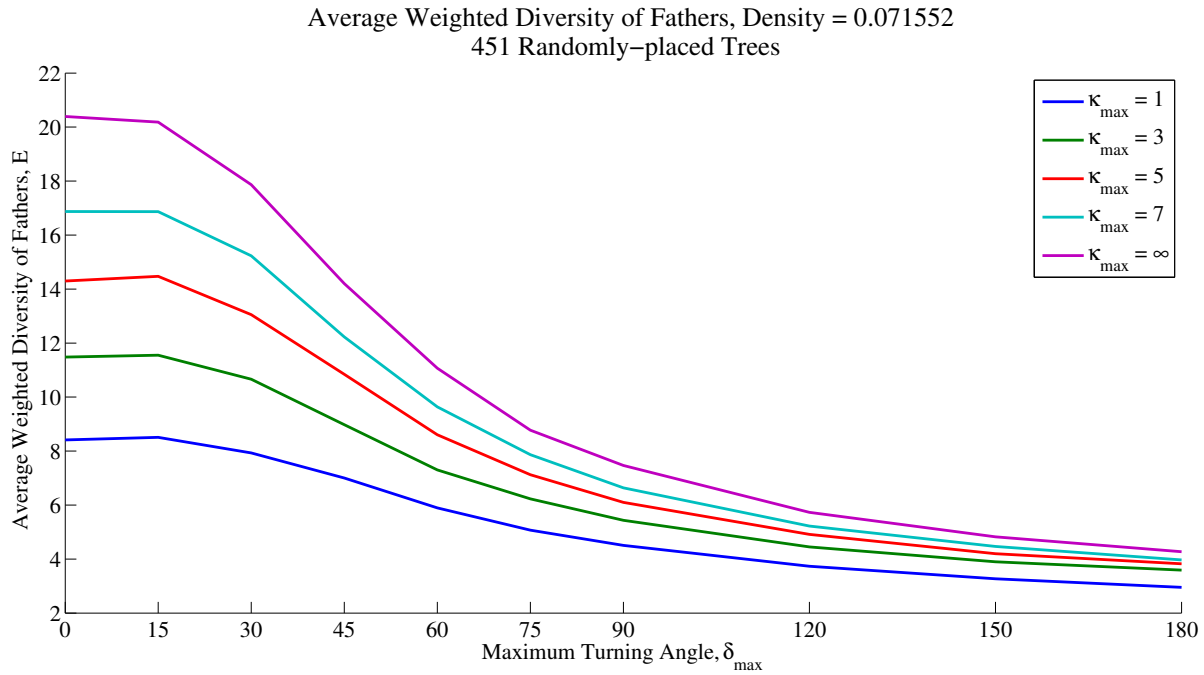


Figure 3.6: *Average weighted diversity of fathers*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

When comparing these data to the data from the Rice Center in Figure 3.7, the distribution has a larger average weighted diversity of fathers. Trees that are in densely packed groups are going to be greatly influenced by surrounding trees so that trees from greater distances away will have less of a comparative impact on the fatherhood of seeds. This comparative impact is characteristic of what the average weighted diversity of fathers describes.

### 3.4 Average pollination distance

The average pollination distance for insects is shown in Figure 3.8. As expected, decreasing the value of  $\delta_{\max}$  increases the average pollination distance. Also as expected, increasing  $\kappa_{\max}$  increases the average pollination distance.

Using Rice Center data, if  $\delta_{\max}$  is close to  $0^\circ$ , the average pollination distance is greater

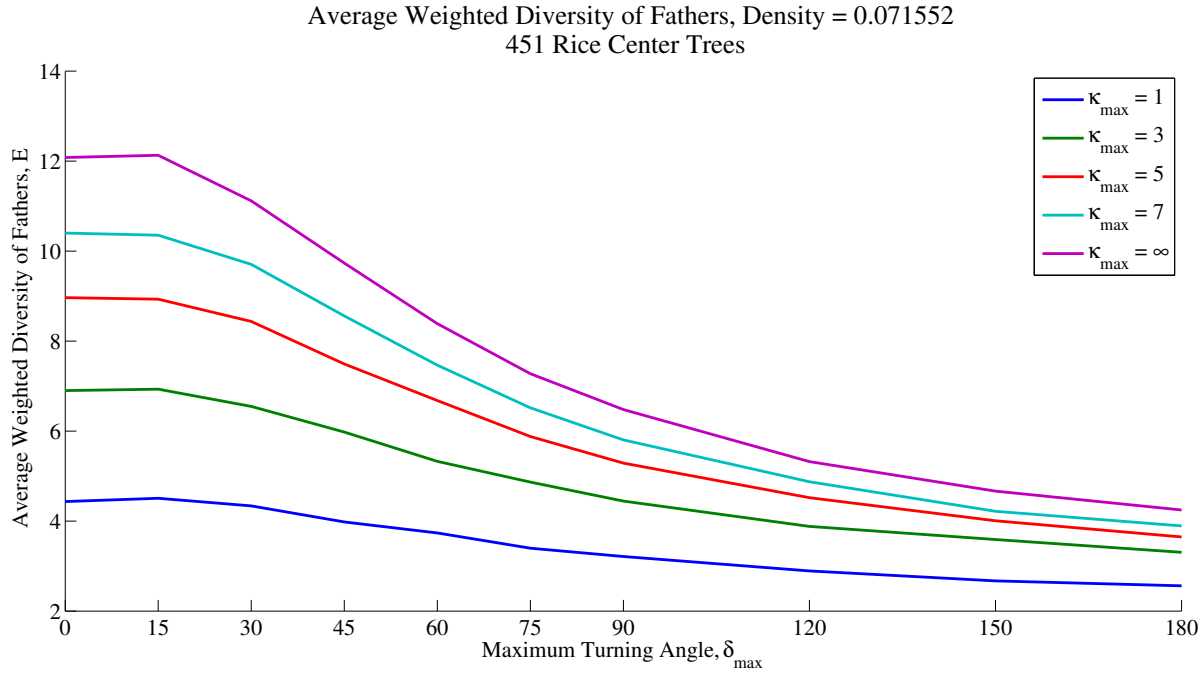


Figure 3.7: *Average weighted diversity of fathers*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

than that of randomly-placed trees. However, if  $\delta_{\max}$  is close to  $180^\circ$ , the average pollination distance using Rice Center data is less than that of randomly-placed trees.

If  $\delta_{\max}$  is close to  $0^\circ$ , this is representative of an insect pollinator traveling in nearly a straight line. The average distance between trees an insect visits is greater where there are large empty areas. For example, if an insect passes by a group of trees in nearly the same place, it may only be able to pollinate one flower before moving on to the next group of trees. The average distance between these groups of trees will be greater than the average distance between individual trees in an environment in which trees are equally spaced.

If  $\delta_{\max}$  is close to  $180^\circ$ , this is representative of insects that remain close to where they started and closely resembles wind dispersal of pollen. Even though some insects will pass by clusters of trees, other insects may not be able to visit any trees. Still others may only be able to visit a few trees. These insects would have a smaller average pollination distance,

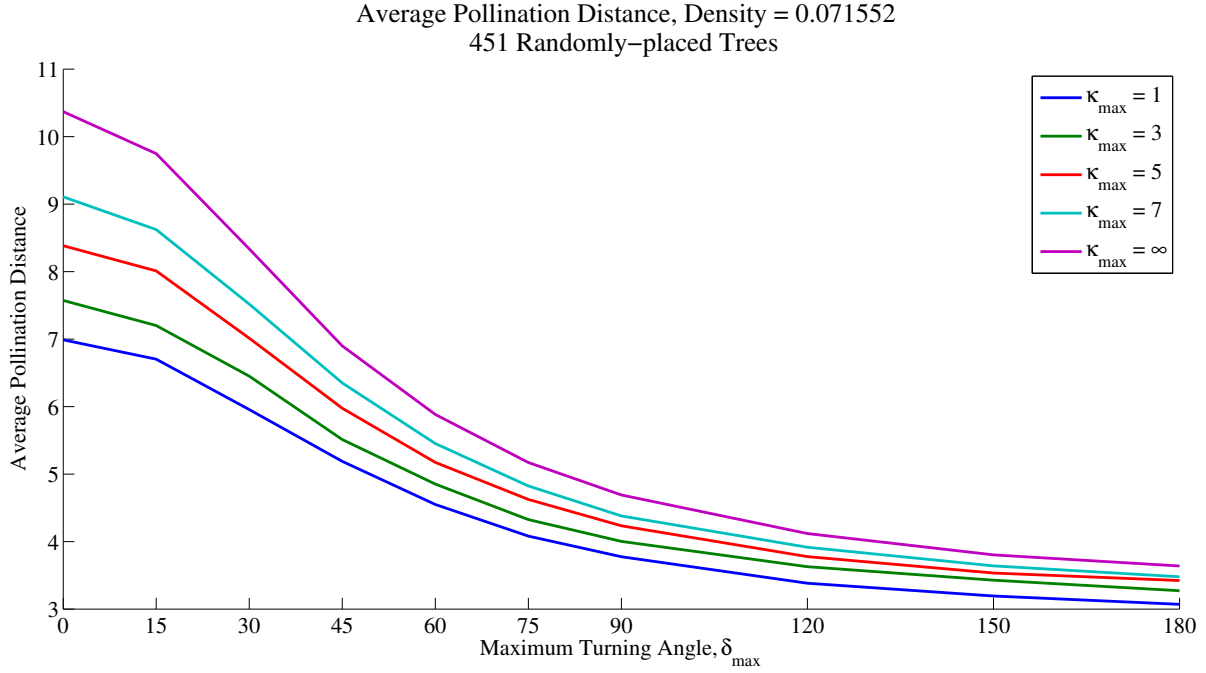


Figure 3.8: *Average pollination distance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

lowering the average pollination distance among all insects.

If the probability of an insect creating a pollination event remains constant such that  $P_{\kappa} = \rho$  for all  $\kappa \leq \kappa_{\max}$ , and pollen carryover is unlimited such that  $\kappa_{\max} = \infty$ , the resulting average pollination distance curve would be as in the top curve on Figure 3.10. However, this would imply that an insect could carry an enormous amount of pollen, which is unrealistic. This demonstrates the importance of defining  $P_{\kappa}$  such that it is monotonically decreasing.

### 3.5 Average maximum pollination distance

The importance of defining  $P_{\kappa}$  such that  $P_{\kappa} = \rho(1 - \rho)^{\kappa-1}$  for all  $\kappa \leq \kappa_{\max}$  is further demonstrated by observing the effects of setting  $P_{\kappa} = \rho$  for all  $\kappa \leq \kappa_{\max}$ . In Figure 3.11, if  $\kappa_{\max} = \infty$ , the average maximum pollen dispersal distance for an insect is limited only by

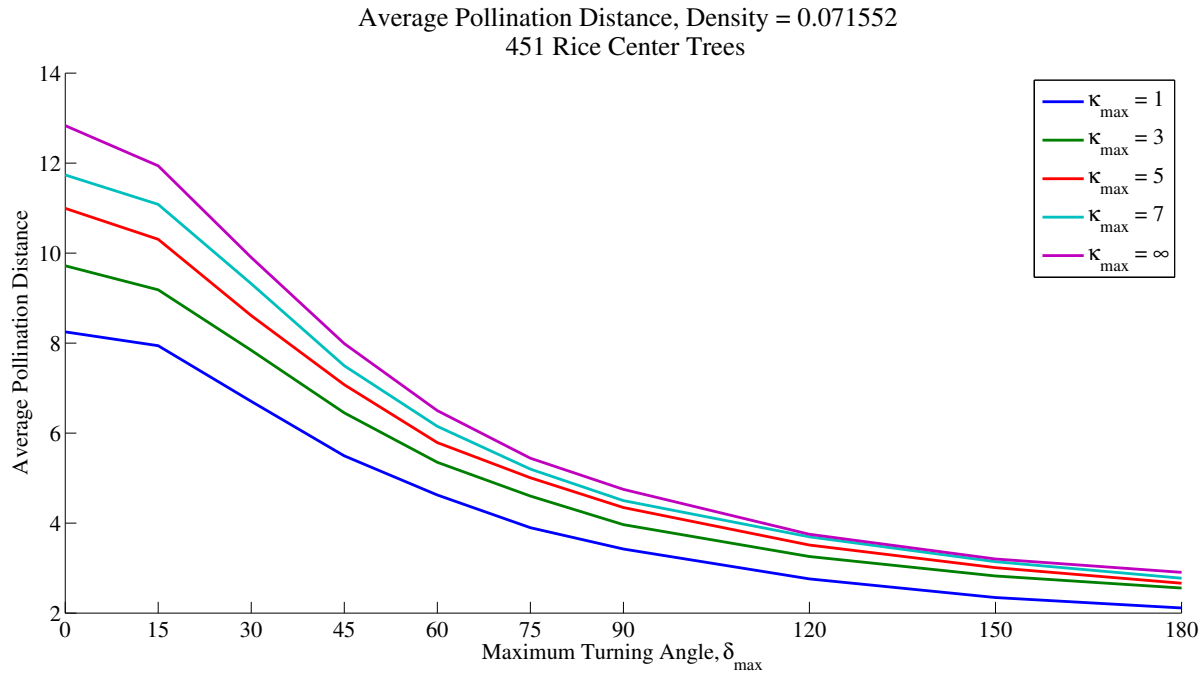


Figure 3.9: *Average pollination distance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

the size of the field for  $\delta_{\max}$  small. A reasonable average maximum pollen dispersal curve is shown in Figure 3.12 by setting  $P_{\kappa} = \rho(1 - \rho)^{\kappa-1}$  for all  $\kappa \leq \kappa_{\max}$ .

