Holly Bok April 14, 2014

The effect of interspecific and intraspecific competition on floral fidelity in pollinator bee species

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
of the requirements of the degree of
Bachelor of Sciences with Honors

Environmental Science

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Acknowledgements

Thank you to my advisor, Berry Brosi. Thank you to my committee members Christopher Beck and Thomas Gillespie. Thank you to everyone in the lab, especially to Emily Dobbs, Carolyn Ayers, and Travis Dynes. Lastly, thank you to Emory University and the entirety of the Environmental Science department.

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Abstract

Global declines in pollinator species bring particular attention to the role of competition networks in plant-pollinator communities. As pollinator species decline, interspecific competition between remaining bee species may decrease, which may cause shifts in the floral fidelity of pollinator species. Decreases in floral fidelity, in turn, may have serious consequences for biodiversity-ecosystem functioning relationships because specialized plant-pollinator relationships are important for plant reproduction. Here I examine the relationship between interspecific and intraspecific competition and short-term floral fidelity in pollinator bee species. I explore the effect of interspecific competition on short-term floral fidelity, complementarity, and energy uptake in four pollinator species: *Apis mellifera, Bombus impatiens, Osmia lignaria, and Megachile rotundata*. I predicted that an increase in interspecific competition would result in an increase in floral fidelity, and that increases in intraspecific competition would have the opposite pattern. *Megachile rotundata* and *A. mellifera* individuals did not forage normally in the laboratory enclosure, so I do not report results for those species. I found that interspecific competition has a positive relationship with floral fidelity for *B. impatiens*, but, in contrast, that interspecific competition has a negative relationship with floral fidelity for *O. lignaria*. I found that intraspecific competition had the opposite effect, with a positive relationship with *B.*

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Introduction

Interspecific competition has been shown to cause environmental and resource niche partitioning and to shape specialization in plant and animal species, but this has been thought of in terms of an evolutionary time scale rather than an ecological time scale. Competition (specifically interspecific competition) as a framer of specialization is a widely accepted mechanism for biodiversity ecosystem functioning (BDEF). This is generally thought of in terms of an *evolutionary* time scale. Specialization, particularly niche partitioning, is thought to develop over long periods of time as species evolve to fill differing spatial and temporal resource spheres. However, interspecific competition may shape specialization over an *ecological* time scale. Species have been shown to exhibit phenotypic plasticity, or the ability to change phenotypically in response to changes in the environment (Miner et al. 2005). Changes in interspecific competition may result in short-term, behavioral phenotypic plasticity and cause changes in specialization over short, ecological time scales. In order to explore the effects of interspecific competition on short-term specialization we examined interactions between four pollinator bee species *Apis* *mellifera* (honeybees)*, Bombus impatiens* (bumblebees)*, Osmia lignaria* (blue orchard bees)*, and Megachile rotundata* (alfalfa leafcutter bee).

Pollinator bee species are suitable model organisms for the study of competition driven interactions for several reasons. First, pollinator bee species are generalists, meaning they forage on many different flower types (Waser et al. 1995). Second, bee species have plastic foraging preferences and are able to transition those preferences (Waser et al. 1995). These two things allow for bee species to have the potential for measurable changes in foraging behavior. Lastly, bee species are suitable model organisms for this study because they have been shown to be responsive to competition over short time scales (Fontaine et al. 2008, Fründ et al. 2013, Brosi & Briggs 2013, Inouye 1978, Morse 1977).

Pollinator species in both feral and managed communities have been shown to be declining over a very broad geographic range, which has serious potential consequences for ecosystem functioning. Pollinators are in widespread decline due to anthropogenic sources such as habitat fragmentation, climate change, changes in land use, and agricultural management (Potts et al. 2010, Wardell et al. 1998, Kearns et al. 1998). The loss of pollinator species has potentially catastrophic consequences for plant species populations, both in managed agricultural and natural populations, because plant species require pollination to successfully reproduce (Potts et al. 2010, Wardell et al. 1998, Kearns et al. 1998). The potential effect of pollinator decline on plant reproduction has brought considerable attention to pollinator species interactions because shifts in pollinator interactions may result in serious changes in plant-pollinator relationships. Declines in pollinator species change the interactions between species by reducing interspecific competition. If reductions in interspecific competition result in short-term changes in resource specialization, then pollinator declines will change plant-pollinator relationships, which could potentially seriously affect ecosystems and BDEF relationships.

