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Generalist and Specialist Pollination Syndromes: When are they Favoured? A Theoretical Approach to Predict the Conditions Under which a Generalist or Specialist Pollination Syndrome is Favoured.

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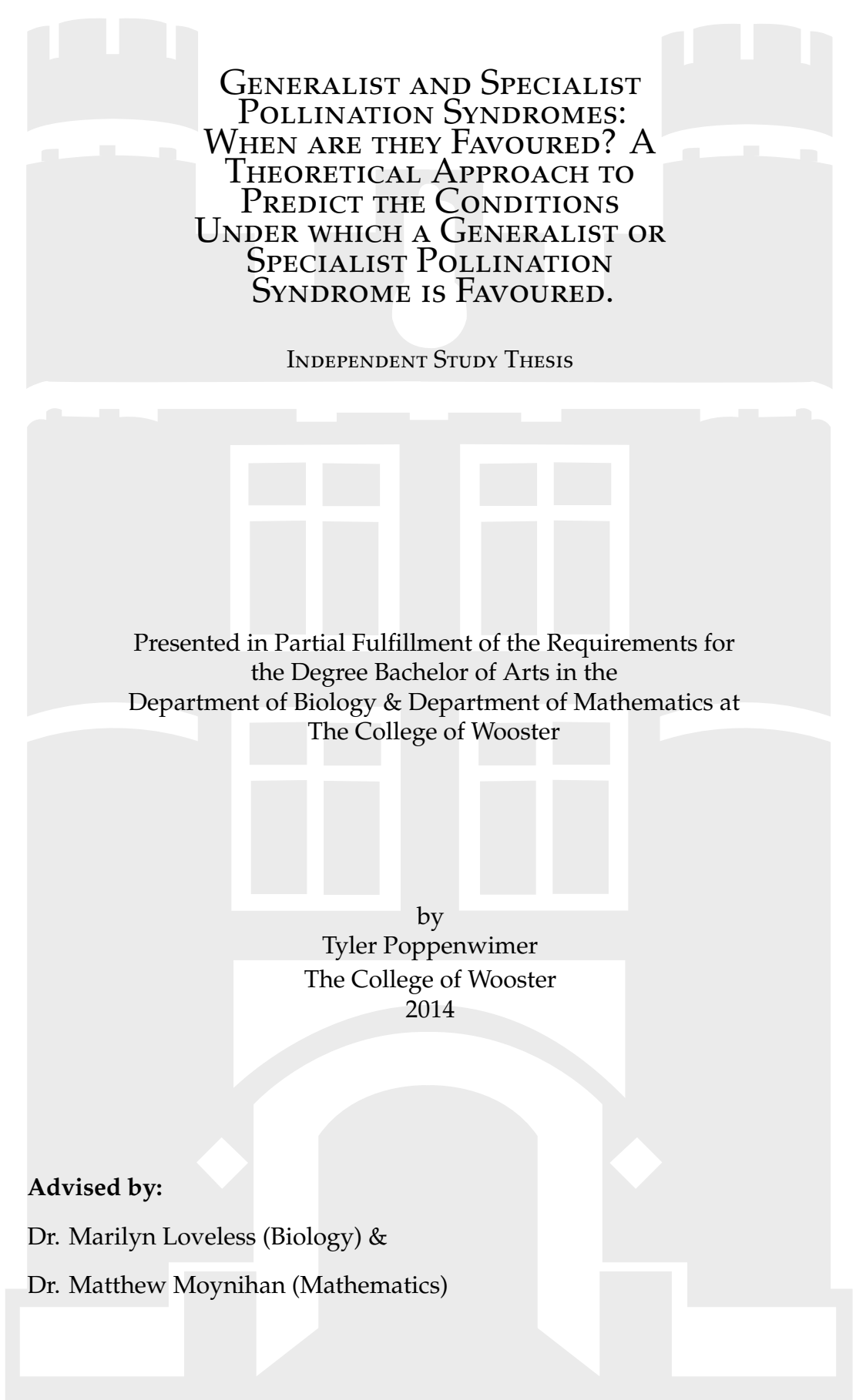
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GENERALIST AND SPECIALIST
POLLINATION SYNDROMES:
WHEN ARE THEY FAVOURED? A
THEORETICAL APPROACH TO
PREDICT THE CONDITIONS
UNDER WHICH A GENERALIST OR
SPECIALIST POLLINATION
SYNDROME IS FAVOURED.

INDEPENDENT STUDY THESIS

Presented in Partial Fulfillment of the Requirements for
the Degree Bachelor of Arts in the
Department of Biology & Department of Mathematics at
The College of Wooster

by
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The College of Wooster
2014

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THE COLLEGE OF
WOOSTER

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ABSTRACT

There are many factors characterizing plants and pollinators that have been shown to correlate to the specialist or generalist pollination syndrome displayed by an angiosperm. Such factors include plant longevity, pollinator efficiency, pollinator abundance, etc. and are essential to understanding a plant-pollinator system. Two distinct models were created to examine the individual effects of each factor, the interactions between factors, and to determine if any values of the factors lead to changes in the frequency of plants displaying a given pollination syndrome. A Java model, utilizing stochastic cellular automata and agent based modeling, simulates a patch of flowers, their pollinators, and the evolutionary progression of each pollination syndrome. A system of differential equation model examines a few factors that are predicted to greatly affect the favoured pollination syndrome. The results indicate the Java model is most sensitive to changes in pollinator efficiency and pollinator abundance and least sensitive to plant longevity. When combining variations in multiple factors, the outcomes could not be predicted from the addition of the effects of each individual factor. The results indicate that the included factors may interact differently under different conditions. Similarly, the results of the differential equation models indicate that there is a great deal of interaction among the included factors. Consequently, while nearly all of the hypotheses proposed in this study were rejected, the results strongly support the hypothesis that the interactions among the factors of a plant-pollinator system are key to understanding and predicting which pollination syndrome is evolutionarily favoured.

This work is dedicated to the future generations of The College of Wooster students.

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CHAPTER 1

INTRODUCTION

The angiosperms, or flowering plants, inhabit nearly every terrestrial habitat and display a startling array of variation. They are the most successful and abundant of all plant phyla (Friis et al. [2006]) and their diversity is unrivaled by any other plant phyla (Govaerts [2001]). Angiosperms are unique among plant phyla in that they utilize flowers which are hypothesized to have coevolved with insects as pollinators (Friis et al. [2006]). Consequently, a majority of angiosperm species require pollinators to transfer pollen between individuals of the same species in order to outcross (Friis et al. [2006]). It has been hypothesized that pollinators are one of the major evolutionary pressures behind the great diversity found among angiosperms (Johnson and Steiner [2000], Niet and Johnson [2012], Pauw [1998], Schemske and Bradshaw [1999]).

The use of flower and pollinators for pollination creates a complex form of symbiotic relationship between plants and their pollinators. This relationship may be beneficial and/or detrimental to the plant. The plant receives a benefit by having its pollen transferred to another flower of the same species, but also incurs a cost by rewarding the pollinator or by maintaining some floral trait that is needed for pollination. Each species of pollinator varies in their ability to transfer pollen and in the floral traits that attract them (Padysakova et al. [2013]). Consequently, the variations in the different qualities of pollinators create a multitude of different

relationships (beneficial or detrimental) between plants and their pollinators. It is these variations in the relationship between flowering plants and their pollinators that are the underlying cause of the evolutionary pressures exerted on angiosperms by their pollinators (Schemske and Bradshaw [1999]).

The variations in the relationships arise from differences in both pollinator efficiency and pollinator abundance (Ollerton [1996]). The efficiency of a pollinator is measured using two concepts: the amount of pollen an individual pollinator will transfer to conspecific flowers after one visit to the flower and the number of calories an angiosperm expends through the maintenance or production of a floral trait (Lau and Galloway [2004]). Some floral traits may be immediately consumed by the pollinator (nectar and pollen) and other floral traits such as scent, colouration, and shape are maintained throughout the flower's life and are not consumed by the pollinator. Consequently, it can be difficult to obtain a per visit caloric expenditure of non-consumed floral traits. Therefore, in many cases, it is useful to measure the amount of pollen and nectar consumed per visit to obtain the caloric expenditure of the flower. These two concepts of pollinator efficiency, while measured individually, produce a ratio of pollen transferred per calorie expended and it is this ratio that is used to determine the efficiency of individuals of a given pollinator species.

The ratio of pollinator efficiency represents a continuous scale where efficiency can take any value ranging from negative to positive (Willmer [2011]). Likewise, the efficiency of one pollinator species may vary between individual plants with a species of pollinator potentially having a negative efficiency for one species of plants and a high efficiency for another (Larsson [2005]). Similarly, because pollinators may not deposit all of the pollen that is taken from a flower (Padysakova et al. [2013]), the efficiency of a pollinator can be measured in probabilistic terms. Hence, there are many factors that can affect the efficiency of a pollinator, which can cause the ratio to take values ranging from negative to positive on a continuous scale.

Although pollinator efficiency is continuous, pollinators can be categorized according to their efficiency. Some species of pollinators are extremely efficient pollinators and each individual greatly increases the fitness of a plant. When an individual of an extremely efficient pollinator species visits a flower, it transfers large quantities of pollen to conspecific flowers while the plant expends minimal calories in producing pollen and nectar. Other pollinators, known as "ugly pollinators," are inefficient and transfer small quantities of pollen to conspecific plants while the plant expends numerous calories (Lau and Galloway [2004]). The small quantity of pollen transferred may be the result of large quantities of pollen gathered but only a small quantity transferred to conspecific plants or the result of a small quantity of pollen gathered. "Ugly pollinators" can, in some situations, exert a negative fitness on the plant by transferring little to no pollen to conspecific plants while the plant expends a large number of calories (Lau and Galloway [2004]). Another group of visitors (these are not considered pollinators, but are still included in many plant-pollinator systems), known as nectar thieves, act as parasites and take nectar without transferring any pollen (Padysakova et al. [2013]) and exert a strong negative pressure on plants.

Pollen transfer between conspecific individuals allows the plant to outcross and reproduce (Waser and Ollerton [2006]). Because the efficiency of a pollinator is measured in the number of pollen grains transferred to conspecifics as compared to the number of calories a plant expends in maintaining a floral trait, the efficiency of a pollinator can be summarized as its one time contribution to the reproductive fitness of the plant (Larsson [2005]). The variation of a pollinator's one time fitness contribution is directly related to its efficiency.

The number of pollinators available for pollination (referred to as abundance) mediates the one time fitness contribution by describing the availability of individuals of a pollinator species for the pollination of the plants. The abundance

of a pollinator species thereby describes the seasonal fitness contribution to the plant from the species of pollinator (Ollerton [1996]). Consider the situation where the abundance of an extremely efficient pollinator is low and the abundance of a moderately efficient pollinator is high. Both species could provide the same overall fitness contribution to the plant even though individuals of one pollinator species are highly efficient and individuals of the other species are moderately efficient. The abundance of pollinators is not always stable and may vary over the flowering life of a plant (Ollerton [1996]). Thus, it is important to understand the effects of pollinator abundance as this too affects the reproductive fitness of the plant.

The variation in the one time fitness contribution between different species of pollinators may result in evolutionary pressures that favour certain floral traits over others. The categorization of these favourable floral traits results in the development of pollination syndromes (Johnson and Steiner [2000], Ollerton [1996], Waser et al. [1996]). Pollination syndromes are arrays of floral traits that attract certain species of pollinators (Willmer [2011]). For example, white or cream coloured flowers which are large and relatively open are indicative of bat pollination while flowers with a honey scent and nectaries buried in thin tubes are indicative of butterfly pollination (Waser [2006]). The floral traits of a pollination syndrome can permit and entice certain species of pollinators to pollinate the flower while also attempting to exclude certain pollinators from pollinating the flower. Such differences in plant preference for pollinator species results in a dichotomous classification of such floral traits into specialist and generalist plant pollination syndromes.

Plants displaying a specialist pollination syndrome are those species of angiosperms that utilize a few highly efficient pollinators. In contrast, plants displaying a generalist pollination syndrome use many moderately efficient pollinators. The existence of the generalist and specialist pollination syndromes have been a widely debated topic in plant ecology. The cause of this debate arises from the

difficulty in studying and accurately defining a generalist and specialist pollination syndrome (Sahli and Conner [2006], Johnson and Steiner [2000], Ollerton [1996], Waser et al. [1996]). Consequently, there have been many studies that have attempted to understand the characteristics of pollinators and plants that correlate to a specialist or generalist pollination syndrome that is displayed by a plant. Similarly, there have been studies that have attempted to examine whether one pollination syndrome is always favoured or if there is a set of characteristics of plants and their pollinators that can predict the favoured pollination syndrome (Johnson and Steiner [2000]).

The direction of evolution, which can be attributed to variations in pollinator efficiency, was originally believed to culminate in angiosperms that were specialized towards their most efficient pollinator (Mitchell et al. [2009], Stebbins [1970], Gomez et al. [2007]). Plants displaying a generalist pollination syndrome were thought to be in a transitory stage in which the plants were slowly becoming more specialized. This theory was based on the idea that the most efficient pollinator contributed the most to the reproductive fitness of the plant. Thus, any mutation to the plant that increased this pollinator's efficiency would allow the plant to have a higher reproductive fitness (Stebbins [1970]). Recently, this argument has come under increased criticism because many angiosperm species are not specialized towards their most efficient pollinator. It is now believed that evolution does not always lead to specialization (Sahli and Conner [2006], Johnson and Steiner [2000]). In fact, most generalist plants are optimally suited to their suite of pollinators and are pressured to remain generalists (Johnson and Steiner [2000]). Consequently, many plant species that have been shown to be generalists are not in an intermediate phase slowly moving towards specialization as was originally believed.

Numerous studies have examined multiple aspects of angiosperm and pollinator characteristics that lead to or correlate to specialization or generalization (Johnson

and Steiner [2000], Bond [1994], Waser et al. [1996], Gomez et al. [2007], Mitchell et al. [2009]). Many of these studies have focused their efforts on understanding how the life history of both angiosperms and their pollinators can result in the evolution of a specialist or generalist pollination syndrome. Two important traits that have reoccurred in multiple studies are the longevity of the angiosperm and the between-season variation in pollinator community makeup and abundance (Johnson and Steiner [2000], Stebbins [1970], Waser et al. [1996], Bond [1994]). Variations in both qualities have been hypothesized to alter the evolutionary pressures towards a given pollination syndrome.

Angiosperms that have long life spans are more likely to be specialists while angiosperms with short life spans are more likely to be generalists (Waser et al. [1996], Bond [1994]). Flowering plants with long lives are able to withstand flowering seasons where they do not reproduce, due to the scarcity or absence of their most efficient pollinator, because they will most likely survive to flower during seasons when their most efficient pollinator species is abundant. Similarly, it is not necessary for long lived plants to reproduce every season since they live for many seasons and can compensate for a low fitness during one season. Thus, they can afford to wait to reproduce during seasons when their pollinators are abundant (Waser et al. [1996]). In contrast, those flowering plants with short lives, especially annuals, cannot withstand flowering seasons where a specific pollinator is absent or rare. These short lived species cannot afford to wait to reproduce since they only live for one or a few seasons. Consequently, generalization can help ensure that at least a few pollinators can be used during any flowering season (Bond [1994]).

The abundance of a flowering plant's most efficient pollinator species has also been correlated to the favoured pollination syndrome (Ollerton [1996]). Consider the case when the abundance, between seasons, of an angiosperm's most efficient pollinator is random. In this situation, the abundance of the most efficient pollinator

species, during any given flowering season, could be low or high. Consequently, a plant specializing towards this pollinator species will not always be guaranteed to reproduce as its pollinator could be absent or rare (Waser et al. [1996]). A plant that is a generalist will be able to take advantage of an increase in this pollinator's abundance, but is not reliant on it being present to outcross. In contrast, consider the case when the abundance of an angiosperm's most efficient pollinator species is relatively constant between seasons. In this situation, a plant that is specializing towards this particular pollinator species will be able to take great advantage of this constant source of pollination since its floral morphology greatly attracts and increases the efficiency of this particular pollinator species (Waser et al. [1996]). In contrast, a generalist plant will only be able to take little advantage of this constant source of pollination since it is not displaying an array of floral traits that attracts and increases the efficiency of this pollinator species.

The longevity of a plant and the abundance of each pollinator species describe factors that portray plant characteristics and pollinator characteristics respectively. While each quality has been described individually, both factors influence a plant-pollinator system simultaneously. Thus, the interaction among these factors could result in correlations to generalist and specialist pollination syndromes that may not arise from a combination of the correlations of each individual factor. Consequently, to accurately understand and examine the outcomes of the evolutionary pressures and determine which pollination syndrome is favoured, the pollination behaviors of pollinators and their interactions with plants must be accurately simulated.

This study takes two distinct modelling approaches to explore the fundamental role pollinators play in the evolution of pollination syndromes. The first approach is a model developed in Java and the second is a system of differential equations that attempts to simplify the complexities of the first model. The Java model utilizes agent based modeling and stochastic cellular automata to capture the main

elements of the fundamental interactions between angiosperms and their pollinators. It utilizes agent based modelling to simulate the movement and interactions of pollinators as they visit a population of flowering plants. The method of stochastic cellular automata is used to simulate the change in the frequency of generalists and specialists plants within a population. While this model accurately captures many aspects of pollinator-plant interactions, it is exceedingly complex and no explicit solution can be found.

To reduce the complexity of the Java model, a second model was developed. This model uses a system of differential equations to simulate the change in frequency of specialist and generalist plants within a population. It is developed around the idea that each syndrome, generalist and specialist, attracts a certain fraction of the total abundance of each pollinator species. This model examines the frequency of each syndrome as well as the contribution of each pollinator to the reproductive fitness of each of the pollination syndromes of the plants. These aspects work in conjunction with one another to accurately reflect the outcomes of the evolutionary pressures. The model determines how the frequency of each pollination syndrome will change over time given a set of values (constant or functions) for plant attractiveness towards each species of pollinator, the abundance of each pollinator species, and the initial population of each plant pollination syndrome.

Although these models are different in their underlying mathematical concepts, both attempt to measure the fundamental interaction between an angiosperm and its pollinators. In this way, the models are designed to tease apart the set of conditions which favour one syndrome over another. The models are run with a given set of initial conditions so that the effects of changes in pollinator populations and changes in plant longevity can be assessed. In this way, the models can simulate how changes in the pollination behavior of pollinators and their interactions with angiosperms alter which syndrome is favoured.