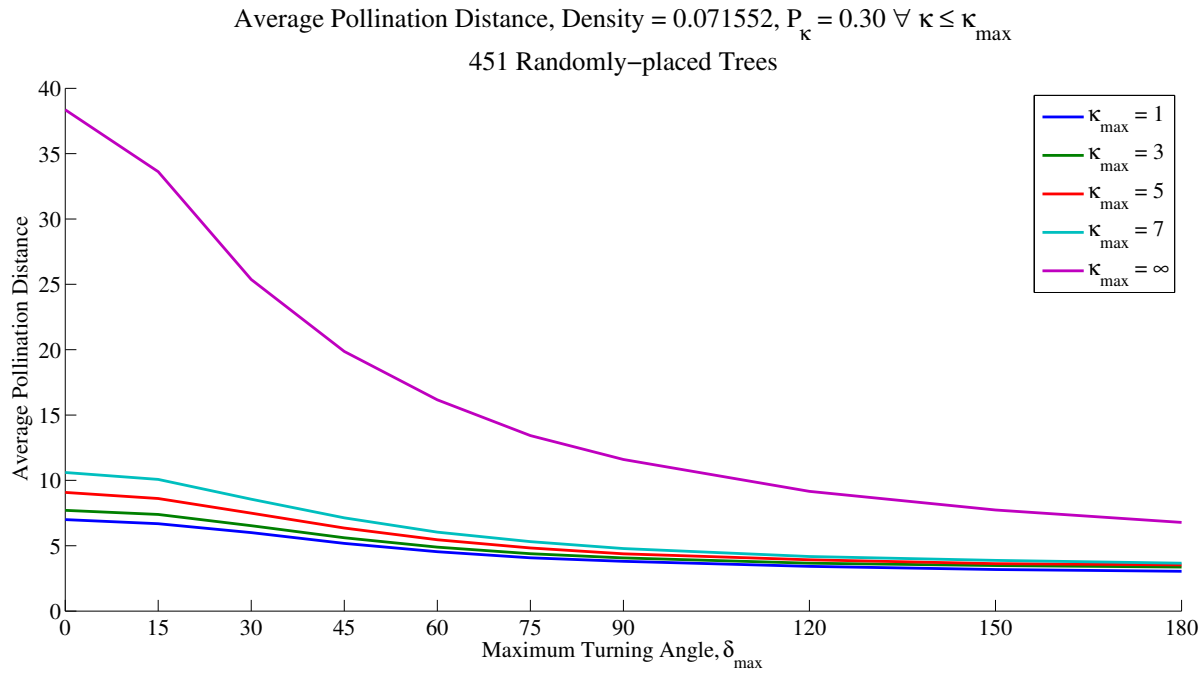


Figure 3.10: *Average pollination distance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance equal for all  $\kappa \leq \kappa_{\max}$ . Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

When comparing the data from the randomly-placed trees in Figure 3.12 with the data from the Rice Center in Figure 3.13, the same inferences can be made about the average maximum pollination distances as were made with the average pollination distances in Figure 3.8 and Figure 3.9.

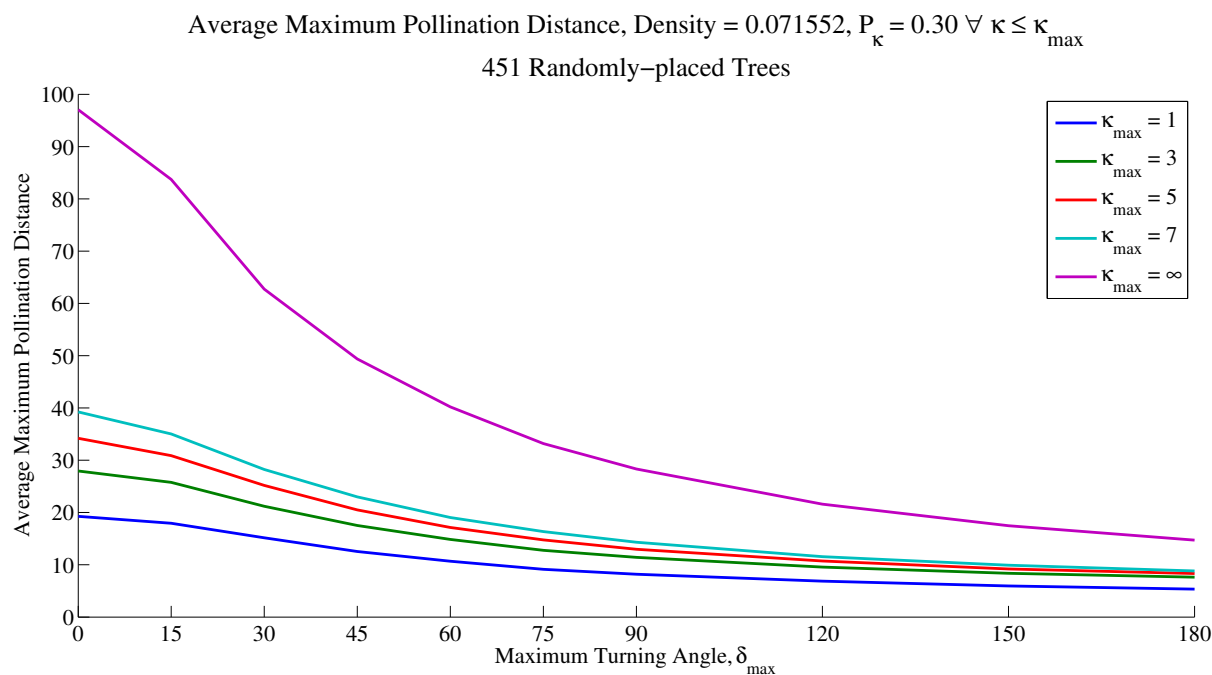


Figure 3.11: Average maximum pollination distance. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance equal for all  $\kappa \leq \kappa_{\max}$ . Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

### 3.6 Clustering coefficient of fathers

As shown in Figure 3.14, for a field of randomly-placed trees, there is a maximum value for the clustering coefficient of fathers,  $C$ . This maximum is between  $60^\circ$  and  $90^\circ$  for all maximum pollen carryover values,  $\kappa_{\max}$ . The reason for this local maximum can be explained by examining the extreme values of  $\delta_{\max}$ . When  $\delta_{\max} = 0^\circ$ , insects travel across the landscape and do not stay in a small neighborhood. Since the clustering coefficient of fathers is an average measure of clustering at a local level, it is natural for  $C$  to be low if insects do not remain in a small neighborhood. At the other extreme, if  $\delta_{\max} = 180^\circ$ , insects do not move around enough to increase the value of  $C$ . The average connectance is significantly lower as shown in Figure 3.4. When  $\delta_{\max}$  is not at an extreme value, the displacement of the insects is high enough to visit many trees, but low enough so that all of

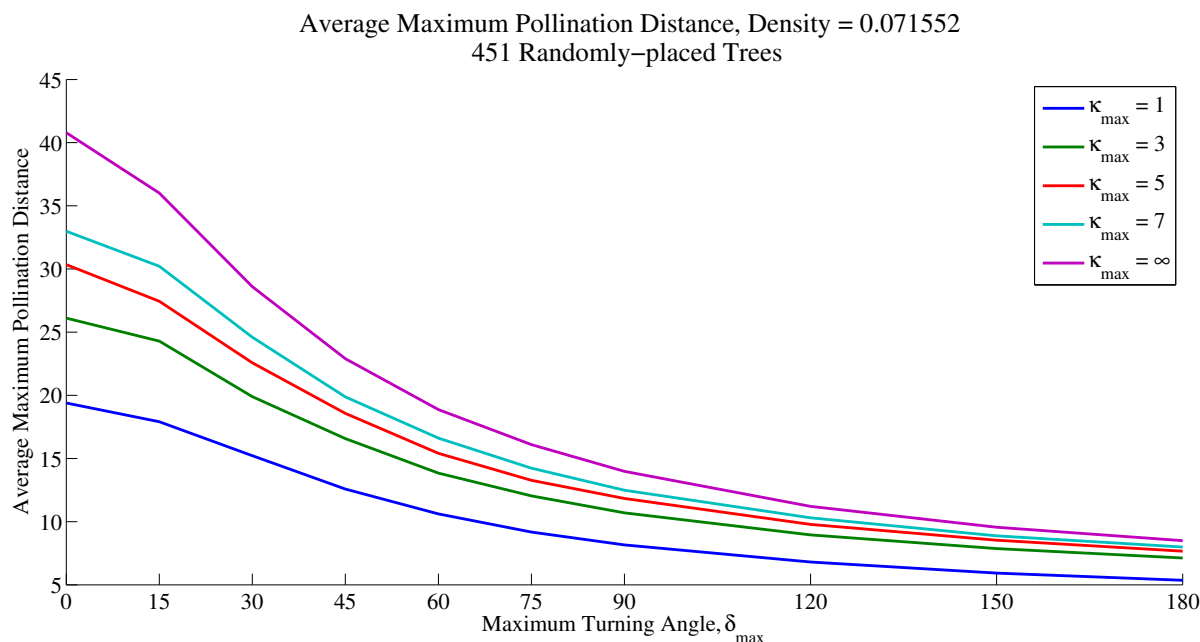


Figure 3.12: Average maximum pollination distance. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

the trees that it visits are within a closer proximity to one another.

Modeled data on the clustering coefficient of fathers,  $C$  from the Rice Center is shown in Figure 3.15. The  $C$  values slowly increase as  $\kappa_{\max}$  increases over the entire interval from  $0^\circ$  to  $180^\circ$ , mostly flattening out for  $\kappa_{\max} > 75^\circ$ . As  $\delta_{\max}$  approaches  $180^\circ$ , insects remain in the same general area. Thus, in locally dense patches of trees, clustering will naturally be higher.

Unexpectedly, varying the tree density,  $\omega$ , did not have a major effect on  $C$ . It would seem that varying  $\omega$  would have the same quantitative effect on  $C$  as varying the maximum insect turning angle,  $\delta_{\max}$ . We suspect that the reason for the relative consistency of values for  $C$  is that the values are based on an average of 10 simulations with random data. The values for  $C$ , varying  $\omega$  and  $\delta_{\max}$ , are shown in Figure 3.16.

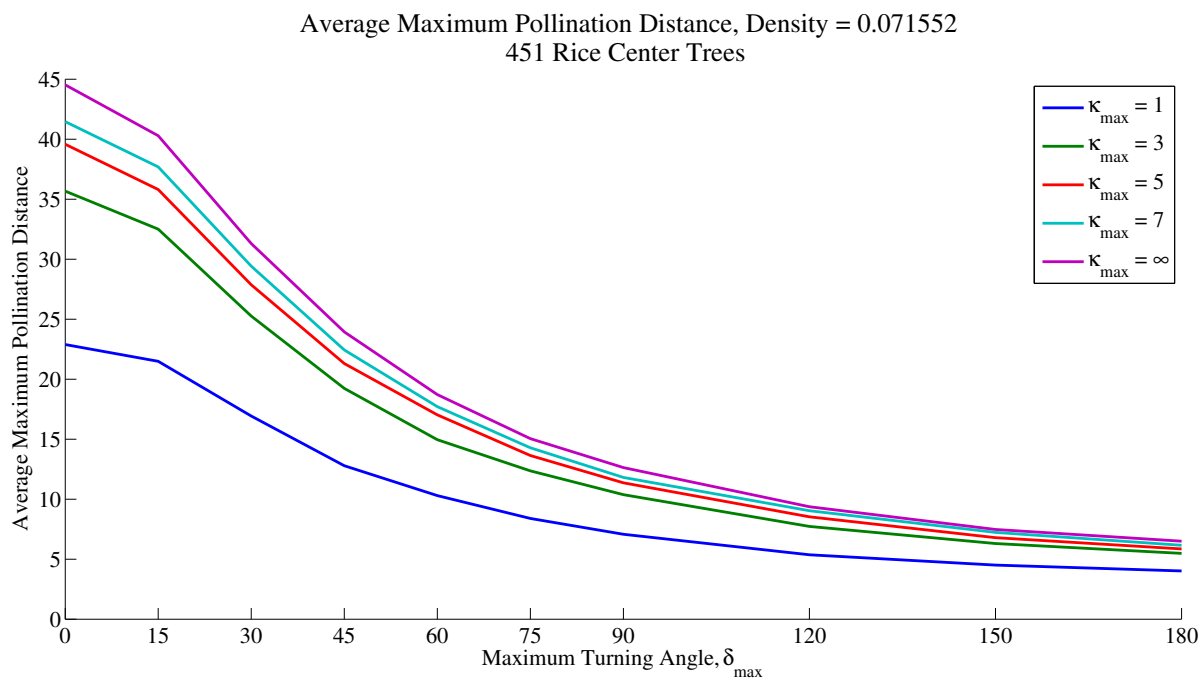


Figure 3.13: *Average maximum pollination distance*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .



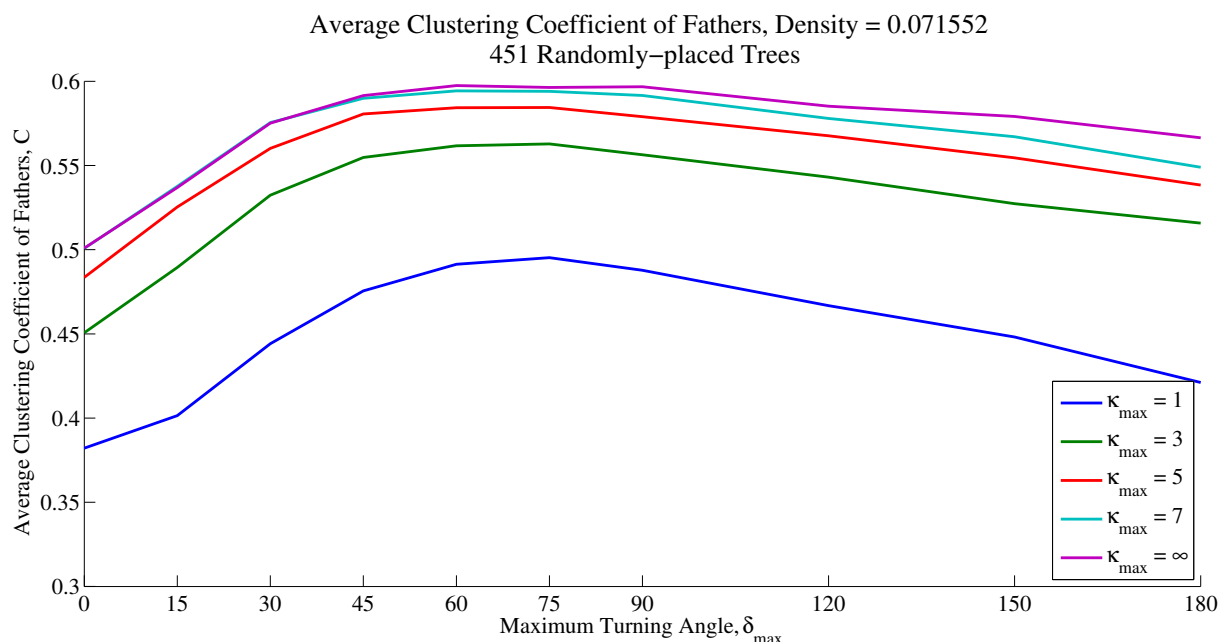


Figure 3.14: *Clustering coefficient of fathers*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