The reduction of interspecific competition has short-term behavioral effects on pollinator species and has serious consequences for ecosystem functioning and the species themselves. Changes in interspecific competition affect resource specialization and diet breadth of bee species over an ecological time scale. More specifically, short-term specialization, or floral fidelity, is behaviorally driven and can be altered in individual bees as a result of the presence or absence of interspecific competition. A decrease in floral fidelity results in a decrease in conspecific pollen transfer, or the deposition of pollen to the correct species of flower (Brosi & Briggs 2013). A decrease in conspecific pollen transfer reduces the amount of successful flower reproduction in an ecosystem, and lowers the ecosystem functioning of that system (Flanagan et al. 2009, Morales & Traveset 2008, Arceo-Gomez & Ashman 2011). In addition, decreases in floral fidelity have consequences for the pollinator species themselves. Pollinators have been shown to benefit from specialized foraging by having greater foraging efficiency and higher energy returns. Short-term specialization, then, has direct impacts on ecosystem functioning and the success of pollinator species.

There are existing studies showing the effect of interspecific competition on specialization in pollinators; these studies have been focused on two main areas: 1) the effect of changes in pollinator diversity on biodiversity ecosystem functioning relationships and 2) the effects of both interspecific and intraspecific competition on specialization. The first body of research has shown that greater pollinator diversity results in an increase of

BDEF (Greenleaf & Kremen 2006, Cardinale et al. 2003, Brittain et al. 2013), but these studies have not necessarily addressed the role of floral fidelity and the conclusions have been varied in the mechanisms that are attributed to the process. The second body of research has explored how interspecific and intraspecific competition affect specialization in pollinators (Morse 1977, Inouye 1978, Pimm et al. 1985). There is little research showing the link between these two areas of focus, or the idea that competition directly affects ecosystem functioning through changes in specialization. However, this link has been explored in field studies that have shown that interspecific competition directly affects the functioning of ecosystems through changes in the specialization of plant-pollinator relationships (Brosi & Briggs 2013, Fründ et al. 2013).

As a result of my study design being extremely controlled, my research has many benefits that previous studies have not had. My experiments were conducted in a laboratory setting using a foraging enclosure, as opposed to a field study. Because the foraging enclosure was highly controlled, I was able to isolate the effect of interspecific competition and did not have the interference of other factors such as fluctuating weather, temperature, or third party species. In addition, I was able to gather information on exact flower sequences traveled by individual bees. This type of information provides data for a variety of tests that field data cannot feasibly provide. Using this data I was able to quantify both the total energy consumed in the system and complementarity in terms of flower evenness.

Complementarity is an effect in which the interactions between species result in complementary niche shifts in resource use that benefit ecosystem functioning. The type of data that I collected includes very specific information about flower sequences traveled by individual bees. This data can be used to determine if complementarity is occurring by showing the range of flower visitation in the system. If we see complementarity occurring we would expect that in the presence of competition there would be more evenness in flower type visits and a higher proportion of visits to lower reward flowers. While my main questions do not directly address how interspecific competition affects ecosystem functioning, complementarity provides a measure of how interactions between species directly affects the functioning of the system through changes in plant-pollinator relationships.

Through my experiments I addressed the following questions: Is the short-term specialization, or floral fidelity, of individual pollinators impacted by changes in the presence of interspecific competition? Does an increase in interspecific competition in the form of pollinator species result in greater specialization in individuals, and, in contrast, does a decrease in interspecific competition result in greater generalization in foraging habits? I hypothesized that interspecific interactions between pollinator species shape short-term specialization, specifically floral fidelity. My prediction was that the loss of interspecific competition leads to decreased plant specialization and increased generalization in foraging habits of pollinator species.