To further examine the hypotheses regarding pollinator abundance two simulations of the Java model and of the system of differential equations model were conducted in which pollinator abundance was varied. In the first simulation, the abundance of each pollinator species was random for any given flowering season. In comparison, the other simulation was characterized by pollinator species that had a constant abundance across all flowering seasons of the model. In previous studies it has been shown that if a plant's most efficient pollinator species has an abundance that is random during any given flowering season, then generalization is more likely to be displayed by the plant (Waser et al. [1996]). In contrast, if the most efficient pollinator species has an abundance that is relatively constant across seasons the plants are more likely to display a specialist pollination syndrome (Waser et al. [1996]). Consequently, it is hypothesized that the results of the model will mimic the predictions of these previous studies.

Similar to the examination of pollinator abundance, two simulations of the Java model were conducted to better examine the hypotheses surrounding plant longevity. During one simulation of the Java model, plants were characterized by a long life span. The results of this simulation were then compared to the other simulation in which plants were characterized by an extremely short life span. It is hypothesized that plants with a short life span are more likely to display a generalist pollination syndrome while plants with a long life span are more likely to be specialists (Waser et al. [1996], Bond [1994]).

While both of the analyses described so far have examined the effect of variations in one parameter, it is also relevant to examine how the model changes given variations in both of these parameters. To accomplish this, four simulations were conducted combining the two variations of pollinator abundance and the two variations of plant longevity. In the first simulation, plants were characterized by a short life span and the abundance of each species of pollinator was random for any

given flowering season. For the second simulation, plants had a short life span but the abundance of each pollinator species was constant across all seasons. In both the third and fourth simulations, plants were characterized by a long life span with the abundance of each pollinator species being random and constant respectively.

Although few modelling studies have been fully devoted to understanding how the interactions among plant longevity and variation in pollinator abundance affect the evolutionary pressures exerted on the plant, it may be possible to add the effects of each individual parameter to predict the outcome of the model. Consequently, I hypothesize that, during the first simulation, plants will be more likely to become generalists since there is a correlation between both short lived plants and random pollinator abundance to plants displaying a generalist pollination syndrome (Ollerton [1996], Waser et al. [1996]). In the second simulation, I would expect more plants to display specialization because, although the plants survive across few flowering seasons, their most efficient pollinator is always present to transfer pollen between plants. For the third simulation, I hypothesize that generalization and specialization will be displayed in relatively equal measures because long lived plants correlates to plants displaying a specialist pollination syndrome while random pollinator abundance correlates to plants displaying a generalist pollination syndrome. In the fourth simulation, I hypothesize that more plants will display a specialist pollination syndrome because long lived plants and constant pollinator abundance both correlate to plants displaying a specialist pollination syndrome (Ollerton [1996], Waser et al. [1996]).

Although pollinator abundances can be random and/or constant, the abundance of a pollinator species may also be cyclic. To examine the effects of cyclic pollinator abundance on the models, five cycles for pollinator abundance in the Java model were created. In each simulation all of the pollinator species within the model followed the same cyclic pattern. I hypothesize that if the plants live longer than

half of the period of any abundance cycle, then the plants will be more likely to become specialists. If the plants live across more than half of the period, then most of the plants will survive to reproduce during a season when the abundance of each pollinator species is at its maximum. During this maximum abundance, the specialist plants can take advantage of this pollinator and thus greatly increase their reproductive success. However, it is not clear whether this large one time increase in reproductive success will be enough to offset the decrease in reproductive fitness during seasons in which pollinator abundance is not at its maximum.

I also hypothesize that if the plant does not survive across half of the period of the cycle of pollinator abundance then more plants will be generalists. This hypothesis was proposed because, in most cases, the plant will not survive to flower during a season in which the pollinator species is highly abundant. Consequently, specialist plants will not be guaranteed to receive the great increase in its reproductive success during the season when the pollinator is most abundant because most plants will not live to flower during the season of high pollinator abundance. Thus, there is little to offset the decrease in reproductive success gained during seasons in which pollinator abundance is not at its maximum.

To further determine if different cycles for each species of pollinator resulted in a different frequency of generalists, the system of differential equations model used multiple sinusoidal functions with differing amplitude and/or periods. Because this model did not account for plant longevity, it is difficult to predict whether specialization or generalization will be favoured. Nevertheless, although a strong prediction cannot be made as to the outcome of the models, it will still provide data which can be compared to the Java model to determine if the complexity of the Java model could be simplified with a system of differential equations.

Not wanting to omit variations in pollinator efficiency from this study, a simulation was conducted in which the efficiency of pollinators was varied. The simulation

was conducted to examine the predictive power of the most efficient pollinator principal. Consequently, the efficiency of individuals of one pollinator species was increased while the efficiency of the individuals of all other pollinator species was decreased. Following the reasoning of the most efficient pollinator principal (Stebbins [1970]), it is hypothesized that the frequency of plants specializing towards this highly efficient pollinator will be much higher compared to simulations in which the efficiency of each pollinator is equal.

To further examine the hypothesis of the most efficient pollinator principal, an additional simulation of the Java model was conducted. In this simulation, the efficiency of individuals of one species of pollinator was increased as well as the abundance of this pollinator species. Consequently, both the abundance and the efficiency were skewed in favour of one species of pollinator. Hence, it is hypothesized that the frequency of plants specializing towards this highly efficient and highly abundant pollinator will be much higher compared to simulations in which the efficiency and abundance of each pollinator was equal.

CHAPTER 2

METHODS

Consider a square patch of flowering plants in the middle of a field, where all of the flowers are the same species. Outside of this square patch of flowers are species of pollinators that may visit and pollinate the flowers. At the beginning of each day, these pollinators will enter the flower patch and will randomly select a flower to land on. Once landed the pollinators proceed to remove nectar and gather pollen from the flowers. After a short amount of time, a random pollinator moves to an adjacent flower. When the pollinator lands, it repeats the same process of removing nectar and gathering pollen. During this process, pollen gathered by the pollinator during its visit to the previous flower is deposited onto the pistil of the flower it is currently occupying. After some time has passed and many moves have occurred, all of the pollinators leave the flower patch. However, new pollinators arrive and quickly replace those that left the patch before them. Once the day has waned, the pollinators leave once again and the plants secrete more nectar and produce more pollen in preparation for tomorrow's pollinators.

The flowers remain open and receive pollinators for several days until the flowering season ends and the flowers wilt. When the flowering season ends, a few of the plants die from natural causes. The remaining plants, during the non-flowering season, produce seeds from the pollen that was transferred between plants by the pollinators. These plants then set their seeds in the spots that were left empty by the dead plants. These new plants may be different from their parents and may specialize towards a species of pollinator or generalize towards all species of pollinators. No matter the pollination syndrome of the plants, these

newly recruited plants grow to maturity rather quickly. As soon as the next flowering season begins, they are fully mature and ready to be pollinated. The pollinators return to the flower patch and the cycle begins once more.

2.1 INTRODUCTION TO THE JAVA MODEL

To simulate the movement of pollinators and the effect they have on the frequency of plants displaying a generalist or specialist pollination syndrome, this model utilizes stochastic cellular automata and agent based modelling. The model is constructed on a square lattice where each cell represents an individual plant with a single flower. Information regarding the flower, the effects each pollinator has on the flower, the phenotype of the flower, and the flower's attractiveness to each species of pollinator is contained in multiple lattices. Cells with the same row and column location in each lattice correspond to the same flower. This square lattice creates an arena for pollination to occur and will henceforth be referred to as the flower patch.

Within the model, plants are characterized by the quantity of pollen and nectar that is removed per visit by each species of pollinator. This characterization is termed a phenotype as the underlying concept is that different floral morphologies, resulting from the physical manifestation of the genes of the plant, result in different quantities of nectar and pollen removed per visit for each species of pollinator. Similarly, pollinators are characterized by the quantity of pollen and nectar removed from each plant during a single visit. A species of pollinator is characterized by its abundance which describes how many individuals of this species of pollinator is in the model. A species of pollinator does not need to be one species but can represent taxonomic groups such as bees, butterflies, birds, etc.

2.2 OVERVIEW OF THE JAVA MODEL

The Java model uses a quadruple nested cycle in which movement periods are contained in days, which are contained in seasons, which are contained within the model (Figure 2.1). At the beginning of each model, all of the plants within the flower patch are identical to one another. These plants display the phenotype of the original population, which is determined by the user prior to the execution of the model.

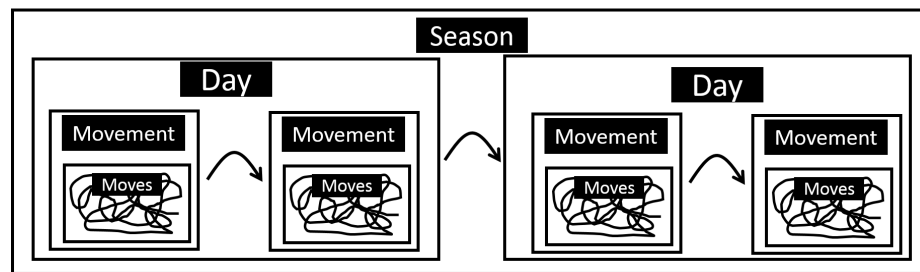


Figure 2.1: The hierarchical configuration of the Java model. The model is composed of seasons which are composed of days, which are composed of movement periods, which are composed of moves.

The deepest cycle within the model is the movement period. At the beginning of each movement period, pollinators are randomly placed in the flower patch. Once placed, the pollinators move among the flowers and then leave the flower patch. A movement period is described by the number of aggregate moves pollinators can make. For example, a movement period of 20 describes a movement period in which 20 pollinator movements occur (this is not the same as each pollinator moving 20 times). When a pollinator moves, it transfers pollen grains from the flower it was on to the next visited flower. This transfer of pollen grains provides a "fitness" increase to both plants. Fitness in the model is referred to as the total number of pollen grains transferred or received. Both plants accrue a fitness increase because, upon delivery of the pollen to the next flower, pollen grains and eggs meet and form seeds that contain the genetic information from both plants. Pollinators also

remove nectar from each flower, without immediate replenishment, which is seen as a cost of pollination.

A day cycle contains multiple movement periods and is described by the number of movement periods contained within each day. At the end of a day, the amount of pollen and/or nectar is refreshed for each flower. The user determines if both pollen and nectar is refreshed or if only one is refreshed. This element of the model reflects the ability of plants to replenish their pollen and nectar throughout a flowering season. Although some plants may replenish pollen and/or nectar constantly during a day, this model amasses this continuous replenishment into a single replenishment occurrence.

Seasons contain multiple day cycles and are described by the number of days in a season. At the end of each season, plants die or survive. Each of the surviving plants has the ability to recruit a new plant which will replace the lost plants. However, the probability of any plant recruiting a new plant is dependent on their fitness accrued through the transfer or acquisition of pollen grains. Only one plant is chosen as the parent plant even though the model requires pollen to be transferred or received to have a probability of recruiting a new plant.

The newly recruited plants can display the same phenotype (recall that phenotype is used to refer to the amount of nectar and pollen removed by each species of pollinator for a given plant) or a different phenotype as its parent. Different phenotypes arise from mutations which result in different floral morphologies for the newly recruited plant. The mutations within the newly recruited plants may also result in the plant developing a generalist or specialist pollination syndrome. A specialist or generalist pollination syndrome is the result of mutations which reflect the key aspects of each syndrome. A plant displaying a specialist syndrome will have more pollen and nectar removed per visit by the species of pollinator it is specializing towards compared to the species it is not specializing towards. In

contrast, a plant displaying a generalist pollination syndrome will have relatively equal amounts of pollen and nectar removed no matter the pollinator species that visits the flower.

After each newly recruited plant has been placed in the flower patch, the quantity of plants displaying the phenotype of the original population, a generalist pollination syndrome, and any of the specialist pollination syndromes within the flower patch is recorded (Figure 2.2). Within the model, each pollination syndrome is denoted by a specific number. The value -1 represents plants displaying a generalist pollination syndrome. Plants displaying the phenotype of the original population are given a 0. For a simulation with three polinator species, plants displaying a specialist pollination syndrome are given a 1, 2, or 3, corresponding to the species they are specializing towards. In this way, it is possible to perfectly record the changes in the quantity of each pollination syndrome over the course of the model.

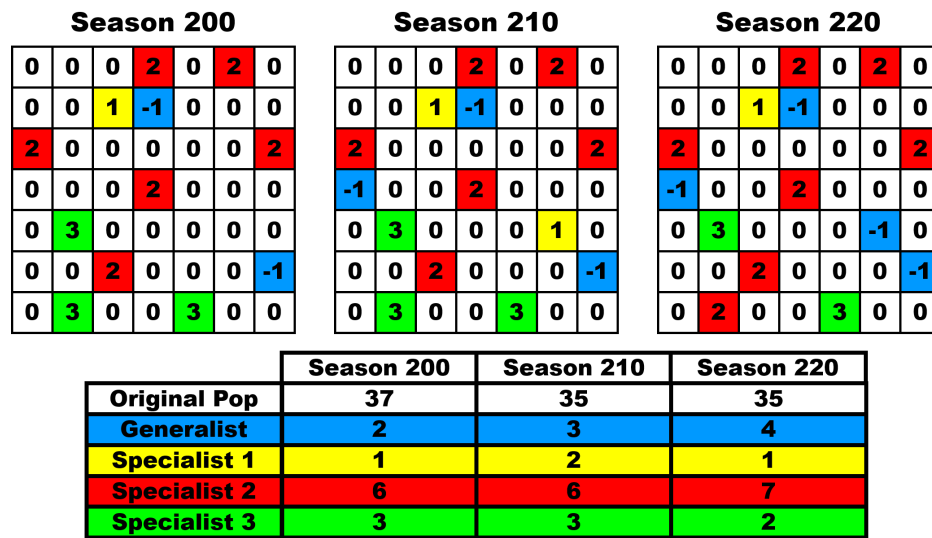


Figure 2.2: An example output of a simulation which contains a 7 by 7 flower patch and 3 pollinators. Notice the changes in plants displaying each pollination syndrome.

The quantity of each pollination syndrome can be used to determine the frequency of each syndrome during any given season. This information is then used to create

a running total and running average for the last several seasons in the model. The number of seasons to be included in the running total and running average is determined by the user. The frequency of each pollination syndrome during each season can also be displayed so that a connected scatter plot displaying the frequency changes of each pollination syndrome (Figure 2.3) can be created.

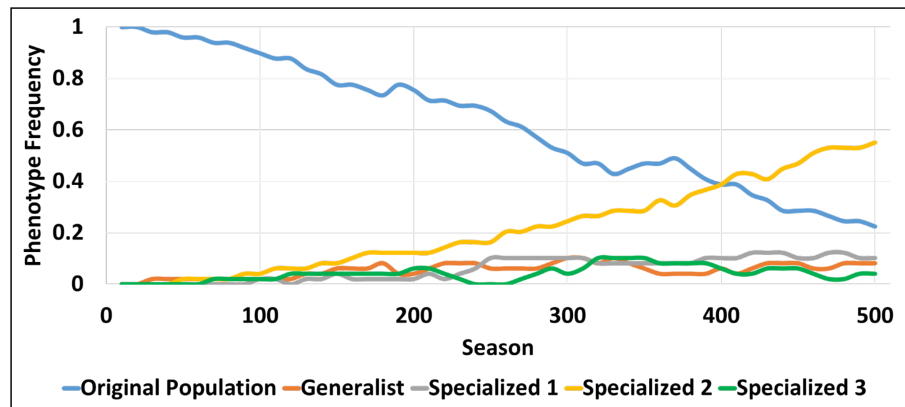


Figure 2.3: A connected scatter plot displaying the change in frequency of each pollination syndrome. This example uses a 7 by 7 flower patch and contains 3 pollinator species.

This model was designed as a framework to simulate the evolution of plant pollination syndromes in a variety of different communities of flowering plants and species of pollinators. Consequently, many parameters are set by the user prior to the execution of the model. This allows for the customization of many factors that characterize both the pollinators and plants.

2.2.1 INITIAL SET UP OF THE JAVA MODEL

Before the model can be executed, the user is required to input specific information. The information required from the user will determine the size of the matrix, the abundance of each pollinator species (which is the number of individuals of each species of pollinator), the initial quantity of pollen and nectar removed per visit for each species of pollinator, the rate of seasonal deaths in the plants, the rate of

mutation in newly recruited plants, whether nectar and/or pollen is replenished in the plants at the end of day, the number of moves in a movement period, the number of movement periods in a day, the number of days in a season, the number of seasons in a simulation, and the number of simulations desired. Once all necessary information has been input, the simulation will begin.

2.2.2 MOVEMENT PERIODS

At the start of a movement period, pollinators are placed on the flower patch. Placement occurs in order of the pollinator species number. Thus, pollinator species 1 is placed onto the flower patch first. Placement occurs at random, where each plant has the same probability of receiving a pollinator. Once all of the individual pollinators of pollinator species 1 have been placed on the flower patch, the individuals of the next pollinator species are added. This process repeats until all individual pollinators are placed onto the flower patch. Individuals were placed at random because the model assumed that the pollinators visiting the flower patch were new visitors or that the individuals did not remember the most rewarding flower. Consequently, each individual pollinator chooses a flower at random.

Once the pollinators have been placed, a single pollinator is selected at random from all of the pollinators present. This pollinator will then move to an adjacent plant, defined as all of the plants immediately surrounding the plant the pollinator is currently on. Since this model uses a square matrix that does not wrap in any direction, there are three distinct cases determining the number of adjacent plants (Figure 2.4). Flowers in the corner of the flower patch have three adjacent flowers, flowers on the edges have five adjacent flowers, and flowers in the "middle" (not an edge or corner flower) have eight adjacent flowers. Thus, the number of "moves" available to the pollinator varies depending on the location of the flower it is currently on. Another limit to the movement of a pollinator is the presence of

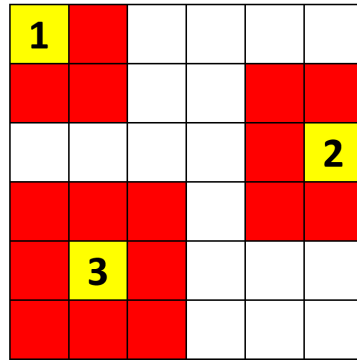


Figure 2.4: The location of the flower a pollinator is on can affect the number of available "moves". A pollinator in the corner (1) will only have three possible moves. A pollinator on the edge (2) will have five possible moves. A pollinator which is not on the edge or corner (3) will have eight possible moves.

a pollinator. Pollinators have rarely been shown to displace a pollinator that is already present on a flower and so a pollinator cannot move to another flower that already has a pollinator present. If all surrounding cells have a pollinator on them, the selected pollinator loses its movement option and another pollinator is chosen to move. This was done to ensure that pollinators could only travel a specified distance.