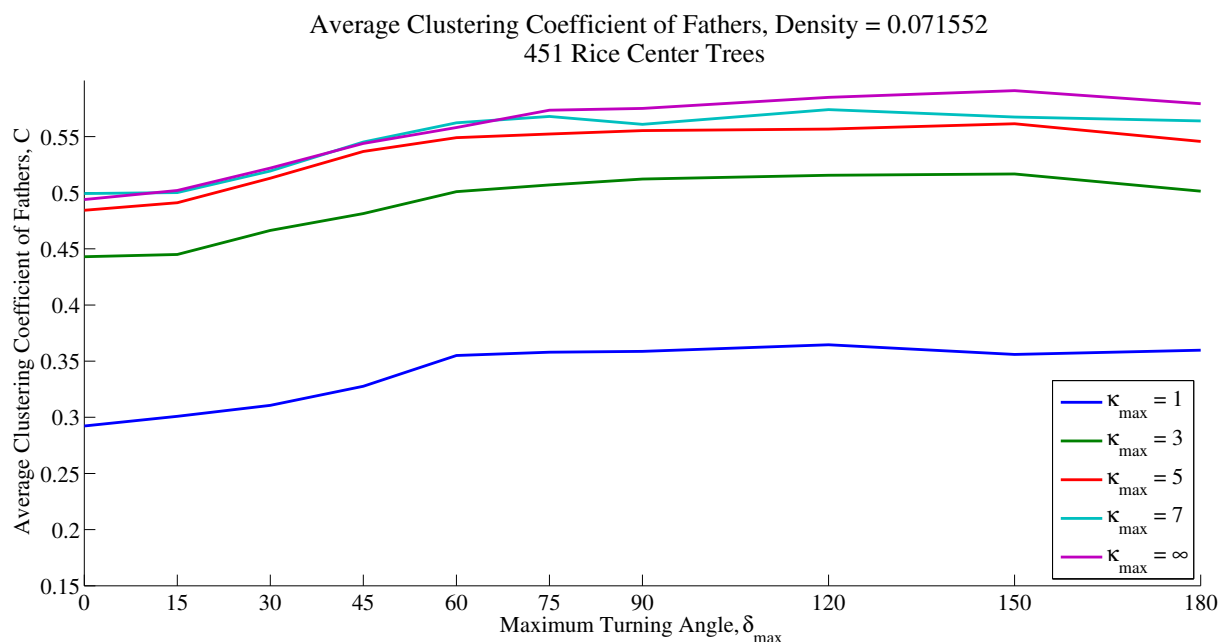


Figure 3.15: *Clustering coefficient of fathers*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

Clustering Coefficient of Fathers, Field Size  $100 \times 100$ , Randomly-placed Trees

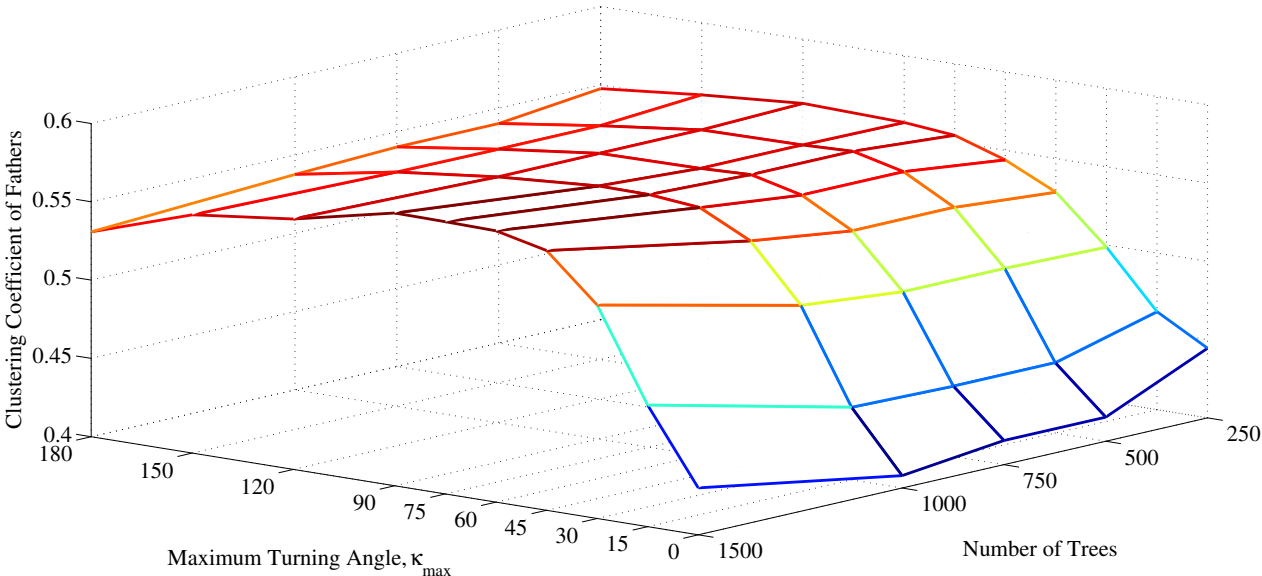


Figure 3.16: *Clustering coefficient of fathers.* Field Size  $100 \times 100$ . Tree density  $\omega = \{0.025, 0.050, 0.075, 0.100, 0.150\}$  ( $\tau = \{250, 500, 750, 1000, 1500\}$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \infty$ .

## Discussion

From the agent-based, correlated random walk model presented, we observe the effects of varying the probability of fertilization,  $P_\kappa$ , the maximum pollen carryover,  $\kappa_{\max}$ , the maximum insect turning area,  $\delta_{\max}$ , and the density of trees,  $\omega$ , on the distribution of pollen within a population of *Cornus florida*.

When the probability of fertilization is constant, i.e.,  $P_\kappa = \rho$  for all  $\kappa \leq \kappa_{\max}$ , simulations do not produce realistic results with large  $\kappa_{\max}$  due to the fact that it is much more likely that a tree will be pollinated by a recently visited tree. If  $P_\kappa = \rho(1 - \rho)^{\kappa-1}$  for all  $\kappa \leq \kappa_{\max}$ , then  $P_\kappa$  is a monotonically decreasing function and we obtain realistic results for all values of  $\kappa_{\max}$ .

When  $\kappa_{\max}$  is varied between  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ , the dispersal distance of pollen changes. For instance, as the maximum pollen carryover,  $\kappa_{\max}$ , increases, we see reasonable increases in the mean and variance in the number of fathers per mother,  $\Phi_m$ , the connectance,  $L$ , the average weighted diversity of fathers,  $E$ , the average pollination distance,  $\bar{D}$ , the average maximum pollination distance,  $\tilde{D}$ , and the clustering coefficient of fathers,  $C$ .

Changing the maximum insect turning angle,  $\delta_{\max}$ , where  $\delta_{\max} \in \{0, 15, 30, 45, 60, 75, 90, 120, 150, 180\}$ , also changes the dispersal distance of pollen. As the maximum insect turning angle,  $\delta_{\max}$ , increases, we see decreases in the network connectance,  $L$ , the average weighted diversity of fathers,  $E$ , the average pollination distance,  $\bar{D}$ , the average maximum pollination distance,  $\tilde{D}$ , and the clustering coefficient of fathers,  $C$ .

When  $\delta_{\max} = 180^\circ$ , pollen is distributed in a purely random walk. This directly results in

random pollen distribution, and is a near representation of pollen dispersal by wind. When  $\delta_{\max} = 0^\circ$ , insects travel in a straight line, only changing direction when bouncing off of the boundary of the field. This leads to a greater spatial displacement for each insect and thus a greater distance that pollen travels, resulting in greater genetic diversity in the *C. florida* population. While neither of these extremes may be biologically relevant in *C. florida* populations, we note that the clustering coefficient of fathers,  $C$ , is maximized when  $\delta_{\max}$  is between  $60^\circ$  and  $90^\circ$ , which could help illuminate some of the biological processes at work in the system.

When the density of randomly-placed trees on a  $100 \times 100$  field is varied in the range  $\omega = \{0.0250, 0.0500, 0.0750, 0.1000, 0.1500\}$ , no major changes are observed in the clustering coefficient of fathers.

Major changes are observed when comparing simulations using randomly-placed trees with simulations using the tree-placement at the Rice Center. When using the Rice Center data, we see a bimodal distribution in the number of fathers per mother, the connectance values are halved, the average weighted diversity of fathers is lower, the average pollination distance is lower when  $\delta_{\max}$  is close to  $0^\circ$  and higher when  $\delta_{\max}$  is close to  $180^\circ$ , and the clustering coefficient of fathers exhibits both quantitative and qualitative differences. All of these differences highlight the need for specificity in describing the tree locations within a specific ecosystem in order to truly understand how pollen is distributed within that ecosystem. The differences in these network indicators is due to the non-uniform distribution of trees at the Rice Center.

## Bibliography

## Bibliography

- [1] F. Bartumeus, J. Catalan, G. M. Viswanathan, E. P. Raposo, and M. G. E. da Luz, *The influence of turning angles on the success of non-oriented animal searches*, J. Theor. Biol. **252** (2008), 43–55.
- [2] R. Bidaux and N. Boccara, *Correlated Random Walks with a Finite Memory Range*, Int. J. Mod. Phys. C **11** (2000) 921–947.
- [3] P. Bovet and S. Benhamou, *Spatial analysis of animal's movements using a correlated random walk model*, J. Theor. Biol. **131** (1988), 419–433.
- [4] J. A. Byers, *Correlated random walk equations of animal dispersal resolved by simulation*, Ecology **82** (2008), 1620–1690.
- [5] E. A. Codling, M. J. Plank, and S. Benhamou, *Random walk models in biology*, J. R. Soc. Interface **5** (2008), 813–834.
- [6] T. J. deJong, P. G. L. Klinkhamer, and M. J. Van Staalduinen, *The consequences of pollination biology for selection of mass or extended blooming*, Functional Ecology **6** (1992), 606–615.
- [7] R. J. Dyer, *Coordinates of C. florida at the VCU Rice Center*, unpublished (2014).
- [8] ———, *Powers of discerning: challenges to understanding dispersal processes in natural populations*, Molecular Ecology **16** (2007), 4881–4882.
- [9] R. J. Dyer, D. M. Chan, V. A. Gardiakos, and C. A. Meadows, *Pollination networks: quantifying pollen pool covariance networks and the influence of intervening landscape on genetic connectivity in the North American understory tree, Cornus florida L.*, Landscape Ecology **27** (2012), 239–251.
- [10] E. Foster, *An agent based gene flow model*, VCU Thesis and Dissertations (2009), paper 1726.
- [11] S. Jha and C. Kremen, *Resource diversity and landscape-level homogeneity drive native bee foraging*, Proc Natl Acad Sci USA **110** (2013), 555–558.
- [12] S. D. Johnson and L. A. Nilsson, *Pollen carryover, geitonogamy, and the evolution of deceptive pollination systems in orchids*, Ecology **80** (1999), 2607–2619.

- [13] S. E. Jørgensen, *Ecosystem Ecology*, Elsevier, Amsterdam, The Netherlands, 2009.
- [14] A. J. Mayor, J. F. Grant, M.T. Windham, and R. N. Trigiano, *Insect visitors to flowers of flowering dogwood, *Cornus florida* L., in eastern Tennessee: potential pollinators*, Proceedings of Southern Nursery Association Research Conference, (1999), 192–196.
- [15] W. F. Morris, *Predicting the consequence of plant spacing and biased movement for pollen dispersal by honey bees*, *Ecology* **74** (1993), 493–500.
- [16] B. R. G. Prasad and R. M. Borges, *Searching on patch networks using correlated random walks: Space usage and optimal foraging predictions using Markov chain models*, *J. Theor. Biol.* **240** (2006), 241–249.
- [17] N. Schieritz and P. Milling, *Modeling the forest or modeling the trees: a comparison of system dynamics and agent-based simulation*, Proceedings of the 21st International Conference of the Systems Dynamics Society, (2003).
- [18] V. L. Sork, P. E. Smouse, V. J. Apsit, R. J. Dyer, and R. D. Westfall, *A two-generation analysis of pollen pool genetic structure in flowering dogwood, *Cornus florida* (Cornaceae), in the Missouri Ozarks*, *Am. J. Botany* **92** (2005), 262–271.

## Appendix A

### Data

#### A.1 Graphs

**A.1.1 Number of fathers per mother. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing. Individual maximum pollen carryovers.**

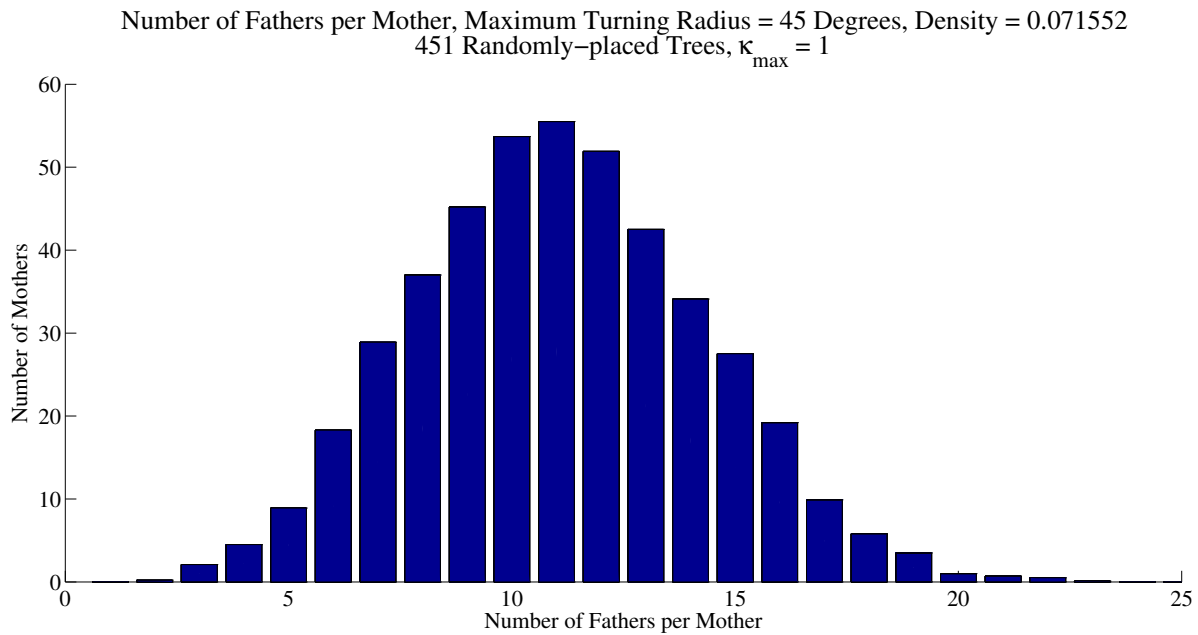


Figure A.1: *Number of fathers per mother.* Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 1$ .



Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Randomly-placed Trees,  $\kappa_{\max} = 3$

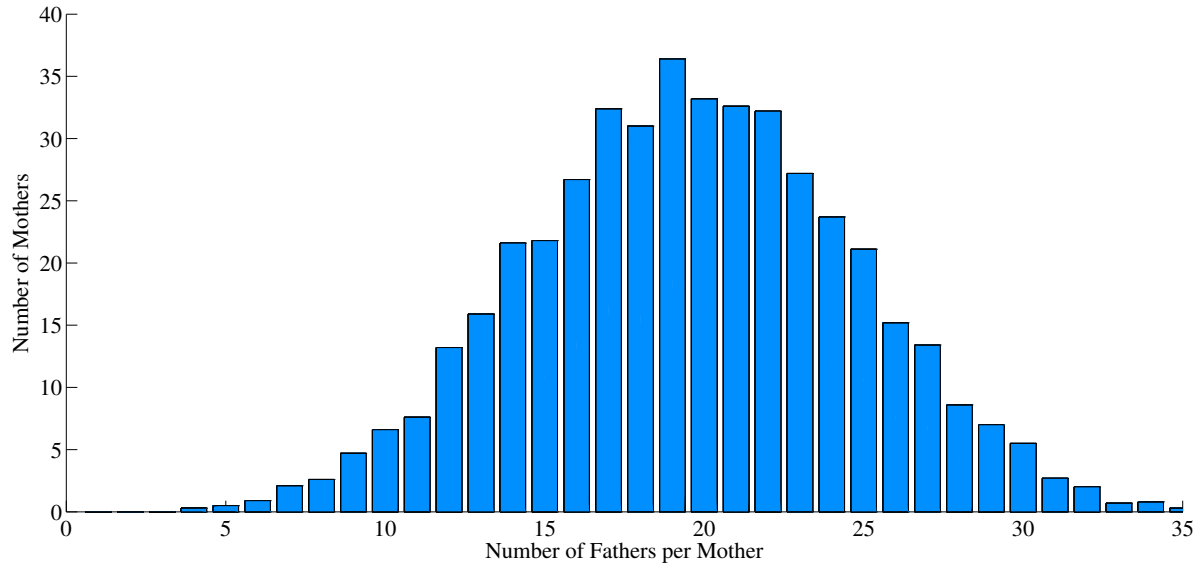


Figure A.2: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 3$ .

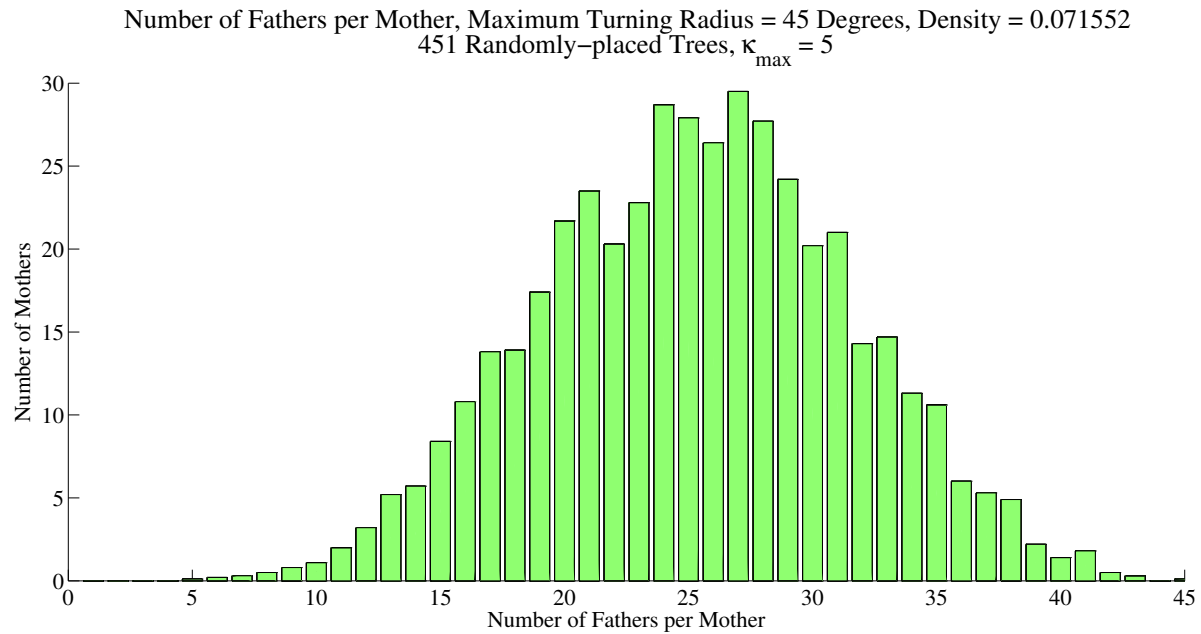


Figure A.3: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 5$ .

Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Randomly-placed Trees,  $\kappa_{\max} = 7$



Figure A.4: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 7$ .

Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Randomly-placed Trees,  $\kappa_{\max} = \infty$

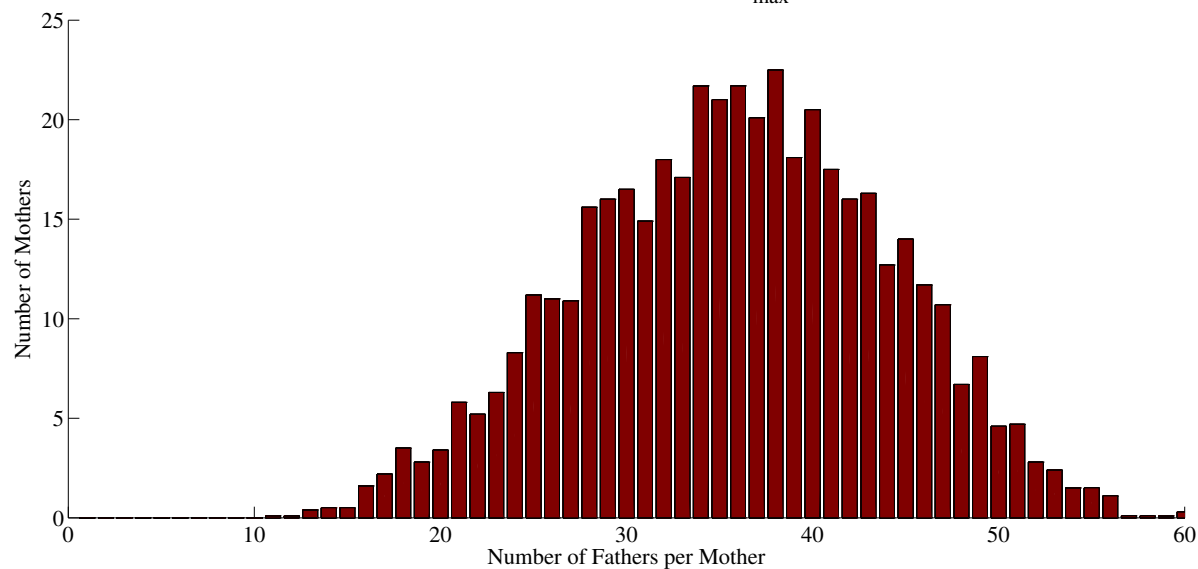


Figure A.5: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \infty$ .

**A.1.2 Number of fathers per mother. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing. Individual maximum pollen carryovers.**

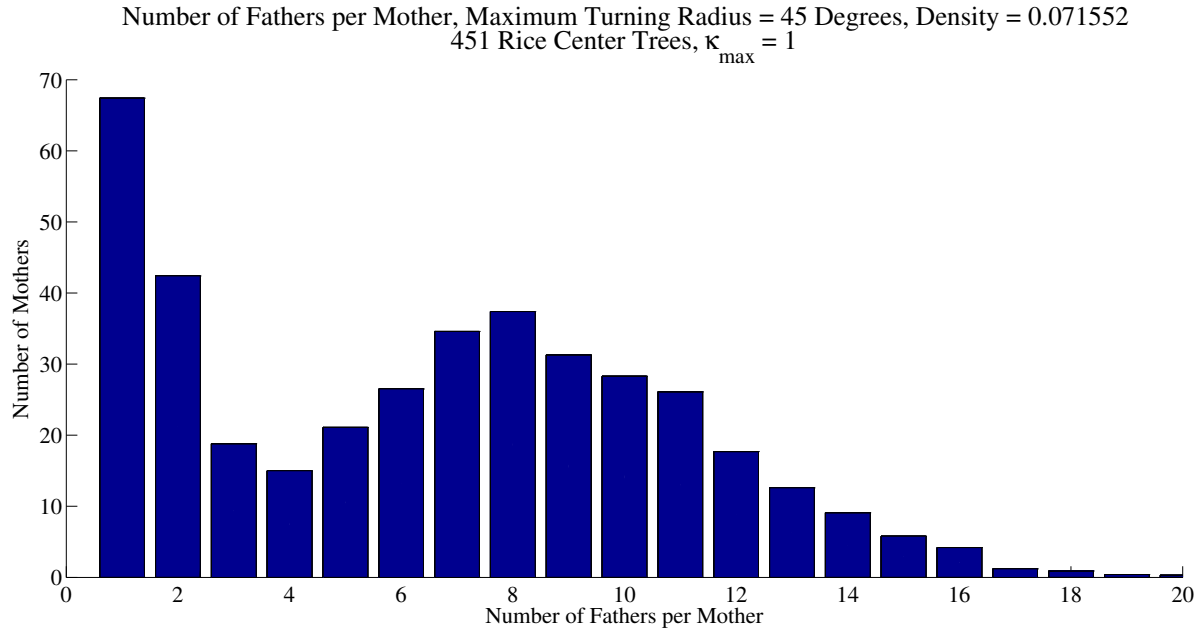


Figure A.6: *Number of fathers per mother.* Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 1$ .

Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Rice Center Trees,  $\kappa_{\max} = 3$

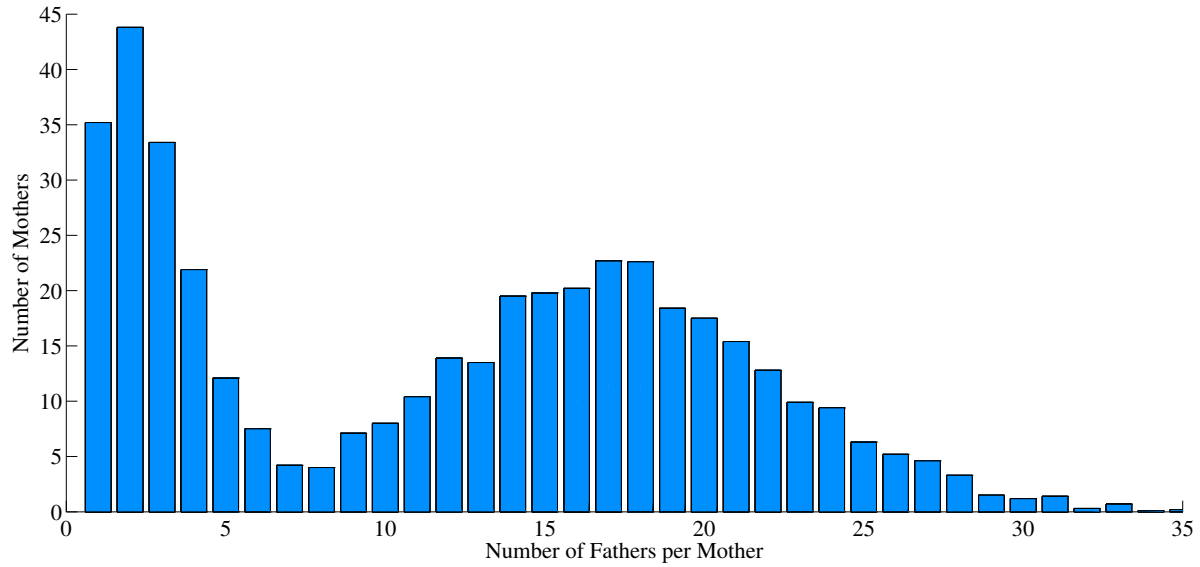


Figure A.7: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 3$ .

Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Rice Center Trees,  $\kappa_{\max} = 5$

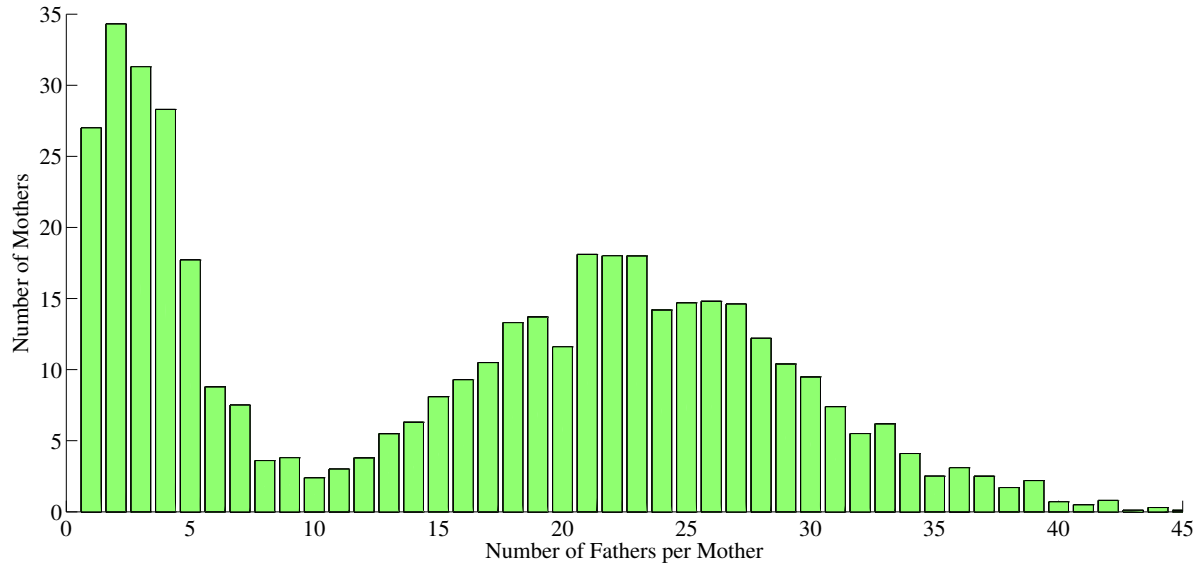


Figure A.8: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 5$ .

Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Rice Center Trees,  $\kappa_{\max} = 7$

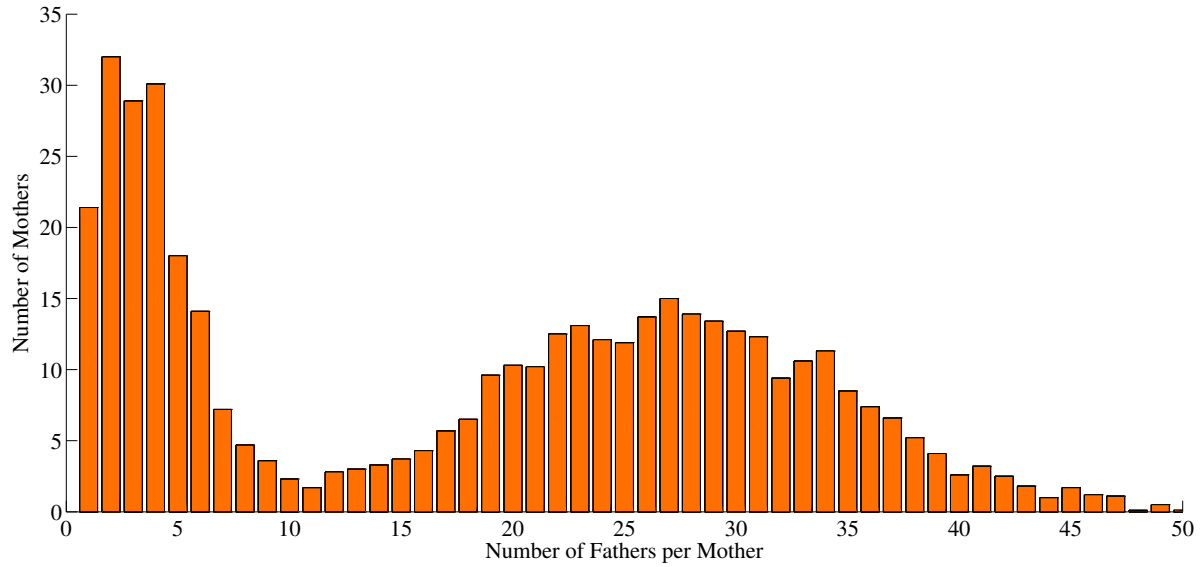


Figure A.9: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = 7$ .



Number of Fathers per Mother, Maximum Turning Radius = 45 Degrees, Density = 0.071552  
 451 Rice Center Trees,  $\kappa_{\max} = \infty$

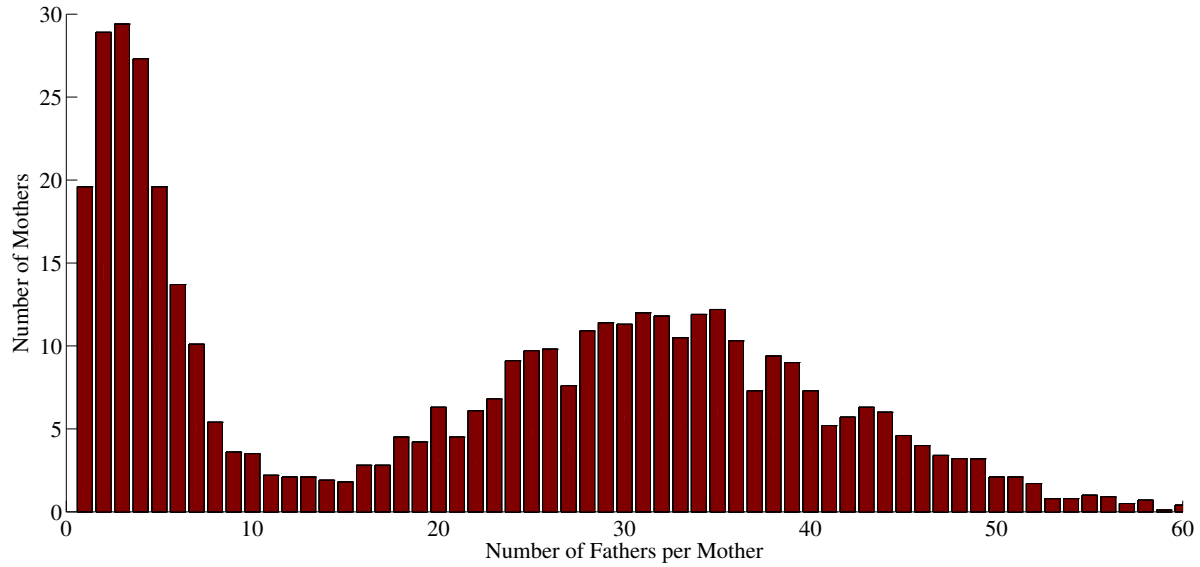


Figure A.10: *Number of fathers per mother*. Field Size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \infty$ .

**A.1.3 Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Pollination chance diminishing.**

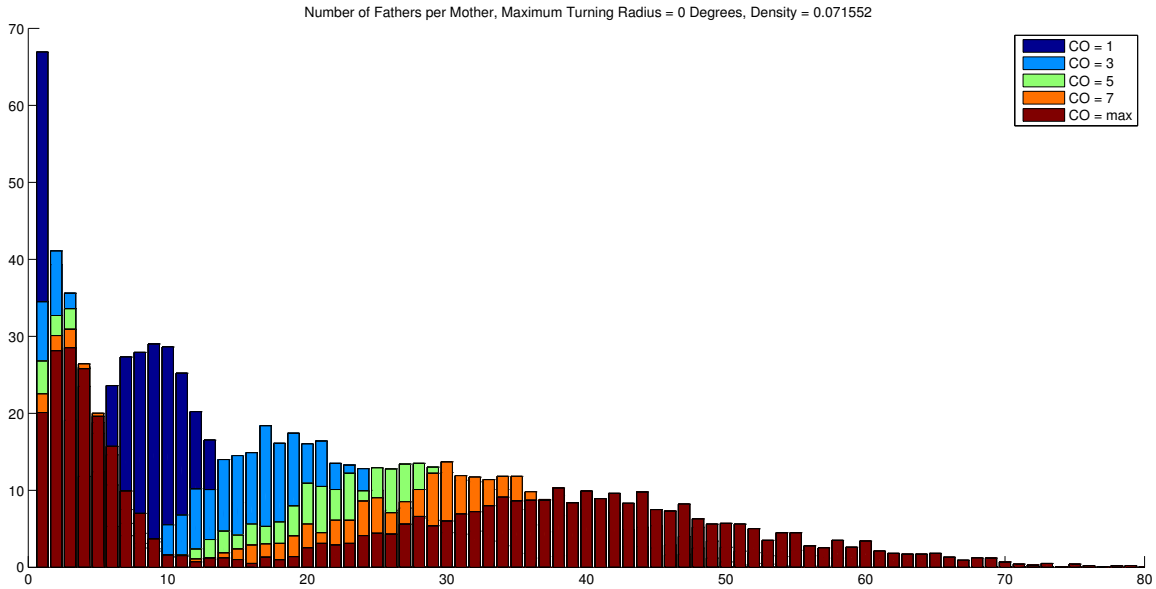


Figure A.11: *Number of fathers per mother*. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 0^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

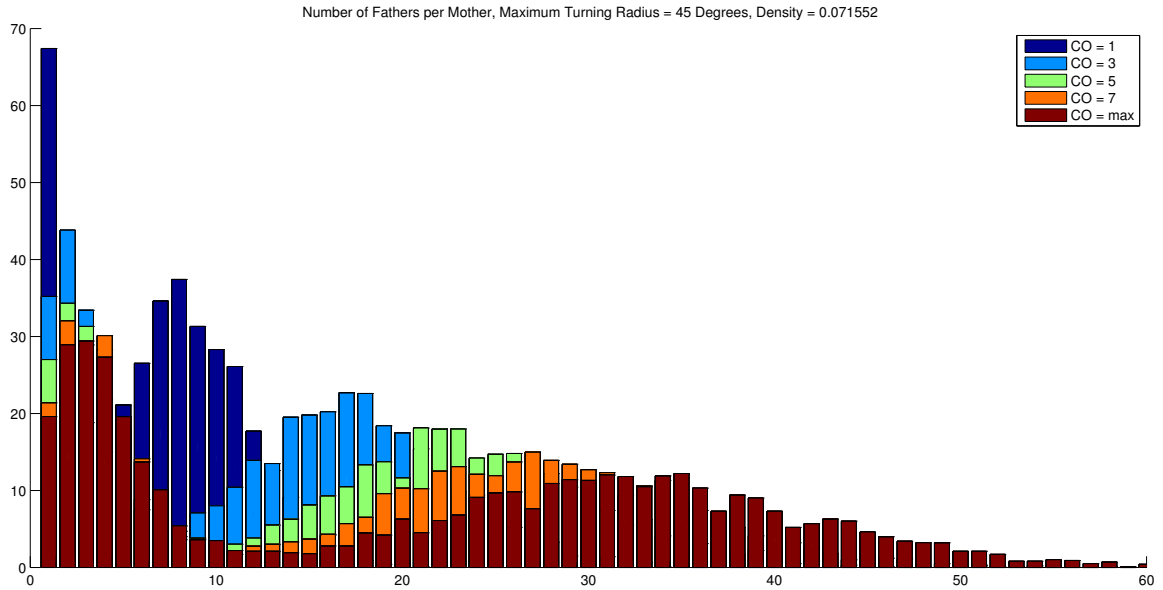


Figure A.12: *Number of fathers per mother*. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

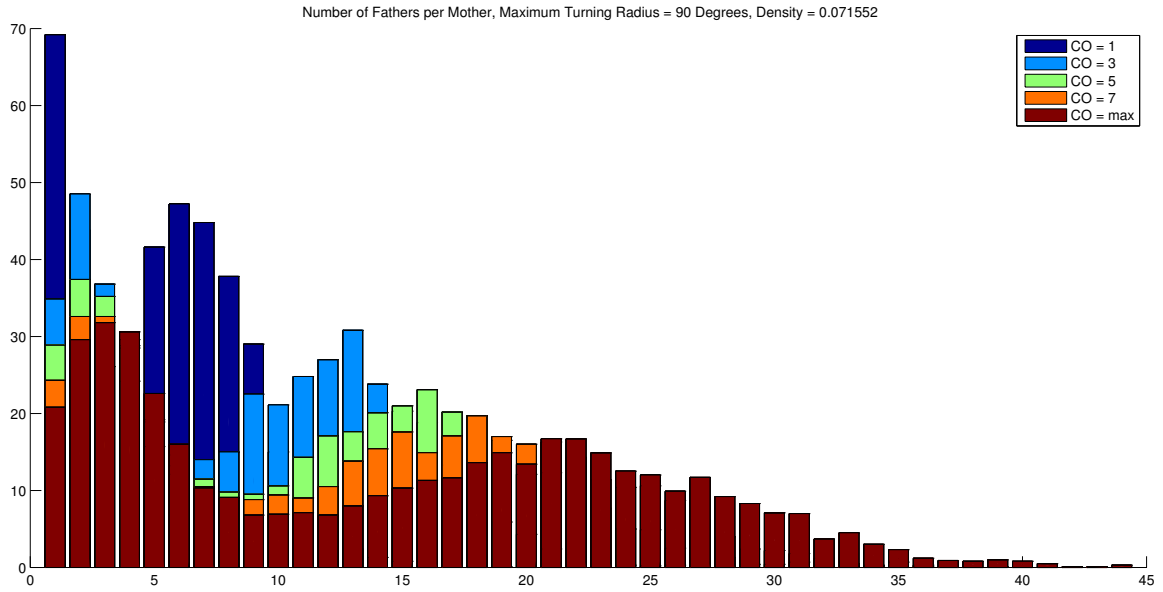


Figure A.13: *Number of fathers per mother*. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 90^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

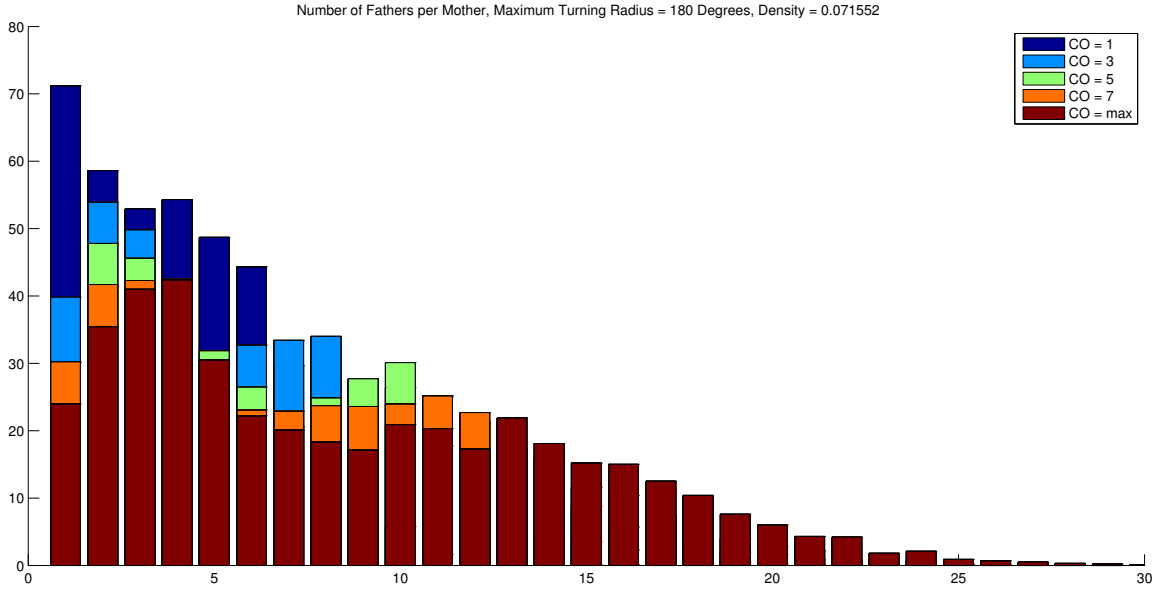


Figure A.14: *Number of fathers per mother*. Field size  $133.2794 \times 47.2927$ . Tree density  $\omega = 0.071552$  ( $\tau = 451$  Rice Center trees). Maximum insect turning radius  $\delta_{\max} = 180^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

**A.1.4 Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees).**

**Pollination chance diminishing.**

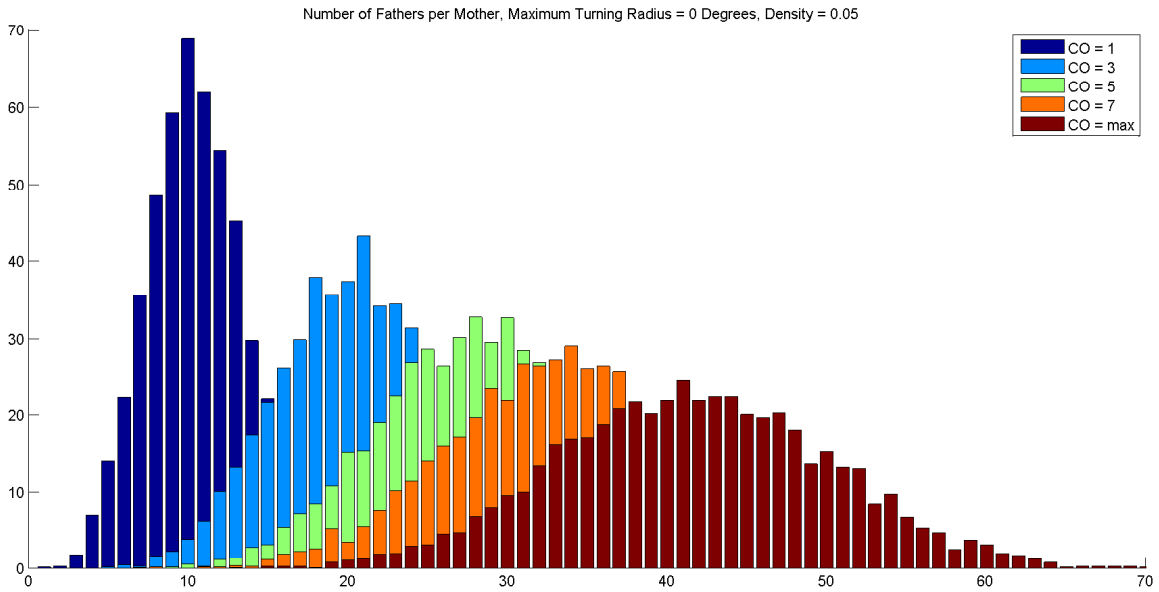


Figure A.15: *Number of fathers per mother.* Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 0^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

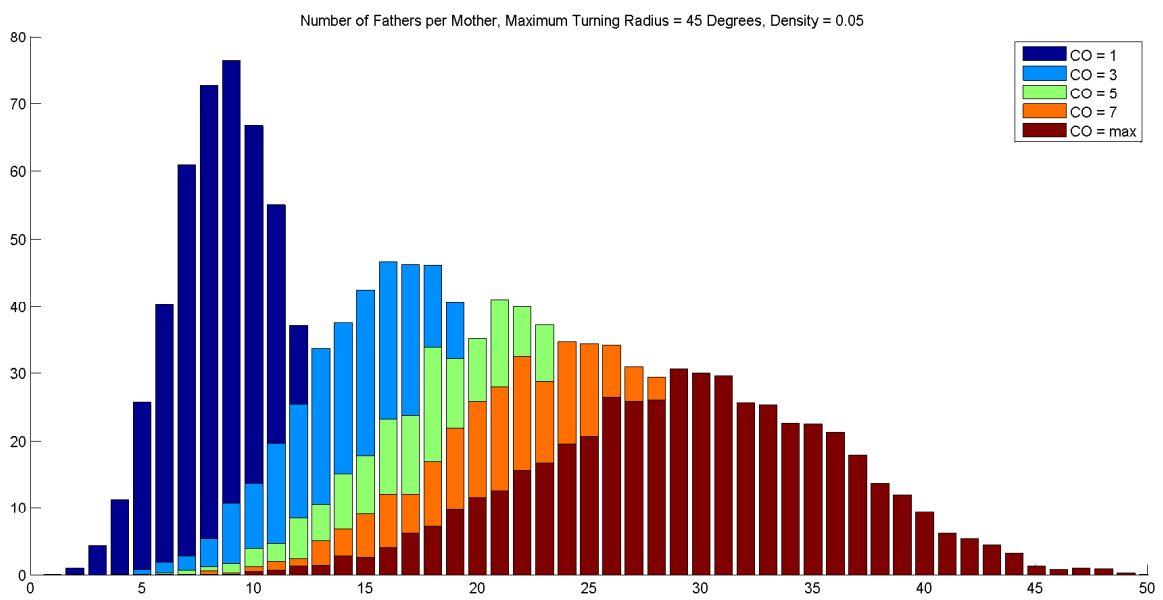


Figure A.16: *Number of fathers per mother*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 45^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

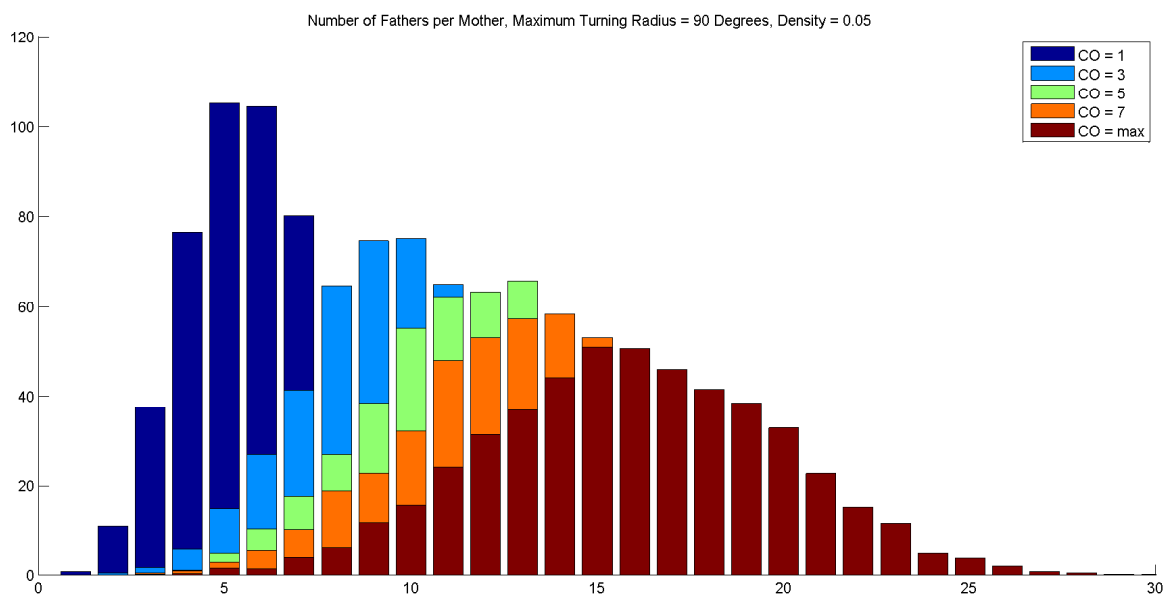


Figure A.17: *Number of fathers per mother*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 90^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .



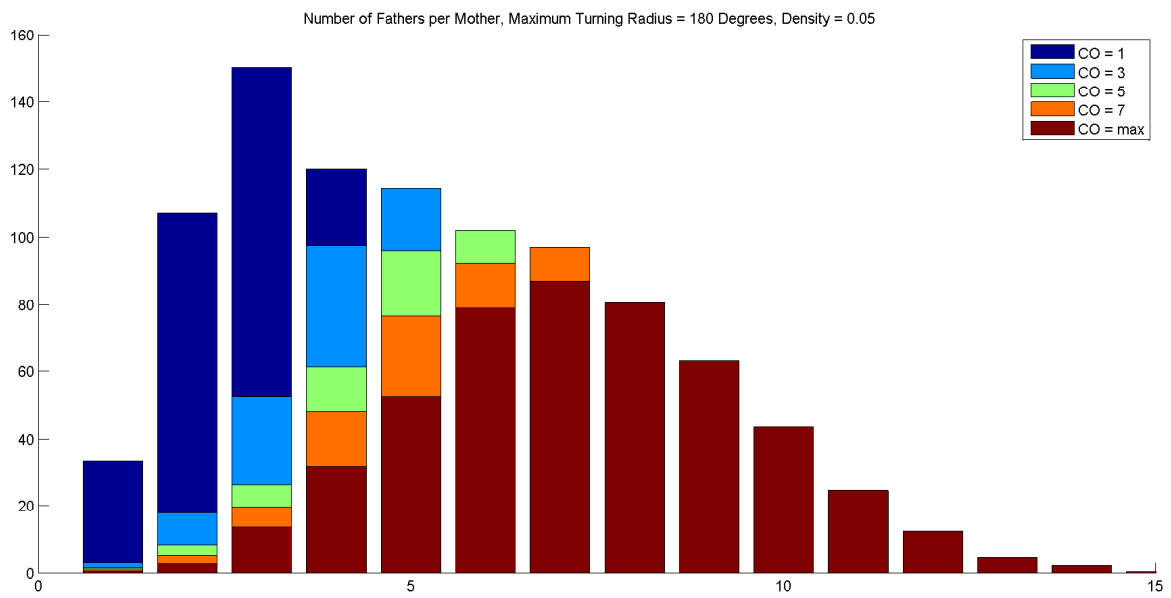


Figure A.18: *Number of fathers per mother*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Maximum insect turning radius  $\delta_{\max} = 180^\circ$ . Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

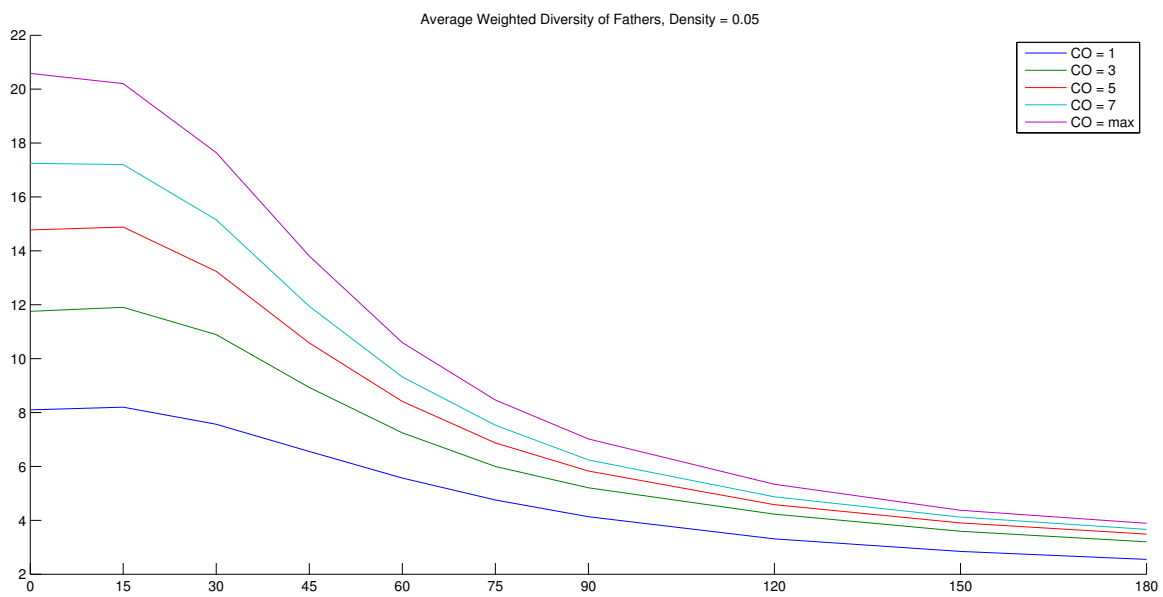


Figure A.19: *Average weighted diversity of fathers*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

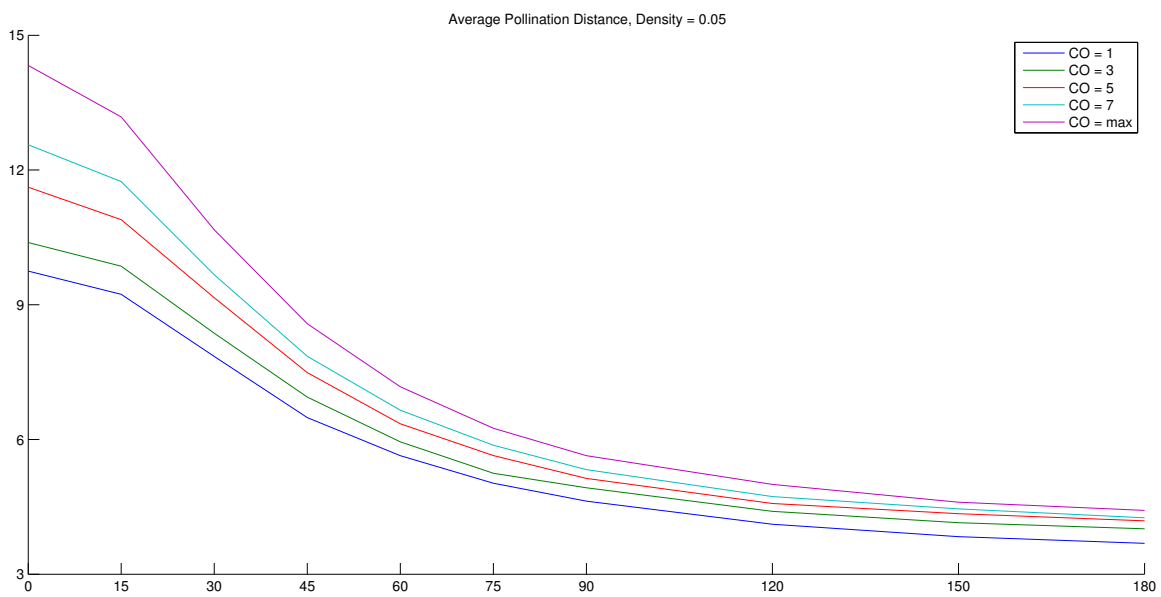


Figure A.20: *Average pollination distance*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