The plant the pollinator moves to is dependent on the amount of nectar the pollinator will receive from each flower as well as the pollination syndrome of the flower. The amount of nectar removed by the pollinator provides the initial probabilities that the pollinator will move to that flower. The pollination syndromes then multiply this probability which either increases, decreases, or maintains the initial probability. If the plant is specializing towards the selected pollinator, the plants probability of receiving the pollinator is doubled. If the plant is a generalist or displays the phenotype of the original population there is no change to its probability. If however, the plant is specializing, but not towards this pollinator species, its probability of receiving the pollinator is halved. As with all probabilities, the highest probability does not guarantee that the pollinator will move to that flower, but gives the plant the best chance to receive the pollinator.

The variation in the multiplication values is a reflection of the floral morphology displayed by the plants in accordance with their pollination syndrome. A plant that is specializing towards a given pollinator will most likely have a floral morphology that entices this specific pollinator to visit it more often. In contrast, a specialist plant will probably have a flower morphology that will not entice those species of pollinators which the flower is not specializing towards. A generalist pollination syndrome does not commonly attract specific pollinators. Instead generalist plants mainly display floral morphologies which attracts many species of pollinators.

Once a destination for the pollinator has been chosen, the pollinator proceeds to move from the flower it is currently on (the source flower) to the chosen flower (the receiver flower). When the pollinator arrives at the next flower, it removes a certain amount of nectar and pollen from the receiver flower. This decreases the remaining pollen and nectar in the receiver flower. The amount removed is dependent on the species of pollinator and the phenotype of the plant. Recall that the phenotype of the plant describes how much pollen and nectar is removed per visit by each species of pollinator. If there is no nectar in the flower, then the pollinator will only remove half of the amount of pollen it would normally remove. This is indicative of a shorter foraging time due to the absence of a nectar reward.

The movement of the pollinator also transfers pollen from the source flower to the receiver flower. This increases the fitness of the source flower because the pollen has been transferred to a conspecific. Similarly, the receiver flower receives a fitness increase because it receives pollen from a conspecific. The fitness increase to both flowers is directly related to the amount of pollen removed by the pollinator. This completes a movement.

After a specified number of aggregate moves, each pollinator is removed from the flower patch. As each pollinator leaves, they decrease the amount of pollen and nectar at their respective flowers. Again, the amount decreased is dependent on the

species of pollinator and the phenotype of the plant. However, there is no fitness increase because the pollinators are leaving the system and, once left, it cannot be guaranteed that these pollinator will transfer pollen to another conspecific. This aspect was included to account for the fact that pollinators will not forage for an infinite amount of time. Consequently, pollinators will leave the flower patch taking nectar and pollen without transferring the pollen to another plant.

2.2.3 DAYS

Days are composed of a specified number of movement periods. After a specified number of movement periods have occurred, the amount of pollen and nectar, in plants that have been visited by a pollinator, has been reduced. This cycle refreshes the amount of pollen and/or nectar to original levels in each plant. The inclusion of a replenishment of pollen and nectar is an attempt to reflect the ability of plants to produce more nectar and pollen. Although plants may continuously produce nectar and or pollen, this model accumulates this continuous production into one replenishment at the end of each day.

Note: Days do not necessarily represent 24 hours. Instead, they represent the frequency of pollen and or nectar replenishment in the plants.

2.2.4 SEASONS

After a specific number of days have transpired, a season ends. At the end of a season, a specified number of plants are selected at random to die. These plants are removed from the flower patch and all relevant information regarding the dead plants are removed. These dead plants are replaced through recruitment, where each surviving plant has a probability of recruiting a new plant. However, each plant may only recruit one new plant. The number of recruited plants is equal to the

number of deaths, thus maintaining the overall population. The probability of any specific plant recruiting a new plant is based on its fitness accrued by receiving and transferring pollen grains. While the plant with the highest fitness is not guaranteed to recruit a new plant, it is most likely to recruit a new plant.

Prior to the placement of the newly recruited plants, the phenotype of each newly recruited plant is determined. Although in nature, genes are the inherited element, this model omits genes and instead focuses on the physical manifestation of these genes. The newly recruited plants can either inherit the same phenotype as their parent plant or can mutate. The rate of mutation is set by the user, prior to the execution of the model. If the newly recruited plant does not display a mutation then it inherits the same phenotype as its parent plant. While in nature it takes two parent plants to produce an outcrossed plant, the model only considers one plant to be the parent in order to reduce the complexity of inheritance. Recall that phenotypes describe the quantity of pollen and nectar removed per visit by each species of pollinator for a given flower. Thus, if the newly recruited plant has the same phenotype as its parent, then no matter the pollinator that visits the newly recruited plant, the same quantity of nectar and pollen are removed as would be removed had the pollinator visited the parent plant. If the newly recruited plant displays a mutation then this will cause a change in the phenotype of the plant.

The phenotypic inheritance of a newly recruited plant is dependent on the phenotype and pollination syndrome of the parent plant. There are three cases of phenotypic inheritance for the newly recruited plants; plants whose parent displays the phenotype of the original population, plants whose parent displays a generalist pollination syndrome, and plants whose parent displays a specialist pollination syndrome. No matter the parental phenotype and pollination syndrome, a mutation will result in a change in the pollination syndrome displayed by the newly recruited plant or a strengthening of the pollination syndrome displayed by the parent.

If the parent of the newly recruited plant displays the phenotype of the original population and the newly recruited plant displays a mutation, then a pollination syndrome (generalist or specialist) is determined for the plant. It is true, that in nature, a phenotype is not "determined", however, the model works under the assumption that a mutation will manifest itself in a floral morphology that is characteristic of a certain pollination syndrome. A mutation will cause any of the possible pollination syndromes with equal probability. The number of pollination syndromes allowed within the model is equal to one more than the number of pollinators present. This is because there is a specialist pollination syndrome that is specializing towards each species of pollinator as well as a generalist pollination syndrome. If, for example, there are three syndromes, generalist, specialist towards pollinator species 1, and specialist towards pollinator species 2, then there is a 33.333% probability of the newly recruited plant displaying any one of the three syndromes (Figure 2.5). If the newly recruited plant does not display a mutation then it will display the same phenotype, and thus have the same pollen and nectar removal rate for each species of pollinator as the original population.

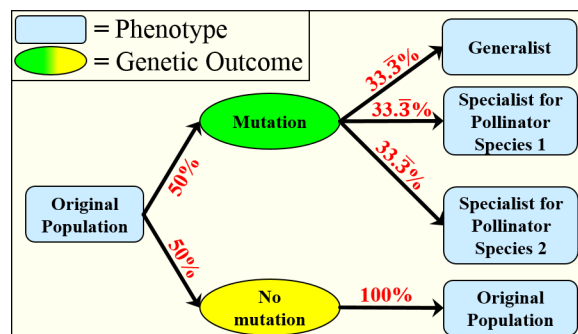


Figure 2.5: How mutations in the original population can cause the emergence of new pollination syndrome. This example is shown with a 50% mutation rate and three pollination syndromes. Each syndrome has the same probability of emerging.

If the parent of a newly recruited plant displays a generalist or specialist pollination syndrome then the newly recruited plant will strengthen the pollination

syndrome of its parent or will maintain the same phenotype as its parent (Figure 2.6). If the recruited plant does not display a mutation then it will display the same phenotype as its parent plant. If the plant displays a mutation, then this mutation will manifest itself through the strengthening of the pollination syndrome of the plant. The mutation is presumed to alter the flower morphology of the plant such that it alters the quantities of pollen and nectar removed for each species of pollinator in a way that reflects the pollination syndrome being displayed.

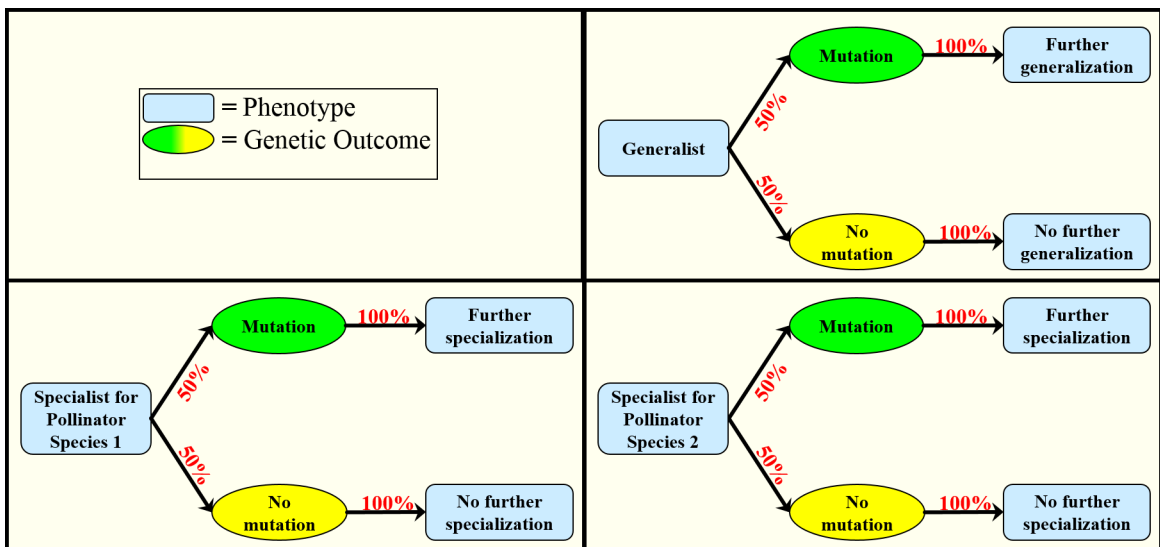


Figure 2.6: The effects of mutations in newly recruited plants whose parents do not display the phenotype of the original population. A mutation will cause a furthering of the pollination syndrome while an absence of mutations will cause the recruited plant to maintain the same phenotype as the parent.

No matter the parental phenotype, the mutations in a newly recruited plant whose parent displayed a generalist pollination syndrome always follow the same guidelines. The mutations will bring the nectar and removal rates of each species of pollinator to the mean nectar and pollen removal rate of all species of pollinators for that plant. If the pollen removal for an individual species of pollinator is lower than the mean pollen removal, there is a 50% chance that the amount of pollen removed per visit will increase (in increments of one) and a 50% chance that it will remain

the same. If the nectar removal for an individual species of pollinator is lower than the mean nectar removal, it follows the same set of rules. If the pollen or nectar removal is above the mean pollen or nectar removal, then there is a 50% chance that the amount of pollen or nectar removed per visit is reduced (in increments of one) and a 50% chance of remaining the same. If the pollen or nectar removal is the same as the mean, the removal rates do not change (Figure 2.7).

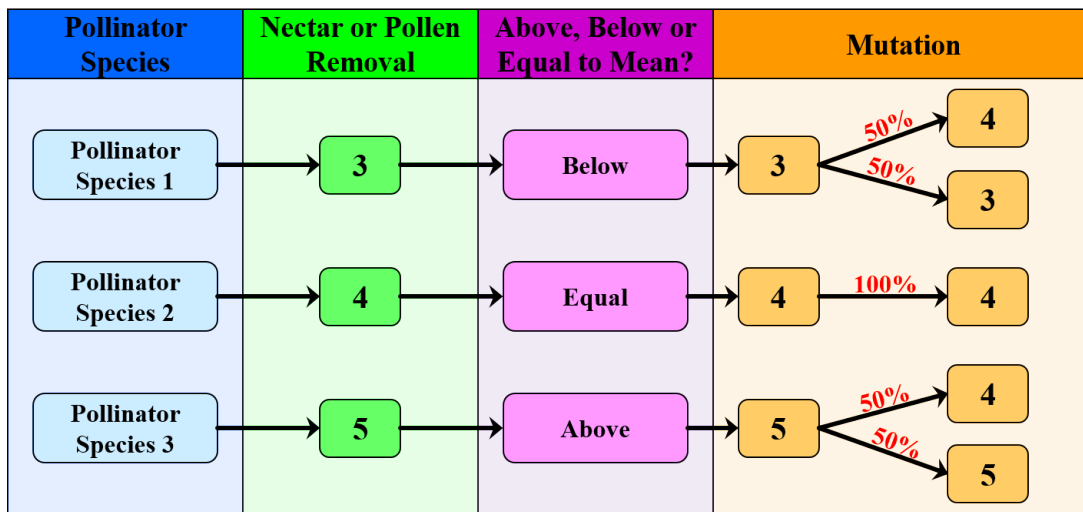


Figure 2.7: The possible results of mutations in a newly recruited plant whose parent displayed a generalist pollination syndrome. In this example, the average pollen and/or nectar removal rate for the parent plant is 4. The newly recruited plant will display a different phenotype from its parent as determined by the rate of mutation and the parental phenotype. In this example, the mutation rate is 50%.

The mutations in a newly recruited plant, whose parent displays a specialist pollination syndrome, will follow the same guidelines regardless of the species of pollinator being specialized towards. The mutations of a specialist pollination syndrome, rather than bringing the amount of pollen and nectar removed per visit for each pollinator species towards the average, increase the amount of pollen and nectar removed for one species of pollinator. The specialist pollination syndrome is said to be specializing towards the species which has its pollen and nectar removal rate per visit increased by the mutations. However, as there can be multiple species of pollinators, mutations will decrease the quantity of pollen and nectar removed

per visit for each of the species not being specialized towards. This is a result of specialization towards one species of pollinator.

For the species being specialized towards, there is a 75% chance that the amount of pollen removed per visit will increase (in increments of one) and a 25% chance that the amount of pollen removed per visit will remain the same (Figure 2.8). The amount of pollen removed per visit increases because this is indicative of a floral morphology which increases the amount of pollen gathered by the pollinator. Conversely, there is a 25% chance that the amount of nectar removed per visit will increase (in increments of one) and a 75% chance that the quantity will remain the same (Figure 2.9). This slower increase in nectar removal per visit reflects the tradeoff between the plant increasing its attraction to the pollinator and increasing the calories required to provide more nectar.

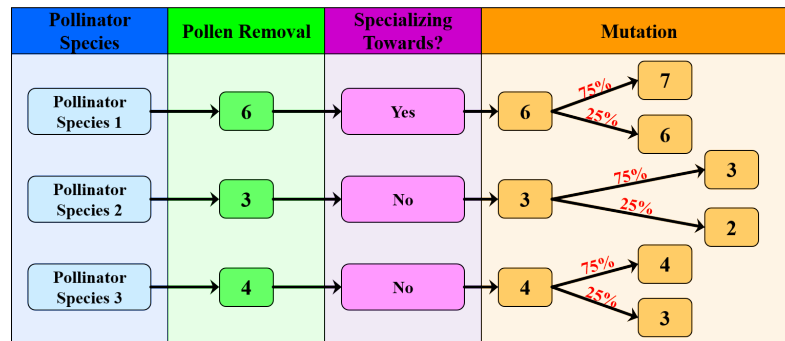


Figure 2.8: The possible mutations to the quantity of pollen removed per visit for a newly recruited plant displaying a mutation and whose parent displays a specialization pollination syndrome. The parent of this plant is specializing towards pollinator species 1.

For the other species of pollinators that the plant is not specializing towards, there is a 25% chance that the quantity of pollen and nectar removed per visit will decrease (in increments of one) and a 75% that the quantity of pollen and nectar removed per visit will remain the same (Figures 2.8 and 2.9). The amount of pollen and nectar removed per visit can only be depressed to one. If the quantity of nectar and pollen removed per visit is already at one, any mutations that cause a decrease in the quantity of nectar and pollen removed per visit will not change the quantity

removed per visit. The mutations for the nectar and pollen removal of the species of pollinator that the plant is not specializing towards represents the decrease in plant attractiveness and decrease in pollinator "fit" in the flower due to the floral morphology displayed by the plant.

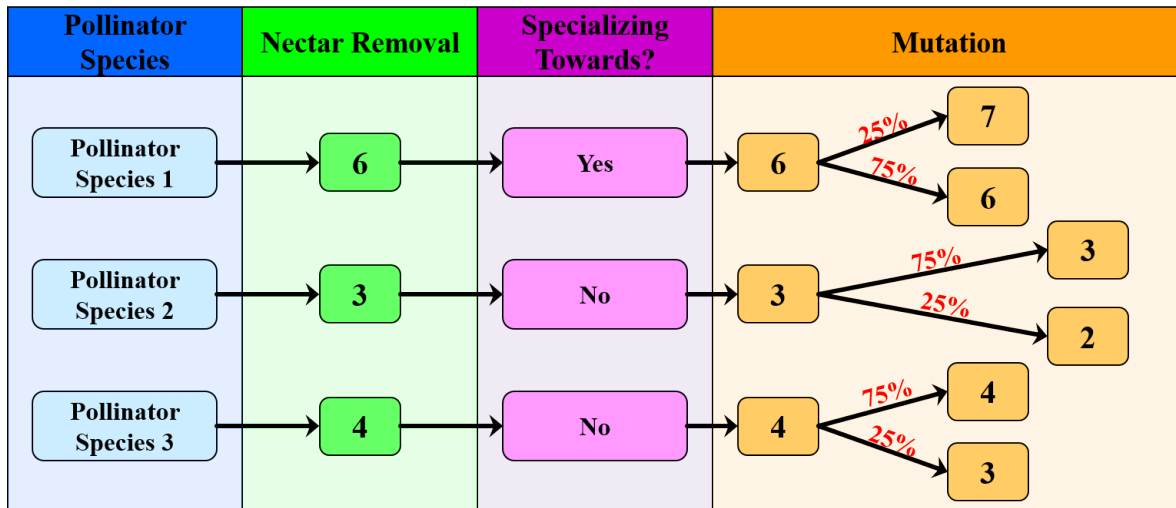


Figure 2.9: The possible mutations of pollinator nectar removal for a newly recruited plant displaying a mutation and whose parent displays a specialization pollination syndrome. The parent of this plant is specializing towards pollinator species 1.

Once the pollination syndromes and the phenotypes of the plants have been determined for the newly recruited plants, these plants are randomly placed in the empty cells left by the dead plants. After the placement of the newly recruited plants, the nectar and pollen are refreshed to initial levels for each plant. The fitness of each plant is reduced to zero as there is no fitness carryover between seasons. This action completes a season and the process repeats with a new season beginning.

2.2.5 ASSUMPTIONS

In any model, a set of assumptions must be made in order to simplify the immense complexity of nature. The following list describes important assumptions that have been made in the Java model.

1. Pollinators move among flowers
2. Pollinators remove nectar and pollen from flowers
3. Pollinators transfer pollen to the next flower they visit
4. Plants receive a fitness increase after a pollinator has transferred their pollen
5. Plants receive a fitness increase after receiving pollen
6. The probability of a plant receiving a pollinator is dependent on the plants pollination syndrome and the nectar removal rate of the pollinator
7. Pollinators forage for a finite amount of time
8. The amount of pollen and nectar in each flower may be replenished
9. Plants die at the end of each season
10. Plants may recruit one new plant
11. The probability of a plant recruiting a new plant is based on its fitness
12. Two plants are required to produce an outcrossed plant, however only one plant is considered to be the parent
13. Recruited plants may display a mutation or maintain the same phenotype as its parent
14. A mutation can cause a newly recruited plant to display a new phenotype and can cause the plant to display a new pollination syndrome
15. There are a finite number of pollination syndromes: generalists or specialist towards a single pollinator species
16. Generalist plants maintain a floral morphology that averages the pollen and nectar removed per visit for all species of pollinators
17. Specialist plants display a floral morphology that increases the pollen and nectar removed per visit for the species of pollinator that is being specialized towards
18. The floral morphology of a specialist plant decreases the pollen and nectar removed per visit for each pollinator species that is not being specialized towards
19. Pollination syndromes are unidirectional; for example, a newly recruited plant whose parent displays a generalist pollination syndrome cannot display a specialist pollination

2.3 ANALYSIS OF THE JAVA MODEL

Multiple simulations of the Java model were conducted to examine the changes in the outcome of the model as a result of parameter variations that reflect certain natural conditions. Although many parameters were varied across the different simulations, other parameters remained stable. These stable parameters describe the aspects of a natural plant-pollinator system that are unlikely to change over the time frame of the model. The parameters that remained constant throughout each analysis are shown in Table 2.1. Other parameters, while varying across some simulations, nevertheless, remained constant across multiple simulations (Table 2.2). When any of the parameters in Table 2.2 were varied for a simulation, the section will indicate which parameters were varied and the new value of each parameter.

Seasons within a model	500
Days within a season	4
Movement periods within a day	3
Moves in a movement period	25
Size of the flower patch	7 by 7 (49 plants)
Mutation rate	50% of newly recruited plants
Pollen per flower at the start of a day	50 pollen grains
Nectar per flower at the start of a day	75 units of nectar

Table 2.1: These are the parameters of the Java model that remained constant during all simulations of the Java model.

For the analysis of each simulation, the outcome of the model was obtained by recording the frequency of the generalist and specialist pollination syndromes in relation to each other at the end of each season. The population of plants displaying the phenotype of the original population was not included in this frequency measurement. The frequency of each syndrome within the last 20 seasons of the model was then used to create a running average of the frequencies for each syndrome. The model was run 50 times for each simulation and thus 50 running

Number of deaths per season	6 plants
Abundance of pollinator species 1	10
Initial pollen removal per visit of pollinator species 1	3
Initial nectar removal per visit of pollinator species 1	4
Abundance of pollinator species 2	10
Initial pollen removal per visit of pollinator species 2	3
Initial nectar removal per visit of pollinator species 2	4

Table 2.2: These are the values of the parameters of the Java model that remained constant during some simulations of the Java model. If any of these parameters were varied, this will be indicated in the relevant section.

averages were obtained. The mean and standard deviation of these 50 running averages produced a final average for the frequency of each syndrome. This final average of the frequency of each syndrome was recorded as the output of the model.

Rather than use the frequency of each syndrome within the last season of the model, this technique allowed the output to be moderately resistant to the stochastic processes inherent in the model. Also, during multiple practice executions of the model, it was noticed that the between-model variation could be quite large. As such, executing the model 50 times and averaging the running average allowed for an output that could resist the large fluctuations in the outcome of the model.

2.3.1 VARIATIONS OF POLLINATOR ABUNDANCE IN THE JAVA MODEL

For this analysis, two simulations were conducted. During the first simulation, the pollinator abundance during any given season was random. The abundance for each pollinator species was randomly selected at the beginning of each season and remained constant throughout that season. The random number could be any integer between and including 1 and 14 with equal probability. The second simulation maintained a constant pollinator abundance across seasons. The abundance for each pollinator species was set at 10 and did not vary during any season. For both simulations, all other parameters maintained the values shown in Tables 2.1 and 2.2.

The outcomes of these simulations were recorded and a two-tailed t-test was conducted. The one tailed t-test compared the frequency of generalist plants between the two simulations. The frequency of generalist plants was compared because the frequency of specialist plants, without considering which pollinator species they were specializing towards, could be found by subtracting the frequency of the plants displaying the generalist pollination syndrome from one. Thus, comparing the frequency of generalists also informs us of the changes in the frequency of specialists, without considering which species they were specializing towards.

2.3.2 VARIATIONS OF PLANT LONGEVITY IN THE JAVA MODEL

Similar to the above analysis of pollinator abundance, this analysis was conducted using two simulations. During the first simulation, the number of plant deaths at the end of a season was set to two. Consequently, the plants had an average life span of approximately 25 ($\frac{49}{2} = 24.5$) seasons which created a simulation in which plants had a long life span. For the second simulation, the number of plant deaths per season was set to 16. Thus, the plants had an average life span of about three ($\frac{49}{16} = 3.0625$) seasons which created a simulation in which plants had a short life span. The outcomes of these simulations were compared with a one-tailed t-test using the average frequency of the plants displaying a generalist pollination syndrome.

2.3.3 VARIATIONS IN POLLINATOR ABUNDANCE AND PLANT LONGEVITY IN THE JAVA MODEL

This analysis combines variations of pollinator abundance with variations in plant longevity resulting in four simulations. During the first simulation, the abundance of pollinators was random during any given season. Pollination abundance could

take any number between and including 1 and 14 with equal probability and was chosen independently for each pollinator species. The random number range did not include numbers after 14 because if, by chance, both pollinator species had an abundance of greater than 14, then there would be more than 28 pollinators in the model. Consequently, a model with more than 28 pollinators will have less than 21 empty flowers which could hinder the movement of pollinators to the point of inaccuracy. During the second simulation, pollinator abundances were kept constant with an abundance of 10 for each species of pollinator. Both of these simulations had plants that were characterized by a short life span and hence the number of plant deaths per seasons was maintained at 16. These simulations were compared using a one-tailed t-test that compared the average frequency of plants displaying a generalist pollination syndrome.

The third and fourth simulations followed the same pollinator abundance design as above, but contained plants which were long lived. Consequently, the number of plant deaths per seasons was set to two which is characteristic of long lived plants. The outcomes of these two simulations were compared using a two-tailed t-test comparing the average frequency of the plants displaying a generalist pollination syndrome.

2.3.4 SKEWED POLLINATOR EFFICIENCY AND/OR ABUNDANCE

Two analyses were conducted to examine the most efficient pollinator principal. The first analysis compares the outcome of simulations in which the efficiency of one pollinator species was increased, while the efficiency of the other pollinator species was decreased. The efficiency of pollinator species 1 was increased by setting the initial pollen removal to seven and initial nectar removal to four. The efficiency of pollinator species 2 was the decreased by setting the initial pollen removal to two and the initial nectar removal to three. All other parameters remained as

described in Tables 2.1 and 2.2. The frequency of specialist plants specializing towards pollinator species 1 of this simulation was compared to the frequency of specialist plants specializing towards pollinator species 1 of a simulation in which all parameters were maintained at the values described in Tables 2.1 and 2.2 using a two-tailed t-test.

The second analysis examines the outcome of simulations in which both the efficiency and abundance of one pollinator species was increased, while the efficiency and abundance of the other pollinator species was decreased. The efficiency of both pollinator species was set to the values described in the paragraph above. However, the abundance of pollinator species 1 was set to 16 while the abundance of pollinator species 2 was set to four. All other parameters remained as described in Tables 2.1 and 2.2. The frequency of specialist plants specializing towards pollinator species 1 of this simulation was compared to the frequency of specialist plants specializing towards pollinator species 1 of a simulation in which all parameters were maintained at the values described in Tables 2.1 and 2.2 using a two-tailed t-test.

2.3.5 CYCLIC POLLINATOR ABUNDANCE IN THE JAVA MODEL

Whereas the simulations prior to this section examined either random or constant pollinator abundance, this simulation was conducted to examine the outcomes of the model when pollinator abundance followed a cyclic pattern. The abundance of pollinators, although varying between seasons, follows the same pattern for the duration of the model. Consequently, it is possible to predict the abundance for each pollinator species during any given season even though it varies across seasons.

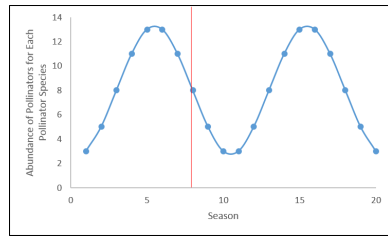
There were five cycles created for this analysis and each is described in Table 2.3 and shown in Figure 2.10. All other parameters were maintained at the values shown in Tables 2.1 and 2.2. Since the number of plant deaths per season was set to

six, the average longevity of the plants within each model is approximately eight ($\frac{49}{6} = 8.1\bar{6}$) seasons. With this lifespan, only during Cycle 1 and Cycle 3 do the plants generally survive through a season of peak pollinator abundance. During all other cycles, there is no guarantee that the plants will survive across a season with peak pollinator abundance. This concept is demonstrated in Figure 2.10 by the red line.

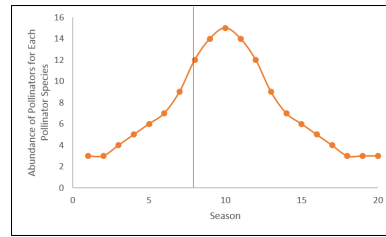
Cycle 1	Cycle 2	Cycle 3	Cycle 4	Cycle 5
3	3	2	3	3
5	3	7	5	3
8	4	13	7	5
11	5	7	9	5
13	6	2	7	8
13	7		5	8
11	9		7	11
8	12		9	11
5	14		12	13
3	15		14	13
	14		14	13
	12		12	11
	9		9	11
	7		7	8
	6		5	8
	5		7	5
	4		9	5
	3		7	3
	3		5	3
			3	

Table 2.3: These are the five cycles of pollinator abundance used to analyze how cyclic pollinator abundance alters the outcome of the model. The abundance of both pollinator species was described using these cycles. Each cycle has a different period length and the abundance of both pollinator species for one full period of each cycle is shown above.

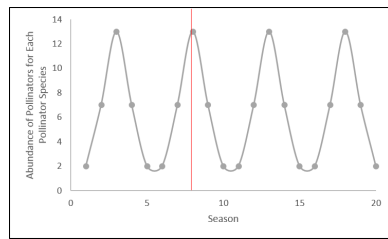
The effects of cyclic pollinator abundance on the outcome of the model were examined using the average frequency of generalist plants. These averages were compared using a single factor ANOVA to measure the difference among the simulations with the five different pollinator abundance cycles.



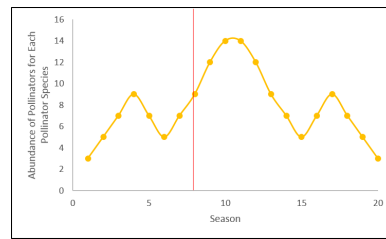
(a) Pollinator Abundance Cycle 1



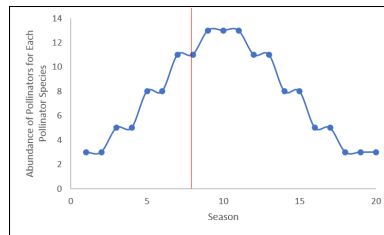
(b) Pollinator Abundance Cycle 2



(c) Pollinator Abundance Cycle 3



(d) Pollinator Abundance Cycle 4



(e) Pollinator Abundance Cycle 5

Figure 2.10: These graphs depict the abundance of both pollinator species across 20 seasons. The red line in each graph is the average lifespan of the plants within the model.

2.3.6 SENSITIVITY ANALYSIS OF THE JAVA MODEL

A one at a time sensitivity analysis is conducted by first running an initial model with a random set of initial conditions for each of the seven parameters in Table 2.2. Each of the parameters selected for variation have a different range of values allowed by the model's design. As part of this one at a time process, each parameter is increased by a certain value during each successive simulation. Hence, it is important to ensure that the increase for each parameter does not force the parameter to exceed its allowed value. Consequently, when selecting the initial value for each parameter, the range of the random number was equal to the range of values allowed minus the change in value for each parameter (Table 2.4).

After the initial parameters are randomly selected, a Java model is executed with the given initial values for each parameter. The mean of the running average of the frequency of the plants displaying a generalist pollination syndrome in the last 20 seasons of 50 simulations was used as the output for this analysis. The frequency of the plants displaying a generalist pollination syndrome is used as the output because this analysis was examining the sensitivity of the model and did not need to output the exact frequency of plants specializing towards a given pollinator. Instead, it was to examine the frequency of plants that were displaying a generalist or specialist pollination syndrome. As such, because there is only one generalist pollination syndrome in the model (there can be multiple specialist pollination syndromes depending on the number of pollinator species in the model), one can obtain the frequency of specialist plants, without regards for which species is being specialized towards, by subtracting the frequency of plant displaying a generalist pollination syndrome from 1. Using a running average of the last 20 seasons, as well as finding the mean of this running average over 50 simulations, allowed the output to withstand the large amount of stochasticity inherent in the Java model

Once the output for the initial simulation is received, the simulation is executed again with the same initial conditions, but with the first parameter changed by a given amount. The output of this simulation, referred to as simulation 1, is obtained and the amount of change in the first parameter is recorded. The output from the initial model is subtracted from the output of simulation 1 and the resulting difference is divided by the amount of change in the first parameter.

Rather than repeat this same process for each variable, which would result in $2 \cdot p$ model simulations (where p is the number of parameters to be varied), this system uses the output of simulation 1, where only the first parameter was changed, as the initial simulation for simulation 2 where the second parameter is changed. Thus, in the second simulation, both the first and second parameters are changed

but the difference is measured between simulation 2 and simulation 1. This process repeats itself and the outcome of the model where parameter one and two are varied becomes the initial run for the model run where parameter three is varied. This process continues for each parameter that is being varied and ends when all of the parameters have been varied once. This type of one at a time sensitivity analysis results in a significant decrease in the number of simulations where the number of required simulations is $p + 1$ instead of $2 \cdot p$. Hence, for the seven parameters used in this one at a time sensitivity analysis, only eight simulations are required rather than 14.

After all of the parameters have been varied once, one complete run of the one at a time sensitivity analysis is completed. This provides one datum point for each of the seven parameters. Consequently, multiple runs of the one at a time sensitivity analysis are conducted to receive as many data points for each parameter as desired. The one at a time sensitivity analysis is conducted a total of 25 times for this analysis. Once all the runs are completed, the mean and standard deviation of each parameter is calculated. The mean represents the importance of the parameter to the model (meaning the model is highly sensitive to changes in this parameter). The standard deviation describes the effects of the parameter on the model. If the standard deviation is high then it illustrates that the given parameter strongly interacts among other parameters or that the effects of the parameters are nonlinear. A small standard deviation indicates that the effects of the parameter are linear or that there is little to no interaction among other parameters.

2.3.7 STEP-BY-STEP DESCRIPTION OF THE ONE AT A TIME SENSITIVITY ANALYSIS OF THE JAVA MODEL

This example illustrates how the analysis was conducted for the Java model, but does so in a general description. An example with numbers, rather than variables,

is presented in the following section, section 2.3.8. In this example, there are seven parameters being varied. The initial values for each parameter are arrayed in a vector referred to as \vec{x}_0 . The vector, $\vec{x}_0 = (x_1, x_2, x_3, x_4, x_5, x_6, x_7)$, where x_n refers to the initial value of the n^{th} parameter.

The function $M(\vec{x}_n)$ is referred to as the model function which takes the values of the parameters in \vec{x}_n and produces an output of the model O_n . Thus, O_n represents the model output given a set of parameters.

The initial output is received by

$$M(\vec{x}_0) = M((x_1, x_2, x_3, x_4, x_5, x_6, x_7)) = O_0.$$

Simulation 1 uses vector \vec{x}_1 where $\vec{x}_1 = (x_1 + \Delta_1, x_2, x_3, x_4, x_5, x_6, x_7)$. The value Δ_1 is the change in the value of parameter 1. In this case, the value of $\Delta_1 = 2$ when x_1 refers to the population of pollinator species. The second output, O_1 , is obtain by

$$M(\vec{x}_1) = M((x_1 + \Delta_1, x_2, x_3, x_4, x_5, x_6, x_7)) = O_1.$$

Now that the values of O_0 and O_1 are obtained, the change in the outcomes can be measured. To do this, simply divide the difference of the two outputs by Δ_1 . Thus, obtaining a measure of change, C_1 , for parameter x_1 by

$$\frac{O_1 - O_0}{\Delta_1} = \frac{M((x_1 + \Delta_1, x_2, x_3, x_4, x_5, x_6, x_7)) - M((x_1, x_2, x_3, x_4, x_5, x_6, x_7))}{\Delta_1} = C_1.$$

The resulting quotient is then recorded and this represents one data point for the sensitivity of the Java model to changes in parameter x_1 .

As mentioned earlier, rather than repeat this same process for each parameter, wherein the model would have to be executed twice per parameter, we instead use the output of simulation 1, O_1 , as the initial output for simulation 2. Consequently,

simulation 2 uses the vector \vec{x}_2 where $\vec{x}_2 = (x_1 + \Delta_1, x_2 + \Delta_2, x_3, x_4, x_5, x_6, x_7)$. Notice that this vector has both Δ_1 and Δ_2 . This is because the initial simulation uses $\vec{x}_1 = (x_1 + \Delta_1, x_2, x_3, x_4, x_5, x_6, x_7)$ to produce the initial output for simulation 2. In order to obtain a point of data for the sensitivity of the Java model to changes in parameter x_2 , we simply repeat the same process as above, but substitute O_2 for O_1 , O_1 for O_0 , and Δ_2 for Δ_1 as the divisor. Thus we obtain,

$$\frac{O_2 - O_1}{\Delta_2} = \frac{M((x_1 + \Delta_1, x_2 + \Delta_2, x_3, x_4, x_5, x_6, x_7)) - M((x_1 + \Delta_1, x_2, x_3, x_4, x_5, x_6, x_7))}{\Delta_2} = C_2.$$

For each of the remaining parameters, this same process is repeated until all parameters have been varied once. Thus, in this example, the process continues until obtaining

$$\frac{O_7 - O_6}{\Delta_7} = C_7.$$

After all of the parameters have been varied once, the first iteration of the one at a time sensitivity analysis is complete.