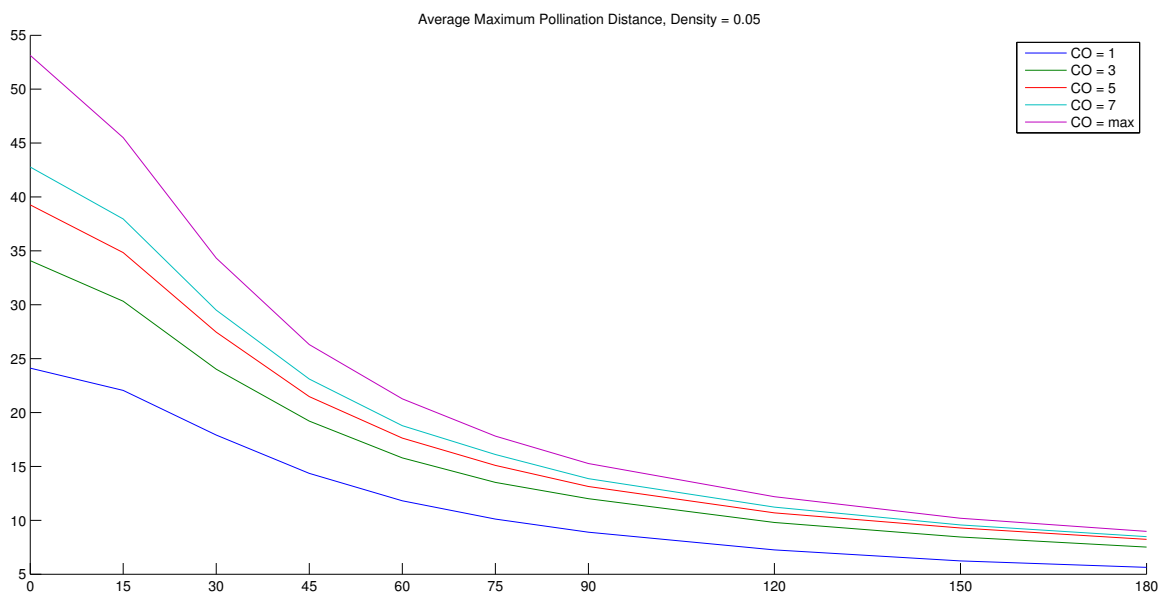


Figure A.21: *Average maximum pollination distance*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

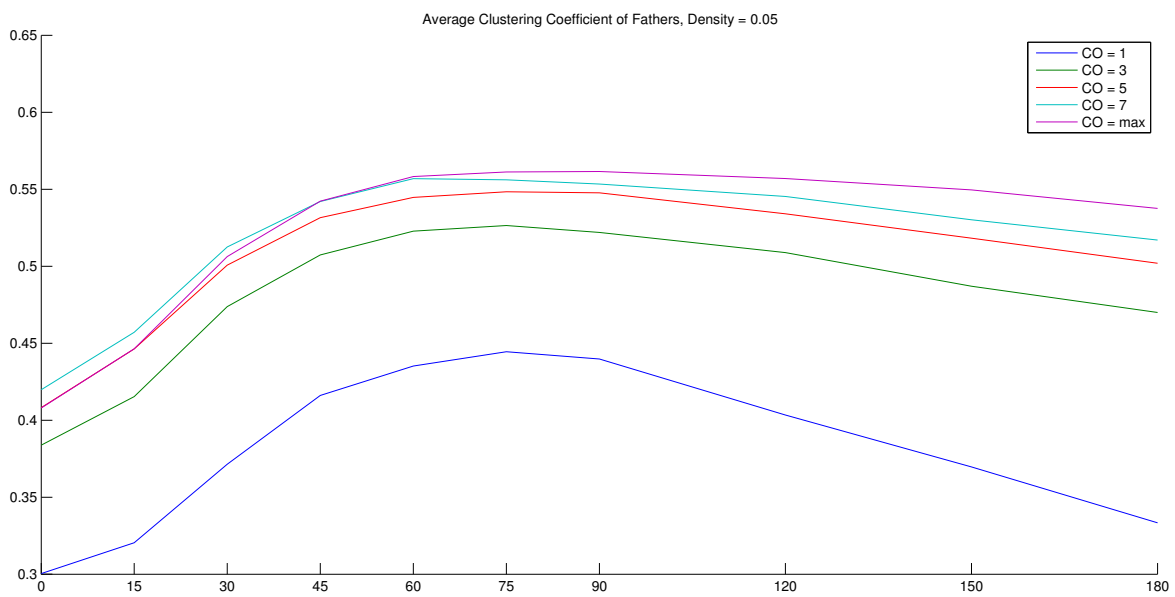


Figure A.22: *Clustering coefficient of fathers*. Field Size  $100 \times 100$ . Tree density  $\omega = 0.050$  ( $\tau = 500$  randomly-placed trees). Pollination chance diminishing with larger carryover. Maximum pollen carryover  $\kappa_{\max} = \{1, 3, 5, 7, \infty\}$ .

Appendix B  
**Original MATLAB Code**

**B.1 Master Files**

**B.1.1 Pollination.m**

```
% Clear workspace
clear all
clc

tic;% For estimating time until completion of runs

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% If using tree coordinates from VCU Rice Center
% -----
% Begin by running Rice.m in current directory or load
% ricetrees.mat
% Original Rice field size 6200*2200 (size determined
% arbitrarily)
% Field scaled by length of diagonals to account for
% a different field size than 100*100
% Scaled by sqrt(2164) = 46.518813398452
```

```

% F=[-66.639704960813901,66.639704960813901,...
% -23.646346921579127,23.646346921579127]
% den=0.071551612903226
% numT=451
% The following to be turned on or off depending on run:

%%%TreeRice=1;
%%%load('ricetrees.mat');
%%%den=TD;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% If using randomly-placed trees on VCU Rice Center field
% -----
% The following to be turned on or off depending on run:

%%%TreeRice=0;
%%%numT=451;
%%%F=[-66.639704960813901,66.639704960813901,...
      %%-23.646346921579127,23.646346921579127];
%%%den=0.071551612903226;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% If using randomly-placed trees on 100*100 field
% -----

```

```

% The following to be turned on or off depending on run:

TreeRice=0;
numT=1000;
F=[0,100,0,100];% F=Field dimensions=[xmin,xmax,ymin,ymax]
den=numT/10000;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

maxstepsize=1;
near=1;
numI=1000;
day=600;
tsdeg=[0,15,30,45,60,75,90,120,150,180];
CO=[1,3,5,7,day];% Max pollination carryover
numruns=10;

ts=pi/180*tsdeg;
rho=0.30;% Chance of a pollination event
% Explicit formula for carryover:
% pchance(p)=rho*(1-rho)^(p-1);
pchance=zeros(1,day+1);
pdim=1-rho;
pchance(1)=rho;
for n=2:day+1
    pchance(n)=pchance(n-1)*pdim;

```



```

    %pch(p)=rho; %For non-diminishing pollination chance
end

% Pre-define size of matrices for program speed
AWDFchart=zeros(length(numT),length(ts));
aapdchart=zeros(length(numT),length(ts));
ampdchart=zeros(length(numT),length(ts));
C=zeros(length(CO),length(ts),numruns);
NumDads0=zeros(length(CO),numT,numruns);
NumMoms0=zeros(length(CO),numT,numruns);
NumDads45=zeros(length(CO),numT,numruns);
NumMoms45=zeros(length(CO),numT,numruns);
NumDads90=zeros(length(CO),numT,numruns);
NumMoms90=zeros(length(CO),numT,numruns);
NumDads135=zeros(length(CO),numT,numruns);
NumMoms135=zeros(length(CO),numT,numruns);
NumDads180=zeros(length(CO),numT,numruns);
NumMoms180=zeros(length(CO),numT,numruns);
AveACCFBDNchart=zeros(length(CO),length(ts),numruns);
AveACCMBDNchart=zeros(length(CO),length(ts),numruns);
AveACCFWDNchart=zeros(length(CO),length(ts),numruns);
AveACCMWDNchart=zeros(length(CO),length(ts),numruns);

% Main program
for kk=1:numruns
    for pp=1:length(CO)

```

```

for jj=1:length(tsdeg)
    % Progress Tracker
    fprintf('Run = %d, Carryover = %d, Radius...
           = %d \n', kk,CO(pp),tsdeg(jj))

% Create matrices tree matrix T and insect matrix I
    if TreeRice==0
        T=RandomTrees(F,numT);
    end

    I=PlaceInsects(F,numI,day);
    I=MoveInsects(F,I,day,ts(jj),maxstepsize);
    I=InsectNearestTree(I,T,day);

% Create Tree Distance Chart for use in other functions
    if TreeRice==0
        TDC=TreeDistanceChart(T);
    end

% Create matrix A, weighted Tree-Insect
% matrix B, weighted Tree(Father)-Tree(Mother)
% aapd, average pollination distance
% ampd, average maximum pollination distance
[A,B,aapd,ampd]=NetMaster(T,I,pchance,...
    near,TDC,CO(pp));

```

```

% Create matrix BinB, unweighted Tree(Father)-Tree(Mother)
    BinB=BinaryB(B);

%Create matrix of connectance values
C(pp,jj,kk)=connectanceTT(B);

%Compute number of parents
if tsdeg(jj)==0
    [NumFathers0,NumMothers0]=...
        NumberParents(BinB,numT);
    NumDads0(pp,:,kk)=NumFathers0;
    NumMoms0(pp,:,kk)=NumMothers0;
end
if tsdeg(jj)==45
    [NumFathers45,NumMothers45]=...
        NumberParents(BinB,numT);
    NumDads45(pp,:,kk)=NumFathers45;
    NumMoms45(pp,:,kk)=NumMothers45;
end
if tsdeg(jj)==90
    [NumFathers90,NumMothers90]...
        =NumberParents(BinB,numT);
    NumDads90(pp,:,kk)=NumFathers90;
    NumMoms90(pp,:,kk)=NumMothers90;
end
if tsdeg(jj)==180

```

```

        [NumFathers180, NumMothers180] ...
            =NumberParents (BinB, numT);
        NumDads180 (pp, :, kk) = NumFathers180;
        NumMoms180 (pp, :, kk) = NumMothers180;
    end

    [ACCFBDN, ACCMBDN] = ACCPBDN (BinB);
    [ACCFWDN, ACCMWDN] = ACCPWDN (B);

    AveACCFBDNchart (pp, jj, kk) = ACCFBDN;
    AveACCMBDNchart (pp, jj, kk) = ACCMBDN;
    AveACCFWDNchart (pp, jj, kk) = ACCFWDN;
    AveACCMWDNchart (pp, jj, kk) = ACCMWDN;

    %Create aapd and ampd charts
    aapdchart (pp, jj, kk) = aapd;
    ampdchart (pp, jj, kk) = ampd;

    %Calculate Average Weighted Density of Fathers (AWDF)
    AWDFa = AWDF (B);
    AWDFchart (pp, jj, kk) = AWDFa;

    end

end

runtime; %Progress tracker

end

```

```

averageaapd=mean(aapdchart,3);
averageampd=mean(ampdchart,3);
averageAWDF=mean(AWDFchart,3);
averageC=mean(C,3);

AveNumDads0=mean(NumDads0,3);
AveNumMoms0=mean(NumMoms0,3);
ND0=AveNumDads0';
NM0=AveNumMoms0';
Pzero=0;
Pmax=length(NumDads0(1,:,1));
while Pzero==0%Scale for plotting purposes
    if sum(ND0(Pmax,:))+sum(NM0(Pmax,:))==0
        ND0(Pmax,:)=[];
        NM0(Pmax,:)=[];
        Pmax=Pmax-1;
    else
        Pzero=1;
    end
end

AveNumDads0=mean(NumDads0,3);
AveNumMoms0=mean(NumMoms0,3);
ND0=AveNumDads0';
NM0=AveNumMoms0';

```

```

Pzero=0;
Pmax=length(NumDads0(1, :, 1));
while Pzero==0
    if sum(ND0(Pmax, :))+sum(NM0(Pmax, :))==0
        ND0(Pmax, :)=[];
        NM0(Pmax, :)=[];
        Pmax=Pmax-1;
    else
        Pzero=1;
    end
end
Px0=1:length(NM0(:, 1));

AveNumDads45=mean(NumDads45, 3);
AveNumMoms45=mean(NumMoms45, 3);
ND45=AveNumDads45';
NM45=AveNumMoms45';
Pzero=0;
Pmax=length(NumDads45(1, :, 1));
while Pzero==0
    if sum(ND45(Pmax, :))+sum(NM45(Pmax, :))==0
        ND45(Pmax, :)=[];
        NM45(Pmax, :)=[];
        Pmax=Pmax-1;
    else
        Pzero=1;
    end
end

```

```

        end
    end
    Px45=1:length(NM45(:,1));

    AveNumDads90=mean(NumDads90,3);
    AveNumMoms90=mean(NumMoms90,3);
    ND90=AveNumDads90';
    NM90=AveNumMoms90';
    Pzero=0;
    Pmax=length(NumDads90(1,:,1));
    while Pzero==0
        if sum(ND90(Pmax,:))+sum(NM90(Pmax,:))==0
            ND90(Pmax,:)=[];
            NM90(Pmax,:)=[];
            Pmax=Pmax-1;
        else
            Pzero=1;
        end
    end
    Px90=1:length(NM90(:,1));

    AveNumDads180=mean(NumDads180,3);
    AveNumMoms180=mean(NumMoms180,3);
    ND180=AveNumDads180';
    NM180=AveNumMoms180';
    Pzero=0;

```

```

Pmax=length(NumDads180(1, :, 1));
while Pzero==0
    if sum(ND180(Pmax, :))+sum(NM180(Pmax, :))==0
        ND180(Pmax, :)=[];
        NM180(Pmax, :)=[];
        Pmax=Pmax-1;
    else
        Pzero=1;
    end
end
Px180=1:length(NM180(:, 1));

averageACCFBDN=mean(AveACCFBDNchart, 3);
averageACCMBDN=mean(AveACCMBDNchart, 3);
averageACCFWDN=mean(AveACCFWDNchart, 3);
averageACCMWDN=mean(AveACCMWDNchart, 3);

%plot AveNumDads MaxTurn=0
figure
hold on
bar3(Px0, ND0)
legend('CO = 1', 'CO = 3', 'CO = 5', 'CO = 7', 'CO = max');
title({'Number of Fathers/Mother, dmax =...
    0 Degrees, w = ', num2str(den)})

%plot AveNumDads MaxTurn=45

```



```

figure
hold on
bar3(Px45,ND45)
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
title({'Number of Fathers/Mother, dmax = ...
      45 Degrees, w = ',num2str(den)})

```

```
%plot AveNumDads MaxTurn=90
```

```

figure
hold on
bar3(Px90,ND90)
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
title({'Number of Fathers/Mother, dmax = 90 Degrees,...
      w = ',num2str(den)})

```

```
%plot AveNumDads MaxTurn=180
```

```

figure
hold on
bar3(Px180,ND180)
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
title({'Number of Fathers/Mother, dmax =...
      180 Degrees, w = ',num2str(den)})

```

```
%plot Connectance vs tsdeg vs CO
```

```

figure
hold on

```

```

plot(tsdeg,100*averageC(:,:))%Expressed as a percentage
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Average Connectance (%)', w = ',num2str(den)})

%plot AAPD vs tsdeg vs CO
figure
hold on
plot(tsdeg,averageaapd(:,:))
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Average Pollination Distance, w = ',num2str(den)})

%plot AMPD vs tsdeg vs CO
figure
hold on
plot(tsdeg,averageampd(:,:))
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Average Maximum Pollination Distance, ...
      w = ',num2str(den)})

%plot averageAWCCF vs tsdeg vs CO
figure
hold on
plot(tsdeg,averageACCFBDN(:,:))

```

```

legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Ave Weighted Clustering Coefficient ...
      of Fathers,w = ',num2str(den)})

%plot averageACCF vs tsdeg vs CO
figure
hold on
plot(tsdeg,averageACCF(:, :))
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Average Clustering Coefficient ...
      of Fathers, w = ',num2str(den)})

%plot AWDF vs density
figure
hold on
plot(tsdeg,averageAWDF(:, :))
legend('CO = 1','CO = 3','CO = 5','CO = 7','CO = max');
set(gca,'XTick',tsdeg)
title({'Average Weighted Diversity ...
      of Fathers, w = ',num2str(den)})

%File name structure:
%First entry:
%Random=100x100 field

```

```

%LgRand=6200x2200 field - Randomly placed trees
%LgRice=6200x2200 field - Rice Center trees
%Second entry:
%'abcd'=Number of trees is abcd
%Third entry:
%Peql=Pollination chance equal
%Pdim=Pollination chance decreasing

save Random1000Pdim.mat

```

### **B.1.2 Rice.m**

```

clear all
clc

originalT=xlsread('DogwoodCoordinates.xlsx','a2:c452');
labelT=originalT(:,1);
oTx=originalT(:,2);
oTy=originalT(:,3);
LabelT=labelT';
OTx=oTx';
OTy=oTy';

rotTx=sin(5*pi/36)*oTx+cos(5*pi/36)*oTy;
rotTy=-cos(5*pi/36)*oTx+sin(5*pi/36)*oTy;

originTx=ones(1,451)*((max(rotTx)+min(rotTx))/2);

```

```

originTy=ones(1,451)*((max(rotTy)+min(rotTy))/2);

transTx=rotTx-originTx;
transTy=rotTy-originTy;

%Scale
rc=sqrt(2164);

T=[transTx;transTy];
T=T/rc;
numT=length(T(1,:));

TDC=TreeDistanceChart(T);

F=[-3100,3100,-1100,1100]/rc;
FieldArea=(F(2)-F(1))*(F(4)-F(3));
den=length(T(1,:))/FieldArea;

clear originalT
clear labelT
clear oTx
clear oTy
clear OTx
clear OTy
clear rotTx
clear rotTy

```

```
clear originTx
clear originTy
clear transTx
clear transTy
clear rc
clear FieldArea

save('ricetrees.mat')
```

## **B.2 Functions**

### **B.2.1 RandomTrees.m**

```
function T=RandomTrees(F,numT)

%Make trees
T=zeros(2,numT);
for t=1:numT
    Tx=rand*(F(2)-F(1))+F(1);
    Ty=rand*(F(4)-F(3))+F(3);
    T(:,t)=[Tx,Ty];
end
```

### **B.2.2 PlaceInsects.m**

```
function I=PlaceInsects(F,numI,day)

% Make insects starting location and initial theta
```

```

% I=[Ix;Iy;theta;nearesttree;distance from nearest tree]
I=zeros(5,numI,day+1);
for i=1:numI
    I(1,i,1)=rand*(F(2)-F(1))+F(1);
    I(2,i,1)=rand*(F(4)-F(3))+F(3);
    I(3,i,1)=rand*2*pi;
end

```

### B.2.3 MoveInsects.m

```

function I=MoveInsects(F,I,day,turn,maxstepsize)

for i=1:length(I(1,:,1))
    for n=2:day+1
        % Determine step size for current time n
        step=rand*maxstepsize;
        Ix=I(1,i,n-1)+step*cos(I(3,i,n-1));
        Iy=I(2,i,n-1)+step*sin(I(3,i,n-1));

        % Determine turning angle for current time n
        % For AMT, use rand; for SDA, use randn
        theta=I(3,i,n-1)+rand*(2*turn)-turn;

        % Keep insects inside field
        if Ix<F(1)
            theta=rand*pi-pi/2;
        elseif Ix>F(2)

```

```

        theta=rand*pi+pi/2;
elseif Iy<F(3)
        theta=rand*pi;
elseif Iy>F(4)
        theta=rand*pi+pi;
end

% New values for insect location and turning angle
I(1,i,n)=Ix;
I(2,i,n)=Iy;
I(3,i,n)=theta;
end
end

```

#### **B.2.4 InsectNearestTree.m**

```

function I=InsectNearestTree(I,T,day)

for i=1:length(I(1,:,1))
    for n=1:day+1
        minITdist=realmax;
        for t=1:length(T(1,:))
            ITdx=T(1,t)-I(1,i,n);
            ITdy=T(2,t)-I(2,i,n);
            ITdist=sqrt(ITdx^2+ITdy^2);
            if ITdist<minITdist
                nearesttree=t;
            end
        end
    end
end

```



```

            minITdist=ITdist;
        end
    end
    I(4,i,n)=nearesttree;
    I(5,i,n)=minITdist;
end
end

```

### **B.2.5 TreeDistanceChart.m**

```

function TDC=TreeDistanceChart(T)
%Creates a symmetric matrix with distance between trees.
TDL=zeros(length(T));
for i=2:length(T(1,:))%Create lower triangular matrix TDL
    for j=1:i-1
        Tdx=T(1,i)-T(1,j);%abs not needed since ...
            values to be squared
        Tdy=T(2,i)-T(2,j);
        Tdz=sqrt(Tdx^2+Tdy^2);
        TDL(i,j)=Tdz;
    end
end
end

TDC=TDL+TDL';
clear TDL;

```

## B.2.6 NetMaster.m

```
function [A,B,aapd,ampd]=NetMaster(T,I,pch,near,TDC,PCO)

day=length(I(1,1,:))-1;
numI=length(I(1,:,1));
numT=length(T(1,:));

Af=zeros(numT,numI);%Network of insects with trees -...
    fathering events
Am=zeros(numT,numI);%Network of insects with trees -...
    mothering events
B=zeros(numT);%Network of tree interactions with trees
apdist=zeros(1,numI);
mpdist=zeros(1,numI);

for i=1:numI
    Ip=zeros(1,day+1);
    for p=1:day+1
        Ip(p)=I(4,i,p);%Nearest tree to insect i ...
            at each time step
    end
    for p=day+1:-1:1%Proximity condition
        if I(5,i,p)>near
            Ip(p)=[];
        end
    end
end
```

```

end
if length(unique(Ip))>1
    pdtotal=0;
    pdnum=0;
    pdmax=0;
    for pm=2:length(Ip)
        pfmin=max(pm-PCO,1);
        for pf=pm-1:-1:pfmin
            if Ip(pm)~=Ip(pf)%Self-sterile condition
                if rand<=pch(pm-pf)
                    %Pollination % chance condition
                    Af(Ip(pf),i)=Af(Ip(pf),i)+1;
                    Am(Ip(pm),i)=Am(Ip(pm),i)+1;
                    B(Ip(pf),Ip(pm))=B(Ip(pf),Ip(pm))+1;

                    pd=TDC(Ip(pf),Ip(pm));
                    pdtotal=pdtotal+pd;
                    pdnum=pdnum+1;
                    if pdmax<pd
                        pdmax=pd;
                    end
                end
            end
        end
    end
end
end
end
if pdnum>0

```

```

        apdist(i)=pdttotal/pdnum;
        mpdist(i)=pdmax;
    end
end
end

A=Af+Am;

for i=numI:-1:1%remove noncontributing insects
    if mpdist(i)==0
        apdist(i)=[];
        mpdist(i)=[];
    end
end

aapd=mean(apdist);
ampd=mean(mpdist);

```

### **B.2.7 BinaryB.m**

```

function BinB=BinaryB(B)

BinB=zeros(length(B));

for bi=1:length(B(:,1))
    for bj=1:length(B(1,:))
        if B(bi,bj)==0

```

```

        BinB (bi,bj)=0;
    else
        BinB (bi,bj)=1;
    end
end
end
end

```

### **B.2.8 connectanceTT.m**

```

function C=connectanceTT(B)

LBi=length(B(:,1));
LBj=length(B(1,:));
observed=0;
possible=LBi*(LBj-1);
for i=1:LBi
    for j=1:LBj
        if B(i,j)>0
            observed=observed+1;
        end
    end
end
end
if observed==0
    C=0;
else
    C=observed/possible;
end
end

```

### **B.2.9 NumberParents.m**

```
function [NumberFathers,NumberMothers]=NumberParents (BinB, TD)

SumFathers=sum(BinB,1);
%Number of fathers for each mother tree
SumMothers=sum(BinB,2);
%Number of mothers pollinated by each father tree

NumberFathers=zeros(TD,1);
NumberMothers=zeros(TD,1);

for nf=1:max(SumMothers)
    NumberMothers(nf)=histc(SumMothers,nf);
end
for nm=1:max(SumFathers)
    NumberFathers(nm)=histc(SumFathers,nm);
end
```

### **B.2.10 ACCPBDN.m**

```
function [ACCFBDN,ACCMBDN]=ACCPBDN(BinB)

dM=sum(BinB,1);
dF=sum(BinB,2);
TM=(dM.*(dM-1));
TF=(dF.*(dF-1));
```

```

tM=diag(BinB' *BinB^2);
tF=diag(BinB^2*BinB');

CCMBDN=tM./TM';
CCFBDN=tF./TF;

for c=1:length(BinB)
    if isnan(CCMBDN(c)) || ~isfinite(CCMBDN(c))
        CCMBDN(c)=0;
    end
    if isnan(CCFBDN(c)) || ~isfinite(CCFBDN(c))
        CCFBDN(c)=0;
    end
end

end

ACCMBDN=mean(CCMBDN);
ACCFBDN=mean(CCFBDN);

```

### **B.2.11 ACCPWDN.m**

```

function [ACCFWDN,ACCMWDN]=ACCPWDN(B)

BinB=BinaryB(B);
dM=sum(BinB,1);
dF=sum(BinB,2);

Wprop=B/mean(nonzeros(B));

```

```

Wtilda=nthroot (Wprop, 3);

TM=(dM.*(dM-1));
TF=(dF.*(dF-1));
ttildaM=diag(Wtilda'*Wtilda^2);
ttildaF=diag(Wtilda^2*Wtilda');

CCMWDN=ttildaM./TM';
CCFWDN=ttildaF./TF;

for c=1:length(B)
    if isnan(CCMWDN(c))||~isfinite(CCMWDN(c))
        CCMWDN(c)=0;
    end
    if isnan(CCFWDN(c))||~isfinite(CCFWDN(c))
        CCFWDN(c)=0;
    end
end

end

ACCMWDN=mean(CCMWDN);
ACCFWDN=mean(CCFWDN);

```

### **B.2.12 AWDF.m**

```

function AWDFa=AWDF(B)

Bden=B;

```



```

tau=sum(Bden,2)';

for t=length(Bden(1,:)):-1:1
    if tau(t)==0
        Bden(t,:)=[];
        tau(t)=[];
    end
end

tausqd=tau.^2;
Fsqd=zeros(1,length(tau));
for t=1:length(Bden(:,1))
    fs=0;
    for a=1:length(Bden(1,:))
        fs=fs+Bden(t,a).^2;
    end
    Fsqd(t)=fs;
end

WDF=Fsqd./tausqd;
WDFinv=1./WDF;
AWDFa=sum(WDFinv)/length(B(:,1));

```

### **B.2.13 runtime.m**

```

function runtime=runtime
runtime=toc;

```

```
secperday=24*60*60;
rundays=floor(runtime/secperday);
LOsecs=runtime-(rundays*secperday);
secperhour=60*60;
runhours=floor(LOsecs/secperhour);
LOsecs=LOsecs-(runhours*secperhour);
secpermin=60;
runmins=floor(LOsecs/secpermin);
runsecs=round(LOsecs-(runmins*secpermin));
fprintf('Total run time is %d days, %d hours...
    , %d minutes, %d seconds.\n'...
    ,rundays,runhours,runmins,runsecs);
```

## **Vita**

James Lee was born on March 10, 1975 in Newport News, Virginia to Bill and Mary Ann Lee. He has always lived in Virginia and is a United States citizen. He married Nicole Plato on September 21, 1996, with whom he has two daughters, Samantha and Elisabeth. He earned an Associate of Applied Science degree in Computer-Aided Design Technology from ITT Technical Institute in Norfolk, Virginia in 1998. At ITT Technical Institute, he graduated with highest honors. In his early career, he worked as a residential architectural designer, designed and sold kitchens, and managed a sales team at a kitchen and bath showroom.

James restarted his college career in 2009. He earned an Associate of Science degree in Math Education from Thomas Nelson Community College in Hampton, Virginia in 2010. At Thomas Nelson, he was a member of the Phi Theta Kappa Honor Society and graduated Summa Cum Laude. He then earned a Bachelor of Science degree in Mathematical Sciences with concentrations in Applied Mathematics and Biomathematics from Virginia Commonwealth University in Richmond, Virginia in 2012. At VCU, he was a member of Phi Mu Epsilon national mathematics honor society, was awarded the Biomathematics Award for the highest GPA in the concentration, and graduated Magna Cum Laude.

James entered graduate school at VCU in 2013. While pursuing his Master of Science degree in Applied Mathematics, he was a recitation instructor for five different math classes, earned a research grant from the VCU Inger and Walter Rice Center for Environmental Life Sciences, and was a graduate teaching assistant.