2.3.8 AN EXAMPLE OF A ONE AT A TIME SENSITIVITY ANALYSIS RUN OF THE JAVA MODEL

Below is an example of one full run (varying the seven parameters of the Java model that have been selected for analysis) of the one at a time sensitivity analysis; it illustrates exactly how the analysis was conducted for the Java model. Table 2.4 describes the variables selected for change, their assigned variable names, the range of values allowed for each parameter, the change in each parameter during any

given sensitivity analysis run, and the range of random numbers used to select the initial values.

Parameter to be Varied	Variable Name	Range of Allowed Values	Change in Value	Random Number Range
Population of Pollinator Species 1	x_1	1 to 12	2	1 to 10
Nectar Removal for Pollinator Species 1	x_2	1 to 5	1	1 to 4
Pollen Removal for Pollinator Species 1	x_3	1 to 5	1	1 to 4
Population of Pollinator Species 2	x_4	1 to 12	2	1 to 10
Nectar Removal for Pollinator Species 2	x_5	1 to 5	1	1 to 4
Pollen Removal for Pollinator Species 2	x_6	1 to 5	1	1 to 4
Plant Deaths Per Season	x_7	1 to 16	2	1 to 14

Table 2.4: Displayed are the seven variables selected for sensitivity analysis, their variable name, the allowed range of values as determined by the model, the change in value as set by the researcher, and the random number range for each parameter.

Prior to the initial simulation of a one at a time sensitivity analysis, the initial values of the seven parameters in Table 2.4 are randomly selected. The initial values for each of the seven parameters are

$$\vec{x}_0 = (5, 3, 3, 4, 4, 4, 2).$$

From here, the same process, as outlined in section 2.3.7, is followed and each Δ_n is selected from the change in values column of Table 2.4.

$$M(\vec{x}_0) = M((5, 3, 3, 4, 4, 4, 2)) = 0.39925$$

$$M(\vec{x}_1) = M((5 + 2, 3, 3, 4, 4, 4, 2)) = M((7, 3, 3, 4, 4, 4, 2)) = 0.3395 = O_1$$

$$\frac{O_1 - O_0}{1} = \frac{0.39925 - 0.3395}{2} = -0.029875 = C_1$$

$$M(\vec{x}_2) = M((7, 3 + 1, 3, 4, 4, 4, 2)) = M((7, 4, 3, 4, 4, 4, 2)) = 0.4062 = O_2$$

$$\frac{O_2 - O_1}{1} = 0.4062 - 0.3395 = 0.0667 = C_2$$

$$M(\vec{x}_3) = M((7, 4, 3 + 1, 4, 4, 4, 2)) = M((7, 4, 4, 4, 4, 4, 2)) = 0.3804 = O_3$$

$$\frac{O_3 - O_2}{1} = 0.3804 - 0.4062 = -0.0258 = C_3$$

$$M(\vec{x}_4) = M((7, 4, 4, 4 + 2, 4, 4, 2)) = M((7, 4, 4, 6, 4, 4, 2)) = 0.3541 = O_4$$

$$\frac{O_4 - O_3}{2} = \frac{0.3541 - 0.3804}{2} = -0.0262 = C_4$$

$$M(\vec{x}_5) = M((7, 4, 4, 6, 4 + 1, 4, 2)) = M((7, 4, 4, 6, 5, 4, 2)) = 0.3625 = O_5$$

$$\frac{O_5 - O_4}{1} = 0.3625 - 0.3541 = 0.0084 = C_5$$

$$M(\vec{x}_6) = M((7, 4, 4, 6, 5, 4 + 1, 2)) = M((7, 4, 4, 6, 5, 5, 2)) = 0.2763 = O_6$$

$$\frac{O_6 - O_5}{1} = 0.2763 - 0.3625 = -0.0431 = C_6$$

$$M(\vec{x}_7) = M((7, 4, 4, 6, 5, 5, 2 + 2)) = M((7, 4, 4, 6, 5, 5, 4)) = 0.3217 = O_7$$

$$\frac{O_7 - O_6}{2} = \frac{0.3217 - 0.2763}{2} = 0.0227 = C_7$$

After each parameter has been varied once, one run of the one at a time sensitivity analysis is complete. Consequently, one point of data, which measures the sensitivity of the model to changes in a given parameter, is obtained. The data points are C_n where n is the n^{th} parameter of the model. This process was repeated an additional 24 times. Once 25 data points for each parameter are obtained, the mean and standard deviation are found.

2.4 SYSTEM OF DIFFERENTIAL EQUATIONS MODEL

To simulate the change in frequency of specialists and generalists within a population of plants, this model utilizes a system of differential equations. The models are developed using a differential equation for the population of plants displaying a generalist or specialist pollination syndrome(s) and includes two species of

pollinators. Each equation takes into account the frequency of the pollination syndrome within the total population of plants, the abundance of each pollinator species, and each pollination syndrome's attractiveness towards each pollinator species. Only two pollinator species were included in the models to simplify the number of equations and number of parameters. It is possible to increase the number of pollinators, but this will also increase the number of parameters and/or the number of equations in each model.

The equations of the model were designed in such a way that our assumptions of the nature of plant-pollinator interactions were upheld. First an equation whose growth was dependent on frequency of the syndrome it described was needed. If, for instance, a plant displaying a certain pollination syndrome was rare within a population we would not expect the frequency of this syndrome to increase in a drastic manner. Rather, we would expect the frequency to slowly increase and gain speed as time progressed. Also, the growth or decline in the frequency of a pollination syndrome is dependent on the abundance of pollinators within the system. If there are no pollinators it would be expected that there would be no change of the frequency of any pollination syndrome. Finally, the rate of attraction of each plant pollination syndrome should alter the growth rate of the frequency of the pollination syndrome. In accounting for the differences in the attraction of each syndrome to a pollinator species, the equations can define a certain generalist or specialist pollination syndrome. A generalist pollination syndrome would have relatively equal attractiveness to each of the pollinator species. In contrast, a specialist pollination syndrome would be much more attractive to the species of pollinator that it is specializing towards while having a low attractiveness towards those species of pollinators it is not specializing towards. Each of these three concepts was incorporated into this model and are reflected in the design of the equations.

Two models were constructed to have both a simple and complex model. The first model constructed uses two differential equations to describe a generalist pollination syndrome and a specialist pollination syndrome. This model is referred to as the two equation model and is described in section 2.4.1. The other model that was developed uses three differential equations to describe a generalist pollination, a specialist pollination syndrome specializing towards pollinator species 1, and a specialist pollination syndrome specializing towards pollinator species 2. This model is referred to as the three equation model and is described in section 2.4.2.

2.4.1 THE TWO EQUATION MODEL

The first model developed uses two equations to describe the relationship between plants displaying a specialist or generalist pollination syndrome, pollinator abundance, and the attractiveness of each pollination syndrome towards a species of pollinators. The two equations represent the rate of change of a generalist and a specialist population of plants. The specialist population is, without loss of generality, specializing towards pollinator species 1. This system of differential equation looks at the interplay between a generalist and specialist pollination syndrome without regards to which species of pollinator the plants displaying a specialist pollination syndrome are specializing towards. The system is described by the following two equations.

$$\frac{dx}{dt} = \frac{x}{x+y} \cdot (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta) \quad (2.1)$$

$$\frac{dy}{dt} = \frac{y}{x+y} \cdot (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta) \quad (2.2)$$

Each equation represents the change in the population of plants displaying a specialist or generalist pollination syndrome. Equation 2.1 represents the change in the population of plants that are displaying a specialist pollination syndrome

and Equation 2.2 represents the change in the population of plants displaying a generalist pollination syndrome. The first part of each equation, $(\frac{x \text{ or } y}{x+y})$, represents the percentage of the total population that the plants displaying a specialist or generalist pollination syndrome represent at a given time. The second part of the equation, $(\alpha_{x \text{ or } y} \cdot p_{\alpha} + \beta_{x \text{ or } y} \cdot p_{\beta})$, represents the fitness gain from the pollinators as dependent on the pollinator abundances and the attractiveness of each syndrome.

Each equation contains four constants. These constants represent the percentage of total visits to plants displaying a given pollination syndrome by each pollinator species and the abundance of pollinator species 1 and 2. The parameters $\alpha_{x \text{ or } y}$ describe the percentage of total visits to each pollination syndrome made by pollinator species 1. Similarly, $\beta_{x \text{ or } y}$ represents the percentage of total visits to the pollination syndromes made by pollinator species 2. As these two constants represent percentages of a total, both numbers must sum to 1. The parameters p_{α} and p_{β} characterize the abundance of pollinator species 1 and pollinator species 2 respectively. Any of these parameters can be described by a constant or a function.

2.4.1.1 CONSTANT PARAMETER MODEL

The variables in the system of differential equations described in section 2.4.1 were given constant values to understand the effects of a static environment on the outcome of the model. The value of α_x was set to 0.9 and the value for β_x was set to 0.1. This was done to reflect the increased attractiveness of plants displaying a specialist pollination syndrome towards pollinator species 1. The values of α_y and β_y were set to 0.5 in order to represent a generalist plant's relatively equal attractiveness to both species of pollinators. The pollinator abundances were varied to examine the effects that differing levels of pollinator population have on the outcome of the model.

Three trials were conducted to examine the effects of variations in pollinator

abundances. The first trial examined the outcome when pollinator species 1 was rare and pollinator species 2 was abundant. In this simulation, the abundance of pollinator species 1 was set to five and the abundance of pollinator species 2 was set to 35. The second simulation examined the reverse of the first. Thus, the abundance of pollinator species 1 was set to 35 and the abundance of pollinator species 2 was set to five. The last pollinator abundance simulation was conducted with both pollinator species being equal in abundance and thus both abundances were set to 20. During each of the described pollinator abundance variations, the initial population of plants displaying a specialist syndrome and plants displaying a generalist pollination syndrome was set to 25. This was done to ensure that all variations in the outcome could be attributed to variation in pollinator abundances.

2.4.1.2 CYCLIC PARAMETER MODEL

During this analysis, the variables describing the abundance of each pollinator species were substituted with sine functions to understand the effects of a variable environment on the outcome of the model. The amplitude and period of the sine functions were varied in numerous ways to examine how the outcome of the model would be affected given a specific amplitude and period. The initial population for each pollinator syndrome remained constant to ensure that any variation to the outcome of the model could be attributed to the cyclic functions. Similarly, the values of α_x , β_x , α_y , and β_y were set to 0.9, 0.1, 0.5, and 0.5, respectively, for the same reasons as described in the previous section.

Table 2.5 depicts the cyclic functions used to describe the abundance of each pollinator species that have the same amplitudes but different periods. Table 2.6 depicts the cyclic functions used to describe the abundance of each pollinator species that have the same periods but different amplitudes. Finally, 2.7 depicts the cyclic functions used to describe the abundance of the pollinator species that have a

different amplitude and different periods. Combinations of cycles were not repeated in multiple analyses. Similarly, after the results of the first analysis, cycles that had the same amplitude and period were not repeated.

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2
$p_\alpha = 10 \cdot \sin(t) + 10$	$p_\beta = 10 \cdot \sin(t/5) + 10$
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 10 \cdot \sin(t) + 10$
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 10 \cdot \sin(t/5) + 10$

Table 2.5: The cyclic functions used to describe the abundance of each pollinator species. The cyclic functions have the same amplitudes but different periods.

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2
$p_\alpha = 5 \cdot \sin(t/5) + 10$	$p_\beta = 10 \cdot \sin(t/5) + 10$
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 5 \cdot \sin(t/5) + 10$

Table 2.6: The cyclic functions used to describe the abundance of each pollinator species. The cyclic functions have different amplitudes but the same periods.

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 10 \cdot \sin(t/5) + 10$
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 10 \cdot \sin(t) + 10$
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 5 \cdot \sin(t/5) + 5$
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 10 \cdot \sin(t/5) + 10$
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 10 \cdot \sin(t) + 10$
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 5 \cdot \sin(t) + 5$
$p_\alpha = 10 \cdot \sin(t) + 10$	$p_\beta = 5 \cdot \sin(t/5) + 5$
$p_\alpha = 10 \cdot \sin(t) + 10$	$p_\beta = 5 \cdot \sin(t) + 5$
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 5 \cdot \sin(t/5) + 5$
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 5 \cdot \sin(t) + 5$

Table 2.7: The cyclic functions used to describe the abundance of each pollinator species. The cyclic functions have different amplitudes and different periods.

2.4.2 THE THREE EQUATION MODEL

This model uses three equations to describe the relationship between plants displaying a certain pollination syndrome, pollinator abundances, and the attractiveness of each pollination syndrome towards a species of pollinator. The equations describe the rate of change of a population of generalist plants and two populations of specialist plants. The first plant population displaying a specialist pollination syndrome is specializing towards pollinator species 1 while the second plant population displaying a specialist pollination syndrome is specializing towards pollinator species 2. Unlike the two equation model, this model examines the outcome of a plant-pollinator system where there are two possible specialist pollination syndromes. This system is described by the following equations.

$$\frac{dx}{dt} = \frac{x}{x + y + z} \cdot (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta) \quad (2.3)$$

$$\frac{dy}{dt} = \frac{y}{x + y + z} \cdot (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta) \quad (2.4)$$

$$\frac{dz}{dt} = \frac{z}{x + y + z} \cdot (\alpha_z \cdot p_\alpha + \beta_z \cdot p_\beta) \quad (2.5)$$

Each equation represents the change in the population of each possible pollination syndrome. Equation 2.3 and Equation 2.4 represent the change in the population of plants displaying a specialist pollination syndrome and Equation 2.5 represents the change in the population of plants displaying a generalist pollination syndrome. The first part of each equation, $(\frac{x, y, \text{ or } z}{x+y})$, represents the frequency of each pollination syndrome within the total population of plants. The second part of the equation, $(\alpha_{x, y, \text{ or } z} \cdot p_\alpha + \beta_{x, y, \text{ or } z} \cdot p_\beta)$, represents the fitness gain from each pollinator species as dependent on the pollinator abundances and attractiveness of each syndrome.

Similar to the two equation model, each equation in this model contains four constants. These constants represent the percentage of total visits to the pollination

syndrome by a given pollinator species and the abundances of pollinator species. $\alpha_{x, y, \text{ or } z}$ describes the percentage of total visits to the pollination syndrome made by pollinator species 1. Similarly, $\beta_{x, y, \text{ or } z}$ represents the percentage of total visits to the pollination syndrome made by pollinator species 2. As these constants represent percentages, both numbers must sum to 1. The parameters p_α and p_β characterize the abundance of pollinator species 1 and pollinator species 2 respectively. These parameters can be described by a constant or a function.

CHAPTER 3

RESULTS OF THE JAVA MODEL

As mentioned in section 2.3, multiple simulations of the Java model with variations in the values of the parameters were conducted to examine the influence of each parameter on the outcome of the model. The outcome of the model, regardless of the pollination syndrome selected to compare, was obtained by a running average of the frequency of the pollination syndrome during the last 20 seasons of each model. For each simulation, 50 models were executed and the resulting 50 running averages were used as the data for a statistical test. These 50 running averages were also used to obtain the means and mean standard errors used to produce the figures in this section.

The sensitivity analysis of the model indicated that the model was most sensitive to changes in the abundance of pollinator species 2 and the initial pollen removal of pollinator species 1. In contrast, the model was least sensitive to changes in the number of plant deaths per season (Figure 3.1). If the abundance of pollinator species 2 was increased by 1, this would result, on average, in a 1.4% decrease in the frequency of generalist plants. An increase of 1 for the initial pollen removal of pollinator species 1 results in an average increase of 1.57% for the frequency of generalist plants. Finally, an increase of the number of plant deaths per season decreased, on average, the frequency of generalist plants by 0.24% (Figure 3.2).

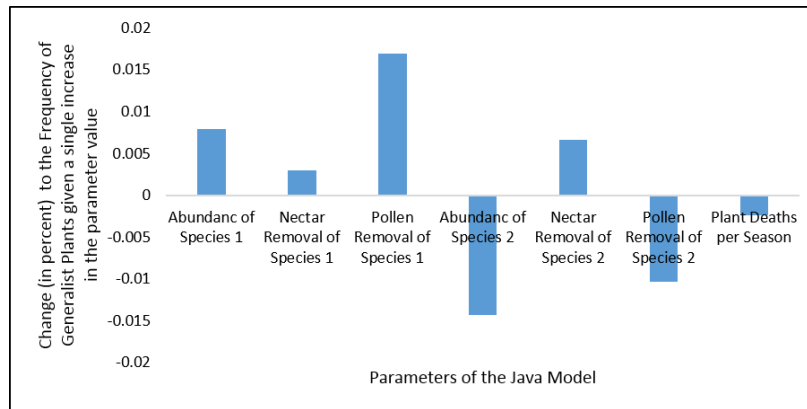


Figure 3.1: The average percent change to the frequency of generalist plants resulting from an increase in the parameters by one. These averages were obtained from the one at a time sensitivity analysis described in section 2.3.6.

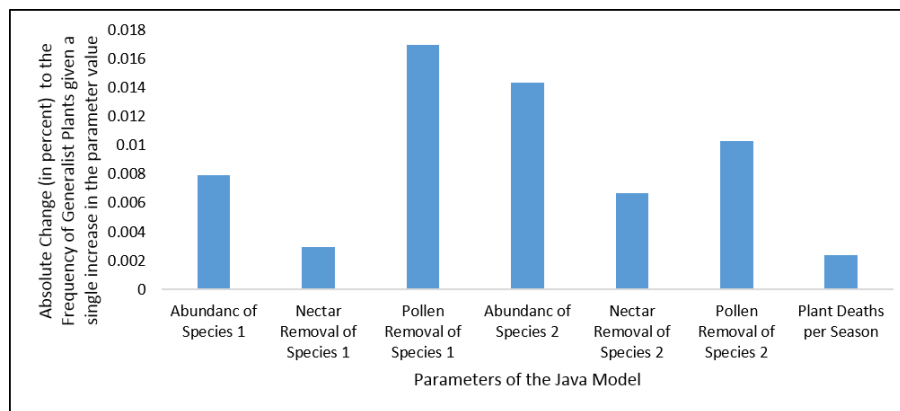


Figure 3.2: The absolute value of averages found in Figure 3.1. This illustrates which parameters the model is most sensitive to and which parameters the model is most resistant to.

There was no significant difference in the frequency of generalists between simulations in which pollinator abundance was constant across seasons and simulations in which pollinator abundance was random during any given season (2 sample two-tailed t-test, $t = -1.23$; d.f. = 98; $p = 0.22$). These results are illustrated in Figure 3.3.

The frequency of generalist plants during simulations with long lived plants was significantly higher (2 sample one-tailed t-test, $t = 4.15$; d.f. = 98; $p = 3.51 \times$

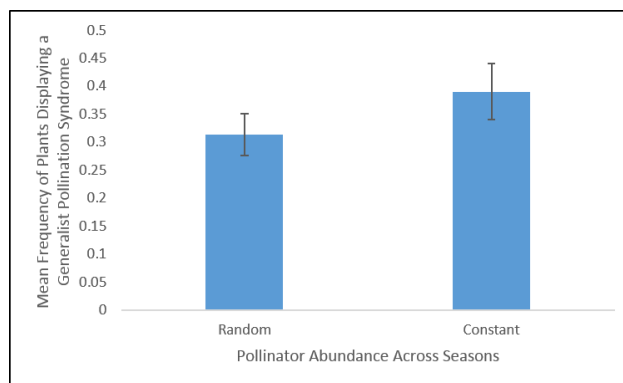


Figure 3.3: The mean frequency of generalist plants in simulations in which pollinator abundance was random during any given season and simulations in which pollinator abundance was constant across seasons. The bars represent mean standard error.

10^{-5}) than simulations containing short-lived plants. Figure 3.4 illustrates the large difference in the frequency of generalist plants.

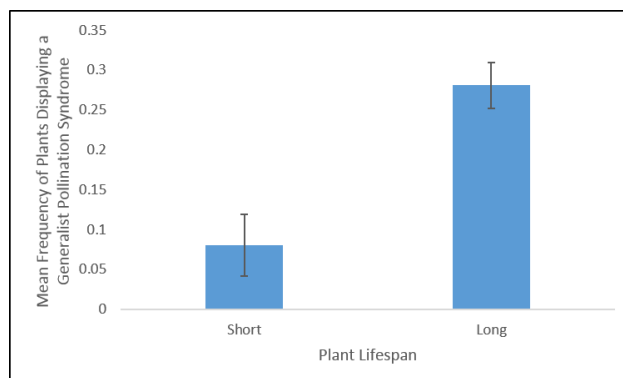


Figure 3.4: The mean frequency of generalist plants in simulations with short lived plants and simulations with longed lived plants. The bars represent mean standard error.

There was a significant increase in the frequency of generalist plants in simulations with a constant pollinator abundance across seasons and short lived plants compared to simulations with random pollinator abundance with short lived plants (2 sample one-tailed t-test, $t = 2.96$; d.f. = 98; $p = 0.002$). These results are illustrated in Figure 3.5.

The frequency of generalist plants between simulations in which pollinator abundance was constant with long lived plants and simulations with random

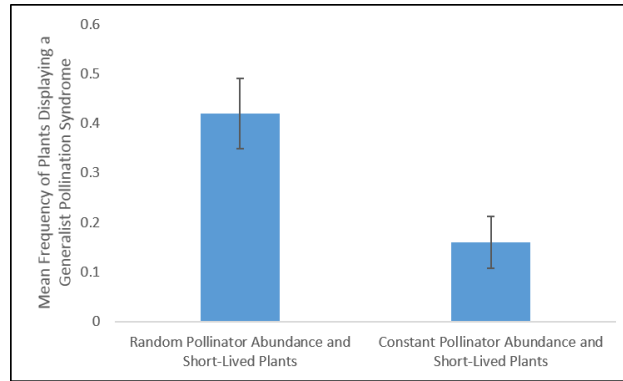


Figure 3.5: The mean frequency of generalist plants in simulations in which pollinator abundance is random during any season with short lived plants and simulations in which pollinator abundance is constant across seasons with short lived plants. The bars represent mean standard error.

pollinator abundance and long lived plants was not significantly different (2 sample two-tailed t-test, $t = 1.13$; d.f. = 98; $p = 0.26$). These results are illustrated in Figure 3.6.

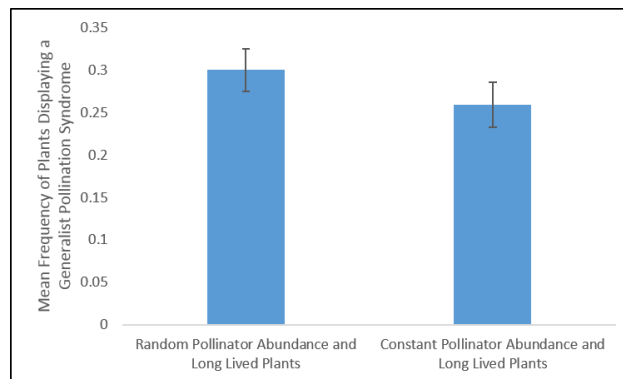


Figure 3.6: The mean frequency of generalist plants in simulations in which pollinator abundance is random during any season with long lived plants and simulations in which pollinator abundance is constant across seasons with long lived plants. The bars represent mean standard error.

During the first simulation of this analysis of skewed pollinator efficiency, pollinator species 1 was characterized in such a way that it was the most efficient pollinator while pollinator species 2 was characterized as having the lowest efficiency. The graph of the output of both simulations illustrates that the frequency of plants

displaying a specialist pollination syndrome specializing towards pollinator species 1 is relatively equal (Figure 3.7). The statistical analysis also indicates that there was no significant difference in the frequency of plants specializing towards pollinator species 1 between simulations with the efficiency of pollinator species 1 increased compared to simulations in which the efficiency of both pollinator species was the same (2 sample two-tailed t-test, $t = 1.66$; d.f. = 98; $p = 0.08$).

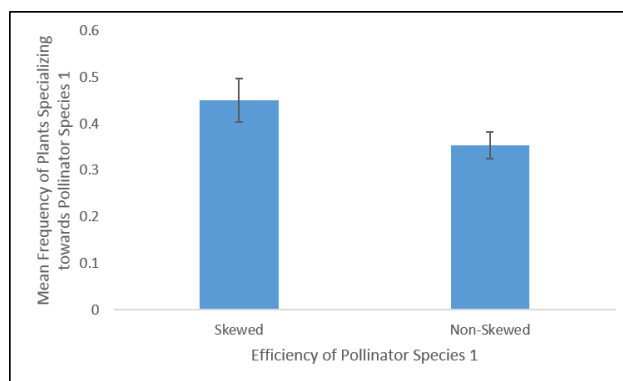


Figure 3.7: The mean frequency of plants displaying a specialist pollination syndrome specializing towards pollinator species 1. The averages were obtained from simulations in which the efficiency of pollinator species 1 was increased and the efficiency of pollinator species 2 was decreased and simulations in which the efficiency of both pollinators was the same. The bars represent mean standard error.

During the simulation with an increase in the efficiency and abundance of pollinator species 1, the simulations were constructed in such a way that pollinator species 1 was the absolute "best" pollinator in the system while pollinator species 2 was the absolute "worst". However, there was no significant difference in the frequency of plants specializing towards pollinator species 1 between the simulations with an increase in the efficiency and abundance of the pollinator species 1 and a decrease in the efficiency and abundance of pollinator species 2 and the simulations with both pollinator species having the same efficiency and abundance (2 sample two-tailed t-test, $t = 0.47$; d.f. = 98; $p = 0.64$). The relatively equal frequency of generalist plants between the simulations is illustrated in Figure 3.8.

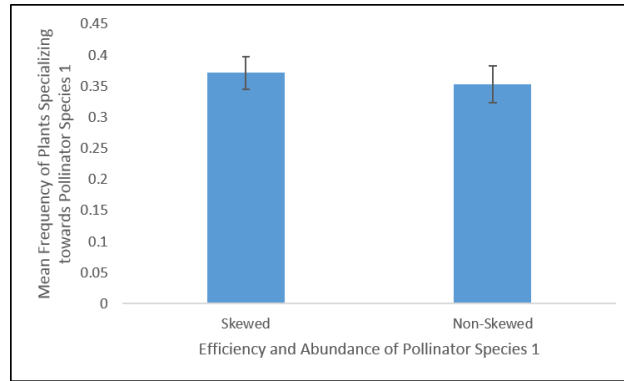


Figure 3.8: The mean frequency of plants displaying a specialist pollination syndrome specializing towards pollinator species 1. The averages were obtained from simulations in which the efficiency and abundance of pollinator species 1 was increased while decreased for pollinator species 2 and simulations in which the efficiency and abundance of both pollinators was the same. The bars represent mean standard error.

There was no significant difference in the frequency of generalists between the simulations with cyclic pollinator abundance ($F(4, 245) = 1.54, p = 0.19$). Figure 3.9 illustrates that the frequency of generalist plants stayed relatively constant across each cycle. Only during Cycle 1 was the average lifespan of the plants longer than the period of the cycle. In Cycle 3 the average lifespan of the plants was longer than half of the period of the cycle. In Cycles 2, 4, and 5, the average lifespan of the plants was shorter than even half of the length of the period.

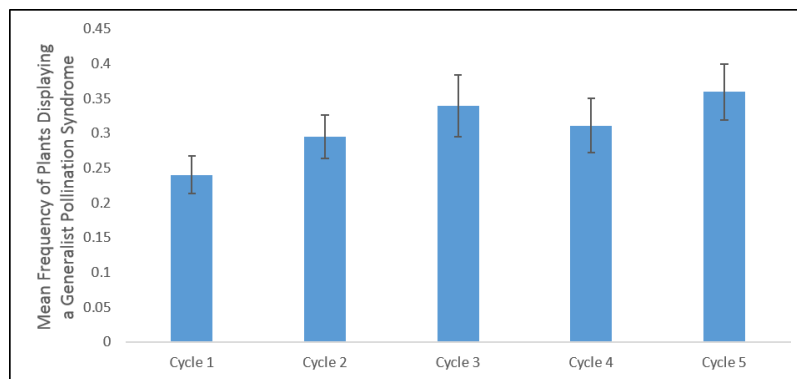


Figure 3.9: The mean frequency of generalist plants during simulations with cyclic pollinator abundance. The bars represent mean standard error. Cycles are defined in section 2.3.5.

CHAPTER 4

ANALYSIS OF THE DIFFERENTIAL EQUATION MODELS

Both of the system of differential equation models described in sections 2.4.1 and 2.4.2 are analyzed to understand how the outcome of the models would change given a set of initial conditions. The two equation model,

$$\frac{dx}{dt} = \frac{x}{x+y} \cdot (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$$

$$\frac{dy}{dt} = \frac{y}{x+y} \cdot (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta),$$

is analyzed in two ways. The first analysis is conducted by finding the derivatives describing the change in the frequency of each pollination syndrome. These equations are then used to examine the conditions under which one would expect to see growth or decline in the frequency of each pollination syndrome. The second analysis looks at the effects of different pollinator abundances on the outcome of the model. The three equation model,

$$\frac{dx}{dt} = \frac{x}{x+y+z} \cdot (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$$

$$\frac{dy}{dt} = \frac{y}{x+y+z} \cdot (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta)$$

$$\frac{dz}{dt} = \frac{z}{x+y+z} \cdot (\alpha_z \cdot p_\alpha + \beta_z \cdot p_\beta),$$

is only analyzed using the same frequency differential equation method as was used for the two equation model. The analysis examining the effects of pollinator abundance is not conducted on the three equation model because of the taxing computational requirements.

4.1 DIFFERENTIAL EQUATION ANALYSIS OF THE TWO EQUATION MODEL

Both equations in the two equation model are used to find differential equations which describe the rate of change of the frequency of each pollination syndrome. This is accomplished using the quotient rule and chain rule. Below is the step-by-step process for finding each differential equation. First, the differential equation of the frequency of the specialist pollination syndrome is found and then the differential equation of the frequency of the generalist pollination syndrome is found. The final equation for each syndrome is numbered.

Set $M = (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$ and set $N = (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta)$.

Then, the equations become $\frac{dx}{dt} = \frac{x}{x+y} \cdot M$ and $\frac{dy}{dt} = \frac{y}{x+y} \cdot N$.

$$\begin{aligned}
\frac{d}{dt} \left(\frac{x}{x+y} \right) &= \frac{\frac{x}{x+y} \cdot M \cdot (x+y) - x \cdot \left(\frac{x}{x+y} \cdot M + \frac{y}{x+y} \cdot N \right)}{(x+y)^2} \\
&= \frac{\frac{x^2 \cdot M + xy \cdot M}{x+y} - \left(\frac{x^2 \cdot M + xy \cdot N}{x+y} \right)}{(x+y)^2} \\
&= \frac{x^2 \cdot M + xy \cdot M - x^2 \cdot M - xy \cdot N}{(x+y)^3} \\
&= \frac{xy \cdot M - xy \cdot N}{(x+y)^3}
\end{aligned}$$

$$\frac{d}{dt} \left(\frac{x}{x+y} \right) = \frac{xy \cdot (M - N)}{(x+y)^3} = \frac{xy \cdot ((\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta) - (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta))}{(x+y)^3} \quad (4.1)$$

$$\begin{aligned}
\frac{d}{dt} \left(\frac{y}{x+y} \right) &= \frac{\frac{y}{x+y} \cdot N \cdot (x+y) - y \cdot \left(\frac{x}{x+y} \cdot M + \frac{y}{x+y} \cdot N \right)}{(x+y)^2} \\
&= \frac{\frac{y^2 \cdot N + xy \cdot N}{x+y} - \left(\frac{xy \cdot M + y^2 \cdot N}{x+y} \right)}{(x+y)^2} \\
&= \frac{y^2 \cdot N + xy \cdot N - xy \cdot M - y^2 \cdot N}{(x+y)^3} \\
&= \frac{xy \cdot N - xy \cdot M}{(x+y)^3}
\end{aligned}$$

$$\frac{d}{dt} \left(\frac{y}{x+y} \right) = \frac{xy \cdot (N - M)}{(x+y)^3} = \frac{xy \cdot ((\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta) - (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta))}{(x+y)^3} \quad (4.2)$$

With each of the differential equations describing the rate of change in the frequency of each syndrome found, the outcomes of the model under different initial populations for each pollination syndrome could be examined. This analysis results in four cases that examine the conditions under which one would see an increase or decrease in the frequency of each pollination syndrome: both the initial populations of the specialist syndrome (variable x) and the generalist syndrome (variable y) are zero, one initial population is zero and the other is greater than zero, and both initial populations are greater than zero.

Case 1: The parameters $x = 0$ and $y = 0$ are the initial conditions. This is a trivial case and both equation (4.1) and equation (4.2) equal zero, denoting that there is no change in the frequency of each pollination syndrome. Although this case is trivial, this result is important as it indicates that the frequency of each syndrome cannot arise from the absence of the syndrome. If either of the equations had shown an increase or decrease, this result would not be consistent with our assumptions of the nature of plant-pollinator systems and the model would be too inaccurate for use.

Case 2: The parameters $x > 0$ and $y = 0$ are the initial conditions. Again, this is a trivial case as both frequency differential equations equal zero; there is no change to the frequency of each pollination syndrome. This case also represents an important result for the model. It shows that the specialist pollination syndrome remains at 100 percent and the generalist pollination syndrome remains at zero percent. This indicates that a syndrome cannot arise from an absence of that syndrome and that the initial syndrome will persist in the environment.

Case 3: The parameters $x = 0$ and $y > 0$ are the initial conditions. This case results

in the same, but inverted, outcome as Case 2. Thus, the results indicate that the specialist syndrome remains at zero percent and the generalist syndrome remains at 100 percent. This result is important for the accuracy of the model because it demonstrates that, once again, a syndrome cannot arise from an absence of that syndrome and that the initial syndrome will persist in the environment.

Case 4: The parameters $x > 0$ and $y > 0$ are the initial conditions. This case results in three different outcomes depending on the values of $M = (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$ and $N = (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta)$.

$$\frac{d}{dt} \left(\frac{x}{x+y} \right) = \begin{cases} > 0 & \text{if } M > N \\ 0 & \text{if } M = N \\ < 0 & \text{if } M < N \end{cases}$$

$$\frac{d}{dt} \left(\frac{y}{x+y} \right) = \begin{cases} > 0 & \text{if } N > M \\ 0 & \text{if } N = M \\ < 0 & \text{if } N < M \end{cases}$$

This result is significant because it indicates that an increase or decrease in the frequency of a pollination syndrome is dependent on the interactions of the pollinator species. It also indicates that the growth or decline of a pollination syndrome can only occur due to the presence of pollinators. This is an important assumption of the model and is a necessary component which increases the accuracy of the model.

Each of the four cases represents how the frequency of a specialist and generalist pollination syndrome will change over time. Although Cases 1, 2, and 3 are

trivial, they nonetheless indicate that the model is functioning as desired. Case 4 is important as it details exactly when the frequency of a pollination syndrome will increase, remain stable, or decrease, given a set of conditions describing pollinator abundances and attractiveness of each syndrome.

4.2 NUMERICAL BASED ANALYSIS OF THE TWO EQUATION MODEL

Using the analysis of Case 4 in the above section, this analysis explores the outcome of the model when pollinator abundances are stable, cyclic with different amplitudes, cyclic with different periods, and cyclic with different amplitudes and different periods. To find which pollination syndrome is favoured in the model, we will find the values of M and N , where $M = (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$ and $N = (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta)$, and apply the conditions from Case 4 to examine which syndrome is favoured.

Throughout each of the variations in pollinator abundance, the values of α_x , α_y , β_x , and β_y remain constant. The initial population of each syndrome also remains constant, although it does vary between certain simulations. The pollinator abundances are constant during some iterations and cyclic during others. When pollinator abundances are constant, the values of M and N are found by simply substituting the constant values into M and N for each of the parameters describing pollinator abundance. When using cyclic functions to describe pollinator abundances, the average value of the function across a given time period is substituted into the corresponding parameter for pollinator abundance. In this way, one number will be substituted for the abundance of each pollinator species in M and N .

For each of the following analyses of the two equation model, $\alpha_x = 0.9$, $\beta_x = 0.1$, $\alpha_y = 0.5$, $\beta_y = 0.5$, and the initial populations of each syndrome were set to 25.

Constant Pollinator Abundance

Table 4.2 displays the values of the abundance for each species of pollinator, the values of M and N , and indicates the favoured syndrome. When the abundance of pollinator species 1 is greater than the abundance of pollinator species 2, the frequency of the specialist plants increases until reaching one (Figure 4.1). In contrast, the frequency of the generalist plants decreases until reaching zero. When the abundance of pollinator species 2 is greater than the abundance of pollinator species 1, the frequency of the generalist plants increases until reaching one. In contrast, the frequency of the specialist plants decreases until reaching zero. If the abundance for both pollinator species is equal, then there is no change to the frequency of either pollination syndrome.

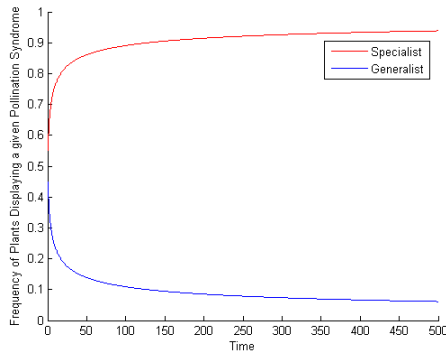


Figure 4.1: The changing frequencies of plants displaying each pollination syndrome when the abundance of pollinator species 1 is 35 and the abundance of pollinator species 2 is five.

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2	Outcome of the Model
35	5	$M > N$, specialization is favoured
5	35	$M < N$, generalization is favoured
20	20	$M = N$, no change

Figure 4.2: The outcome of the two equation model when pollinator abundance is constant.

Cyclic Pollinator Abundance with Different Periods

In this analysis, the functions used to describe the abundance of each pollinator species have the same amplitudes but different periods. For each of the three simulations, there is no change in the frequency of each of the pollination syndromes.

Table 4.1 displays the cyclic functions used to describe the abundance of each species of pollinator and the relationship between M and N .

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2	Average Value of p_α	Average Value of p_β	Outcome of the Model
$10 \cdot \sin(t) + 10$	$10 \cdot \sin(t/5) + 10$	10	10	$M = N$, no change
$10 \cdot \sin(t/5) + 10$	$10 \cdot \sin(t) + 10$	10	10	$M = N$, no change
$10 \cdot \sin(t/5) + 10$	$10 \cdot \sin(t/5) + 10$	10	10	$M = N$, no change

Table 4.1: The outcome of the two equation model when pollinator abundance is cyclic with the same amplitudes but different periods. Average values for p_α and p_β are found across a period of 10π .

Cyclic Pollinator Abundance with Different Amplitudes

In this analysis, the cyclic functions used to describe the abundance of each pollinator species had the same periods but different amplitudes. For each of the three iterations of the model, there was no change in the frequency of each of the pollination syndromes. Table 4.2 displays the cyclic functions used to describe the abundance of each species of pollinator as well as the relationship between M and N .

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2	Average Value of p_α	Average Value of p_β	Outcome of the Model
$5 \cdot \sin(t/5) + 10$	$10 \cdot \sin(t/5) + 10$	10	10	$M = N$, no change
$10 \cdot \sin(t/5) + 10$	$5 \cdot \sin(t/5) + 10$	10	10	$M = N$, no change

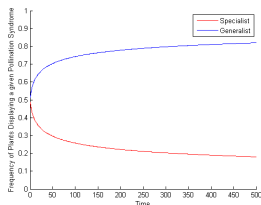
Table 4.2: The outcome of the two equation model when pollinator abundance is cyclic with the same period but different amplitude. Average values for p_α and p_β are found across a period of 10π .

Cyclic Pollinator Abundance with Different Periods and Different Amplitude

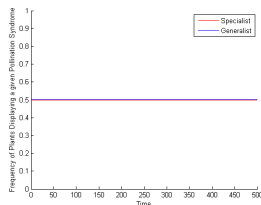
In this analysis, the periodic functions used to describe the abundance of each pollinator species had different periods and different amplitudes. For each of the simulations, generalization is favoured when the midpoint of the cycle describing the abundance of pollinator species 2 is greater than the midpoint of the cycle describing the abundance of pollinator species 1. In contrast, specialization is favoured when the midpoint of the cycle describing the abundance of pollinator species 1 is greater than the midpoint of the cycle describing the abundance of pollinator species 2. Table 4.3 displays the cyclic functions used to describe pollinator abundance as well as the relationship between M and N . Figure 4.3 shows the change in the frequency of each pollination syndrome in three cases from Table 4.3.

Abundance of Pollinator Species 1	Abundance of Pollinator Species 2	Average Value of p_α	Average Value of p_β	Outcome of the Model
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 10 \cdot \sin(t/5) + 10$	5	10	$M < N$, generalization is favoured
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 10 \cdot \sin(t) + 10$	5	10	$M < N$, generalization is favoured
$p_\alpha = 5 \cdot \sin(t) + 5$	$p_\beta = 5 \cdot \sin(t/5) + 5$	5	5	$M = N$, no change
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 10 \cdot \sin(t/5) + 10$	5	10	$M < N$, generalization is favoured
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 10 \cdot \sin(t) + 10$	5	10	$M < N$, generalization is favoured
$p_\alpha = 5 \cdot \sin(t/5) + 5$	$p_\beta = 5 \cdot \sin(t) + 5$	5	5	$M = N$, no change
$p_\alpha = 10 \cdot \sin(t) + 10$	$p_\beta = 5 \cdot \sin(t/5) + 5$	10	5	$M > N$, specialization is favoured
$p_\alpha = 10 \cdot \sin(t) + 10$	$p_\beta = 5 \cdot \sin(t) + 5$	10	5	$M > N$, specialization is favoured
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 5 \cdot \sin(t/5) + 5$	10	5	$M > N$, specialization is favoured
$p_\alpha = 10 \cdot \sin(t/5) + 10$	$p_\beta = 5 \cdot \sin(t) + 5$	10	5	$M > N$, specialization is favoured

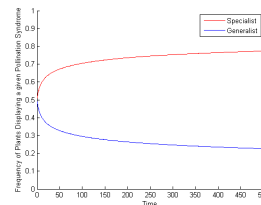
Table 4.3: The outcome of the two equation model when pollinator abundance is cyclic with different periods and different amplitudes. Average values for p_α and p_β are found across a period of 10π .



(a) The frequency differential equations when $p_\alpha = 5 \cdot \sin(t) + 5$ and $p_\beta = 10 \cdot \sin(t/5) + 10$.



(b) The frequency differential equations when $p_\alpha = 5 \cdot \sin(t) + 5$ and $p_\beta = 5 \cdot \sin(t/5) + 5$.



(c) The frequency differential equations when $p_\alpha = 10 \cdot \sin(t) + 10$ and $p_\beta = 5 \cdot \sin(t/5) + 5$.

Figure 4.3: The change in the frequency of each syndrome found using the frequency differential equations found from the two equation model with cyclic pollinator abundance.

4.3 DIFFERENTIAL EQUATION ANALYSIS OF THE THREE EQUATION MODEL

Similar to the differential equation analysis described in section 4.1, each differential equation of the three equation model was used to find a differential equation that describes the rate of change in the frequency of each pollination syndrome in this system. These differential equations describing the frequency were found using the quotient rule and chain rule. Below is the step-by-step solution for each equation with the pollination syndrome specializing towards species 1 solved first, the pollination syndrome specializing towards pollinator species 2 solved second, and the generalist pollination syndrome solved last. The differential equation describing the rate of change in the frequency of each pollination syndrome is numbered.

Set $M = (\alpha_x \cdot p_\alpha + \beta_x \cdot p_\beta)$, set $N = (\alpha_y \cdot p_\alpha + \beta_y \cdot p_\beta)$, and set $O = (\alpha_z \cdot p_\alpha + \beta_z \cdot p_\beta)$.

The equations of this model then become $\frac{dx}{dt} = \frac{x}{x+y+z} \cdot M$, $\frac{dy}{dt} = \frac{y}{x+y+z} \cdot N$,
and $\frac{dz}{dt} = \frac{z}{x+y+z} \cdot O$.

$$\begin{aligned}
\frac{d}{dt} \left(\frac{x}{x+y+z} \right) &= \frac{\frac{x}{x+y+z} \cdot M \cdot (x+y+z) - x \left(\frac{x}{x+y+z} \cdot M + \frac{y}{x+y+z} \cdot N + \frac{z}{x+y+z} \cdot O \right)}{(x+y+z)^2} \\
&= \frac{\frac{x^2 \cdot M + xy \cdot M + xz \cdot M}{x+y+z} - \left(\frac{x^2 \cdot M}{x+y+z} + \frac{xy \cdot N}{x+y+z} + \frac{xz \cdot O}{x+y+z} \right)}{(x+y+z)^2} \\
&= \frac{x^2 \cdot M + xy \cdot M + xz \cdot M - x^2 \cdot M - xy \cdot N - xz \cdot O}{(x+y+z)^3} \\
&= \frac{xy \cdot M + xz \cdot M - xy \cdot N - xz \cdot O}{(x+y+z)^3} \\
&= \frac{xy \cdot M - xy \cdot N + xz \cdot M - xz \cdot O}{(x+y+z)^3}
\end{aligned}$$

$$\frac{d}{dt} \left(\frac{x}{x+y+z} \right) = \frac{xy \cdot (M - N) + xz \cdot (M - O)}{(x+y+z)^3} \quad (4.3)$$

$$\begin{aligned}
\frac{d}{dt} \left(\frac{y}{x+y+z} \right) &= \frac{\frac{y}{x+y+z} \cdot N \cdot (x+y+z) - y \left(\frac{x}{x+y+z} \cdot M + \frac{y}{x+y+z} \cdot N + \frac{z}{x+y+z} \cdot O \right)}{(x+y+z)^2} \\
&= \frac{\frac{xy \cdot N + y^2 \cdot N + yz \cdot N}{x+y+z} - \left(\frac{xy \cdot M}{x+y+z} + \frac{y^2 \cdot N}{x+y+z} + \frac{yz \cdot O}{x+y+z} \right)}{(x+y+z)^2} \\
&= \frac{xy \cdot N + y^2 \cdot N + yz \cdot N - xy \cdot M - y^2 \cdot N - yz \cdot O}{(x+y+z)^3} \\
&= \frac{xy \cdot N + yz \cdot N - xy \cdot M - yz \cdot O}{(x+y+z)^3} \\
&= \frac{xy \cdot N - xy \cdot M + yz \cdot N - yz \cdot O}{(x+y+z)^3}
\end{aligned}$$

$$\frac{d}{dt} \left(\frac{y}{x+y+z} \right) = \frac{xy \cdot (N - M) + yz \cdot (N - O)}{(x+y+z)^3} \quad (4.4)$$

$$\begin{aligned}
\frac{d}{dt} \left(\frac{z}{x+y+z} \right) &= \frac{\frac{z}{x+y+z} \cdot O \cdot (x+y+z) - z \left(\frac{x}{x+y+z} \cdot M + \frac{y}{x+y+z} \cdot N + \frac{z}{x+y+z} \cdot O \right)}{(x+y+z)^2} \\
&= \frac{\frac{xz \cdot O + yz \cdot O + z^2 \cdot O}{x+y+z} - \left(\frac{xz \cdot M}{x+y+z} + \frac{yz \cdot N}{x+y+z} + \frac{z^2 \cdot O}{x+y+z} \right)}{(x+y+z)^2} \\
&= \frac{xz \cdot O + yz \cdot O + z^2 \cdot O - xz \cdot M - yz \cdot N - z^2 \cdot O}{(x+y+z)^3} \\
&= \frac{xz \cdot O + yz \cdot O - xz \cdot M - yz \cdot N}{(x+y+z)^3} \\
&= \frac{xz \cdot O - xz \cdot M + yz \cdot O - yz \cdot N}{(x+y+z)^3} \\
\frac{d}{dt} \left(\frac{z}{x+y+z} \right) &= \frac{xz \cdot (O - M) + yz \cdot (O - N)}{(x+y+z)^3} \tag{4.5}
\end{aligned}$$

With each of the differential equations describing the rate of change of the frequency of each pollination syndromes, the outcomes of the model, when the presence or absence of each of the pollination syndromes are varied, can be examined. In doing this, eights cases arise that describe how the outcome of the model will change given the presence or absence of a pollination syndrome. These eight cases are addressed below and each is analyzed to determine the conditions under which one would see an increase or decrease in the frequency of each pollination syndrome.

Case 1: The parameters $x = 0$, $y = 0$ and $z = 0$ are the initial conditions. This is a trivial case in which all three pollination syndromes have a population of zero and the resulting differential equations equal zero. This indicates that there is no change in the frequency of the pollination syndrome and that no syndrome emerges in the model. Although trivial, this case illustrates what is expected of the model.

Case 2, Case 3, Case 4: In each of these cases, the initial population of one pollination syndrome was greater than zero while the initial population of both of the remaining pollination syndromes was equal to zero. In each case, the differential equations are equal to zero, which indicates that there is no change in the frequency of the pollination syndromes. Consequently, whichever pollination syndrome has an initial population greater than zero will remain at 100 percent frequency throughout the model.

Case 5, Case 6, Case 7: In each of these cases, the initial population of two pollination syndromes was greater than zero while the one remaining pollination syndrome had an initial population of zero. In each case, the values of M , N , or O dictate whether there is an increase or decrease in the frequency of the pollination syndrome similar to how M and N determine which syndrome is favoured in Case 4 in section 4.2. The pollination syndromes which have an initial population above zero dictates whether M and N , N and O , or M and O are used. No matter which two pollination syndromes have an initial population above zero, the differential equation for the rate of change of the frequency of the syndromes follows the same pattern as described in Case 4 of section 4.1; simply substitute M , N , or O when necessary.

Case 8: The parameters $x > 0$, $y > 0$ and $z > 0$ are the initial conditions. In this final case, the value of the differential equations which describe the rate of change of the frequency of each pollination syndrome are dependent on the values of M , N , and O as well as the population of each of the plants displaying a given pollination syndromes, x , y , and z at that time. The cases describing the changes in the values of the differential equations are displayed below.

$$\frac{d}{dt} \left(\frac{x}{x+y+z} \right) = \begin{cases} > 0 & \text{if } M \cdot (y+z) > y \cdot N - z \cdot O \\ 0 & \text{if } M \cdot (y+z) = y \cdot N - z \cdot O \\ < 0 & \text{if } M \cdot (y+z) < y \cdot N - z \cdot O \end{cases}$$

$$\frac{d}{dt} \left(\frac{y}{x+y+z} \right) = \begin{cases} > 0 & \text{if } N \cdot (x+z) > x \cdot M - z \cdot O \\ 0 & \text{if } N \cdot (x+z) = x \cdot M - z \cdot O \\ < 0 & \text{if } N \cdot (x+z) < x \cdot M - z \cdot O \end{cases}$$

$$\frac{d}{dt} \left(\frac{z}{x+y+z} \right) = \begin{cases} > 0 & \text{if } O \cdot (x+y) > x \cdot M - y \cdot N \\ 0 & \text{if } O \cdot (x+y) = x \cdot M - y \cdot N \\ < 0 & \text{if } O \cdot (x+y) < x \cdot M - y \cdot N \end{cases}$$

The six conditions of Case 8, illustrated above, indicate that there is a great deal of interaction among the pollination syndromes and their pollinators. Unlike the other cases, the population of plants displaying a given pollination syndrome is important in determining whether or not there is growth or decline in the frequency of a given pollination syndrome.

The eight cases described above, indicate that these frequency differential equations are more dynamic than those of the two equation model. In Case 8, the change in the frequency of each syndrome is dependent on the abundance of each pollinator species as well as the population of each pollination syndrome at that time. Similarly, the frequency differential equations indicate that the influence of the population of each syndrome and the abundance of each pollinator species is not a summation of each factors affects. Consequently, the frequency differential equations are controlled by the interaction between the populations of each pollination syndrome and the abundance of each pollinator species.

CHAPTER 5

DISCUSSION

There are many characteristics of plant and pollinators that have been shown to correlate to the generalist or specialist pollination syndrome displayed by a plant. In multiple studies it has been shown there is a correlation between the abundance of a plants most efficient pollinator species or group and the syndrome the plant displays (Bond [1994], Waser et al. [1996]). In another study, it was similarly indicated that the longevity of a plant is correlated to the pollination syndrome displayed by the plant (Ollerton [1996]). With these correlations in mind, it was hypothesized that the Java model would be most sensitive to changes in the parameters that describe pollinator abundance and plant longevity. Hence the parameters of abundance of pollinator species 1, abundance of pollinator species 2, and the number of plant deaths per season, which describes plant longevity, were predicted to influence the Java model in a much larger way than any other parameters.

While pollinator efficiency is a key component of pollination (Larsson [2005], Padysakova et al. [2013]), the efficiency of a pollinator species is moderated by the abundance of the pollinator species (Ollerton [1996]). Consequently, although pollinator efficiency is important, because the efficiency of a pollinator species can be decreased or increased based on the abundance of that species, it was not hypothesized to have as strong of an influence as pollinator abundance. Similarly, the lifespan of the plant mediates the plants ability to receive pollinators. Again, the

efficiency of a pollinator species can be increased or decreased based on the lifespan of the plant, which may alter the ability of pollinators to visit the flower.

The results of the sensitivity analysis indicate that, in rejection of the proposed hypothesis, the Java model is most sensitive to changes in the abundance of pollinator species 2 and the initial pollen removal of pollinator species 1. The Java model is least sensitive to changes in plant longevity. The frequency of generalist plants, the measure used for the outcome of the model, increased the most when the initial pollen removal of pollinator species 1 was increased. The frequency of generalist plants decreased the most as a result of an increase in the abundance of pollinator species 2. In contrast, the frequency of generalists was only very slightly depressed by an increase in the number of plant deaths per seasons. These results suggest that, individually, the efficiency of a pollinator species (measured, in the model, as the ratio of the quantity of pollen removed to the quantity of nectar removed per visit) and the abundance of a pollinator species are the most important factors in determining which pollination syndrome is favoured.

Even though the results of the sensitivity analysis do not support the proposed hypothesis, they are indicative of hypotheses from other studies. It has been predicted that the evolution of a specialist pollination syndrome in flowering plants arises under conditions when pollinators exert selective pressures on the plant and when pollinators vary in their efficiency (Gomez and Zamora [2006]). A pollinator species exerts selective pressures on the plants through its efficiency as well as its abundance. Consequently, it can be hypothesized that pollinator abundance and pollinator efficiency are two of the most important factors in determining which pollination syndrome is evolutionarily favoured (Gomez and Zamora [2006]). Thus, when using this framework, it is not surprising that the results of the sensitivity analysis indicate that the Java model is most sensitive to changes in the parameters describing pollinator abundance and pollinator efficiency.

Although the Java model is sensitive to changes in pollinator abundance and pollinator efficiency, as has been hypothesized in previous studies, the direction of the change to frequency of generalist plants, as a result of changes in the parameters, is surprising. As mentioned previously, an increase in the abundance of pollinator species 2 decreased the frequency of generalist plants. However, the same increase in the abundance of pollinator species 1 increased the frequency of generalist plants.

This discrepancy in the changes to the frequency of generalist plants, as a result of changes in pollinator species abundance, could be attributed to the mechanism of initial pollinator placement during movement periods. During the initial placement, all of the individuals of pollinator species 1 are placed before the individuals of species 2 are placed. Thus, a plant is slightly more likely to receive an individual of pollinator species 1 than pollinator species 2. Although this probability is very small, this placement occurs 3000 times during a single simulation of the model described in Table 2.1. This repeated occurrence of the same mechanism could compound the slight increase in probability. Consequently, pollinator species 1 could be slightly favoured by the plants which could explain why an increase in the abundance of pollinator species 1 increased the frequency of generalist plants. Recall, that generalist plants should have an equal probability of receiving each pollinator species. However, this favouritism towards pollinator species 1 could increase a generalist plant's probability of receiving an individual from pollinator species 1. This in turn could make any changes in the characteristics of pollinator species 1 have a different and/or more drastic influence on generalist plants.

The argument that a slight favouritism, within a model, towards a species of pollinator alters this species influence on the model is further strengthened by the results of the system of differential equations models. In the two equation model, if the abundance of pollinator species 2 was increased, the frequency of generalist plants either decreased much slower or increased. If the abundance of pollinator

species 1 was increased then the frequency of generalist plants decreased very quickly. Thus, an increase in one species of pollinator had the opposite effect on the outcome of the two equation model as did an increase in the other species of pollinator even though both pollinator species are identical in efficiency.

In the three equation model, an increase in pollinator abundance almost always resulted in a decrease in the frequency of generalist plants. This model, unlike the two equation model, does not favour any one pollinator species over another. While one can alter the parameters characterizing the attractiveness of each pollination syndrome to each pollinator species, this does not change how the three equation model treats each pollinator. Consequently, when comparing the two differential equations models, the sensitivity of each model to changes in a given parameter is quite varied and may in part be the result of favoritism towards pollinator species 2 in the two equation model.

Similar to the different direction of the effects of pollinator abundance, the effects of an increase in initial pollen removal for each species of pollinator also results in different directions of change to the frequency of generalist plants in the Java model. Whereas an increase in initial pollen removal of pollinator species 1 resulted in an increase in the frequency of generalist plants, an increase in initial pollen removal of pollinator species 2 resulted in a decrease in the frequency of generalist plants. Again, this difference could be attributed to the slight favouritism towards pollinator species 1. Because generalist plants were slightly more likely to receive an individual of pollinator species 1, an increase in the initial pollen removal of pollinator species 1 will have a stronger effect than an increase in the initial pollen removal of pollinator species 2. This may allow more pollen to be removed by pollinator species 1 as a whole, which could increase the fitness of generalist plants more than would be increased by pollinator species 2.

Unfortunately, this argument of the different influences of pollinator efficiency

cannot be supported nor rejected by the results of the differential equations models. Neither differential equation model accounted for pollinator efficiency but instead focused on the effects of abundance. Consequently, to further examine the effects of an increase in pollinator abundance and initial pollen removal on the outcome of the Java model, I suggest that the number of pollinator species within the Java model be increased. By increasing the number of pollinator species, one would be able to examine whether the effects of favouritism was skewing the effects of an increase in abundance or initial pollen removal. If an increase in the abundance and/or initial pollen removal of any other pollinator species resulted in a decrease in the frequency of plants displaying a generalist pollination syndrome it would be a strong indicator that favoritism towards pollinator species 1 was skewing this species effects on the model. If the opposite occurred, and an increase in abundance or initial pollen removal of any other pollinator species resulted in an increase in the frequency of of generalist plants, it would demonstrate that favoritism may not be the cause of the discrepancy in the sensitivity of the Java model and more work would be needed to explore possible explanations.

Whereas the Java model was most sensitive to changes in the abundance and efficiency of a pollinator species, it was least sensitive to changes in the number of plant deaths per season. This is not to say that the outcome of the model was not completely resistant to changes in plant longevity. Instead, an increase in the number of plant deaths per season caused a very slight change in the frequency of generalist plants within the model. The frequency of generalist plants was only changed by approximately 0.24 percent when the number of plant deaths per season was increased by one.

It was originally hypothesized that an increase in longevity would favour specialization simply because the longer a plant lives the more flowering seasons they experience, which provides more chances that the pollinator species being

specialized towards will be present during a season (Bond [1994], Waser et al. [1996]). However, the results of the sensitivity analysis and the data from variations in plant longevity (Figure 3.4) indicate that an increase in plant longevity decreased the frequency of generalist plants. Longevity in the Java model is determined by the number of plants that die at the end of each season. Consequently, a simulation in which plants have a short lifespan is characterized by a high number of plant deaths per season and vice versa. This characteristic of plant longevity causes more opportunities for reproduction in models with short lived plants. Specialist plants have, on average, a higher fitness when pollinator abundance is constant across seasons, as it was during these simulations. Consequently, this increased fitness allows specialist plants to have a higher reproductive success rate than the generalist plants. Since, there are more opportunities for plants to recruit new plants during seasons in simulations in which plant longevity is low, the specialist plants may take greater advantage of these opportunities than generalist plants. This could allow specialization to be favoured when plant longevity is low. In contrast, when plant longevity is high, there are very few opportunities to recruit new plants during each season and the slight increase in fitness of specialist plants might not be as compounded.

The results of the simulations in which both pollinator abundance (random or constant) and plant longevity (short and long) indicates that the combination of variations in the parameters alters the individual effects of each parameter. The simulations with short lived plants and random pollinator abundance showed a marked increase in the frequency of generalist plants compared to the frequency of generalist plants in simulations with short lived plants and constant pollinator abundance. A possible explanation for this difference is that in the simulations with random pollinator abundance, the benefits of specializing are outweighed by the costs of not always having pollinators present. During any given season,

the abundance of a pollinator species may be low or high with equal probability. Consequently, specialist plants, which invest a majority of their fitness gain in one species of pollinator, may not gain as much fitness from the species it is specializing towards if its abundance is low (Ollerton [1996]). This represents a problem for plants that only live across a few seasons as there is less of a chance that any plant will live during a season in which the species being specialized towards is highly abundant. If the abundance of the species of pollinator being specialized towards is high during a season, then the specialist plants reap the benefits of specialization, but this benefit is negated by the fact that a majority of plants will die and not be able to recruit new plants. Consequently, specialization may not be as favourable under these conditions as generalization, because generalist plants do not invest their fitness gain in one species of pollinator.

This problem of greatly needing pollination in short lived plants is not as much of a problem for long lived plants because they survive across many seasons. This is supported by the fact that, there was no significant difference in the frequency of generalist plants between simulations with long lived plants and random pollinator abundance and simulations with long lived plants and constant pollinator abundance. A plant which lives across many seasons has a higher probability of living during a season in which the abundance of a pollinator species is high (Ollerton [1996]). Consequently, the frequency of specialist plants can withstand seasons in which little to no fitness is gained because they will, in all probability, survive across a season in which pollinator abundance is high which can drastically increase their fitness. Even during seasons in which the fitness of specialist plants is low, which gives them a lower probability of recruiting a new plant, there are few opportunities to reproduce and hence the frequency will not be decreased by much.

The results of the simulations in which both pollinator abundance and plant longevity was varied illustrates how the interaction among factors can result in

outcomes that may not arise from a simple combination of the individual effects of each parameter. From the results of simulations with varied pollinator abundance, there was no significant difference in the frequency of generalists between the two simulations. In contrast, there was a significant increase in the frequency of generalists in simulations with long lived plants compared to simulations with short lived plants. Consequently, if variations in pollinator abundance were combined with short lived plants, it is reasonable to predict that the results would show that there was no difference between the two simulations. However, the actual results indicate that there was a significant increase in the frequency of generalist plants in models with random pollinator abundance and short lived plants.

For further illustration of the unexpected results from the interaction among parameters describing pollinator abundance and plant longevity one need only look at the results of the simulations in which pollinator abundance was varied with long lived plants. There was no significant difference in the frequencies of generalist plants between the two simulations. Although this result supports the proposed hypothesis, it nevertheless illustrates that a combination of multiple varied parameters can result in outcomes that do not arise from the simple combination of the individual effects of each parameter.

The frequency differential equations obtained from the equations of the three equation model also indicate that pollinator abundance may not interact with other factors in an additive manner. From the frequency differential equations, the abundance of each pollinator species interacts with the population of plants displaying a given pollination syndrome in both a multiplicative and additive manner. This indicates that the effects of each pollinator abundance varies drastically depending on the values of pollinator abundance and population of plants displaying a given pollination syndrome. Consequently, the predictions of the favoured syndrome, when assuming a simple addition of the influences of each individual

factors, will not be accurate. However, this equation provides a much stronger predictive power and illustrates that the interaction among pollinator abundance and the population of plants displaying a given pollination syndrome can result in outcomes that were not originally hypothesized to occur.

Variations in the parameters describing pollinator efficiency and abundance, when combined, similarly produce results that deviate from the expected results of a combination of both parameters. It was hypothesized that, in the simulations with efficiency and/or abundance skewed in favour of pollinator species 1, there would be an increase in the frequency of plants specializing towards pollinator species 1. This follows from the most efficient pollinator principal which hypothesizes that plants will specialize towards their most efficient pollinator (Stebbins [1970]). However, in the simulation in which the efficiency of pollinator species 1 was increased, there was no significant difference in the frequency of plants specializing towards pollinator species 1. Similarly, there was no significant difference in the model in which the abundance and the efficiency of pollinator species 1 was drastically increased. Thus, both the proposed hypothesis and the most efficient pollinator principal are not supported by the results.

The most efficient pollinator principal has come under increasing criticism because it belies the other factors that characterize a plant-pollinator interaction (Aigner [2001], Padysakova et al. [2013], Johnson and Steiner [2000]). Consequently, it is not surprising that the results of the simulations in which the efficiency and abundance of pollinator species 1 was skewed did not support the proposed hypothesis. Although the hypothesis of the most efficient pollinator principal is not supported, the results support the hypothesis that the interaction among the factors of a plant-pollinator interaction are the essential elements underlying the favourability of one pollination syndrome over another. Similarly, the results also support the hypothesis that the interaction among different parameters will result

in changes to the outcome of the model that do not arise from the summation of the effects of each individual parameter.

The results of each of the simulations discussed so far have been cases of extremes in the parameters. To strengthen the hypotheses that the interactions among parameters are the essential elements of a plant-pollinator interaction and that results of most of the interactions between parameters do not arise from the summation of each factor's individual affects, it is important to consider models in which the parameters are not at an extreme, but are at a value somewhere in between. Similarly, it is important to examine the results of models in which the interaction among parameters is constantly changing throughout the model. The simulations in which pollinator abundance was cyclic represent models that exhibit both of these qualities. During the simulations, the abundance of each pollinator was constantly changing throughout the model and was neither extremely low nor extremely high. In addition, the interactions between pollinator abundance, plant longevity, and pollinator efficiency constantly changed through each season of the model.

It was hypothesized that only when the average lifespan of the plant was longer than half of a full cycle would specialization be favoured. Consequently, it was predicted that there would be a significant difference between the frequency of generalist plants in Cycles 2, 4, and 5 as compared to Cycles 1 and 3. Contrary to this prediction, there was no significant difference in the frequency of generalist plants among any of the cyclic pollinator abundance simulations. If there had been a significant difference, it would support the concept that the parameters of pollinator abundance, plant longevity, and pollinator efficiency interact in a cumulative manner despite continuous changes in one parameter. However, this was not the case and so it is hypothesized that the interaction among these parameters is not cumulative and varies depending on the value of, at least, the abundance of a pollinator species.

The result of the simulations of cyclic pollinator abundance indicates that the value of the parameters affect the interaction between the parameters. It can be hypothesized that changes in values over time may result in different scales of the interaction or altogether different interactions between the parameters. Consequently, it is not only important to recognize the values during one moment in time, it is also important to recognize how these parameters vary so that the changes in the interactions can be understood and predicted.

From the cumulative results of this study, it can be hypothesized that the interactions between the factors that exert evolutionary pressures on a flowering plant are, in most circumstances, the most important elements in understanding the evolution of a specialist or generalist pollination syndrome in flowering plants. As demonstrated by multiple findings of this study, the interactions among parameters influence the outcome of the model in ways that may not be predicted from the summation of the individual effects of each parameter. In most simulations, understanding how, individually, each factor influences a plant-pollinator interaction did not provide an accurate prediction of the favoured pollination syndrome during simulation in which two parameters were varied. However, when applying the hypothesis that the interactions are most important, the results were more easily predicted and an examination into the results yielded more understanding of why the results occurred.

It is not surprising, that many of the initial hypotheses were not supported in the simulations of the Java model, as most were based on the theory that the effects of multiple parameters could be understood by summing their individual effects. It was predicted that if, for example, an individual increase in pollinator abundance and an individual increase in plant deaths yielded a higher frequency of generalist plants then together, their effects should be compounded and the results should indicate that there is a much higher frequency of generalist plants.

However, the addition of the effects of each individual parameter did not yield accurate predictions when variations of the parameters were combined.

Numerous studies (Ollerton [1996], Aigner [2001], Waser et al. [1996], and Padysakova et al. [2013]) have similarly proposed that the effects of multiple factors cannot be found by simply summing their individual effects. In particular it has been shown that the interaction among pollinator species can increase or decrease the efficiency of a pollinator depending on how it interacts with other pollinators (Aigner [2001]). Thus, the overall efficiency of a pollinator species can be altered by the abundance of other pollinator species but not in an additive way. Similarly, the spread of plants and the specialization of a pollinator can interact in ways that results in an alteration to the evolutionarily favoured syndrome as predicted by summing each factor's effects (Feinsinger [1983]). While individually each factor may exert selective pressures on the plant favouring one syndrome over another, the effects of the interaction between multiple factors can change which syndrome would be favoured under a simple addition of the effects of each individual factor.

The Java model and the system of differential equation models attempted to accurately capture these interactions in order to understand how the interactions alter which syndrome is evolutionarily favoured. Both models accomplish this by first accurately accounting for the effects and behaviours of factors governing pollinator abundance, pollinator efficiency, and plant longevity. The models then allow these parameters to interact in a perceived natural condition. Although the models include multiple factors involved in pollination, there are certain aspects of pollination, pollinator behaviour, and plant behaviour that were simplified or omitted to reduce the complexity. In future studies it would be crucial to expand the complexity of both models so that more factors of a plant-pollinator system could be included. Although including additional factors would drastically increase the complexity, it would allow the model to account for more interactions among

additional factors as well as increase the accuracy of the simulated effects of the interactions already contained within the model.

One interaction that was simplified within the Java model, which could be included in future models, is the interaction between different pollinator species. It has been theoretically shown that the interaction among pollinators can sometimes result in a decrease or increase in pollinator efficiency (Aigner [2001]). However, the Java model assumes that if a pollinator is already present at a flower, then the flower is not receptive to another pollinator. Consequently, no new pollinators can visit that flower until the present pollinator departs. This mechanism of pollinator movement removes most of the interactions between pollinators. The approach attempted to simulate interaction among pollinators, but it does not fully capture the interaction among pollinators as proposed by Aigner [2001]. Consequently, in any future models it would be beneficial to include a more accurate description of the interaction among pollinators which would increase the accuracy of the model.

The transfer of pollen grains between flowers is another aspect of a plant-pollinator system that was simplified in the Java model. Within the model, the total amount of pollen taken from a flower by a pollinator was transferred to the next visited flower and contributed to the fitness increase in both plants. However, in many situations not all of the pollen is transferred nor does all of the pollen reach the pistils of the receiving flower (Padysakova et al. [2013]). Similarly, because there was only one species of flowering plants in the model, there was no risk of having pollen transferred to another species of flower or of a flower receiving pollen from another species of flower. To increase the realism of the model, one could alter the description of the transfer of pollen between flowers in such a way that the amount of pollen transferred was probabilistic but still dependent on the amount gathered. Also, including multiple species of flowering plants would allow a greater dynamic between the plants and their pollinators.

Whereas the Java model represents a complex simulation of a pollination system, the differential equation models represent a very simplified simulation. While the simplifications of the differential equation models allows for frequency differential equations to be found, the models omit numerous aspects of a pollination system that may compromise the accuracy of the models. Consequently, in future studies it would be crucial to slightly increase the complexity of the differential equation models but still ensure that a frequency differential equations could be found. One way to increase the accuracy of the models would be to include a population limit on the total number of plants allowed in the models. As it stands, the models allow for unlimited growth in the populations of plant displaying a generalist or specialist pollination syndrome. While accurate for a succession of plants into a new environment, it does not accurately reflect most pollination systems.

To strengthen the accuracy of the system of differential equation models, it is important for future models to include a death rate. Including a death rate for the plants would allow the models to fluctuate about the set population limit. The death rate would also produce more interactions among plant pollination syndromes and their pollinators. Similarly, the system of differential equations models could be used as a comparison for the more complex Java model.

Increasing the complexity of both models would allow a better examination of the effects of interactions among different parameters. In addition to this increased complexity, it would be informative to analyze the results from simulations in which more than two parameters are changed at a time. Similarly, adding stochasticity or controlled variations (as in the simulations with cyclic pollinator abundance) to parameters during the simulations would allow for a deeper examination of interaction among parameters. With additional complexity in the system of differential equations, comparing the results of these models to the outcomes of the Java model would provide a method for assessing the accuracy of both models. It

would be useful to compare the results of both models to know if the less complex system of differential equation model could predict the same outcomes as the complex Java model. If both predicted the same outcome, then it may indicate that an element of a plant-pollinator interaction can be potentially simplified in the Java model.

Although all of the models omitted certain aspects of a pollination system, they nevertheless captured numerous facets of plant-pollinator interactions. From the results of many of the simulations, it is proposed that the effects of the interactions among the factors that influence the evolutionary pressures on a flowering plant are extremely important for understanding the evolution of pollination syndromes. Similarly, the effects of multiple parameters cannot, in most cases, be understood by summing the individual effects of each parameter. While the models suggests it is important to examine the interaction among plant longevity, pollinator efficiency, and pollinator abundance, it also suggests that understanding the interaction among additional factors of a plant-pollinator system is paramount to understanding which syndrome is evolutionarily favoured. A greater understanding of the interactions among the factors in a plant-pollinator system could increase the accuracy of our predictions of the evolution of a generalist or specialist pollination syndromes in flowering plants.

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