Methods

Bees Utilized in Experiments

For my experiments I used four bee species (*A. mellifera, B. impatiens, O. lignaria,* and *M. rotundata*). I gathered the *A. mellifera* foragers twice weekly from a managed colony on the property of Emory University by catching active individuals near the colony with a bee net. I gathered *B. impatiens* colonies from a pollinator supply company (*Beneficial Insectary* Redding, CA), and ordered the *O. lignaria* and *M. rotundata* through agricultural sources (*O. lignaria* from *Ruhl Bee Supply* Gladstone, OR; *M. rotundata* from *USDA Collaborators* Logan, UT). The *O. lignaria* and *M. rotundata* arrived in cocoons and had to be hatched out. I incubated the *M. rotundata* at 29.1°C for 14-21 days or until they hatched. I placed the *O. lignaria* directly into a holding enclosure (ambient temperature ~21°C) in which male individuals hatched in 1-3 days and females hatched in 4-7 days. I kept all bees in species-specific enclosures that contained water, small amounts of ground pollen in order to provide protein for young individuals, and “training flowers.”

The training flowers served two functions: first, they provided sources of nectar for the bees, and, second, they were exact replicas of the artificial flowers used in the experimental foraging enclosure. Exposure to training flowers allowed for learning of artificial flower handling and the development of preferences between different artificial flower types. I placed a heating pad underneath the *A. mellifera* holding enclosure to maintain a hotter temperature to mimic the inside of their natural hive.

Foraging Enclosure

The experiments were conducted in a foraging enclosure that was modeled after a natural system. The foraging enclosure (length: 2.286m, width: 0.762m, height: 0.6604m) was encased in hard plastic with white, opaque walls, a transparent top and windows, and a flat, green base. The enclosure was fitted with two constantly rotating fans to provide ventilation. Four heating lamps were run along the top of the enclosure and an electric blanket set at the highest setting was run underneath the base. The combination of the heating lamps and electric blanket kept the enclosure between 25-29°C. The entirety of the top of the enclosure was covered by a dark blue tarp to filter out flickering of fluorescent lighting, which has been shown to irritate *A. mellifera*.

The enclosure contained a series of 32 artificial flowers. Artificial flowers were in 4 straight rows of random type. The system contained 4 types, or "species," of flower (Table 1). In order for bees to be able to easily differentiate between them, each type varied in color, scent, and concentration of sucrose or "sugar reward."

Each flower was connected to a sucrose pool through a valve and tubing system. 50mL luer slip syringes were attached to the exterior of the enclosure and filled with 10ml of sucrose solution each. Each syringe was attached to a solenoid valve that opened to release the solution. The valve released sucrose solution to a silicone tube that ran to an artificial flower and would dispense a droplet (10uL) of "nectar" to the inside of the artificial flower through a pipette tip.

The operation of the valve and the release of sucrose solution was done through an Arduino system. I outfitted each individual bee with a small, Radio Frequency Identification

("RFID") tag (Microsensys GmbH, Erfurt, Germany) which corresponded to a unique ID. RFID readers inside of each artificial flower were prompted by the presence of a bee's RFID tag and triggered the Arduino system to open the solenoid valve and release a droplet of sucrose solution to the flower. Once a droplet was released by the Arduino system it could not be triggered by the same bee ID to release another droplet for a period of 30 seconds. This was to prevent an individual bee from visiting only one flower and from consuming sucrose solution at too fast of a rate.

The RFID tags on each bee were also used to record foraging patterns. The information for each flower visit picked up by the RFID readers was stored in an external computer through the Arduino system. For each bee visit, information was recorded for the unique bee ID, the ID of the flower that had been visited, and the time of the visit.

Experimental Trials

I manually selected individuals from each colony from their holding enclosures. Only females of each species were utilized because male bees do not forage. Once selected, I placed the bees in a refrigerator (set at 50°F, with fluctuation between 45°-55°F) to temporarily immobilize them and to stimulate hunger. The *A. mellifera* and *M. rotundata* were left in the refrigerator for approximately 30 minutes, while the *B. impatiens* and *O. lignaria* were left for approximately 60 minutes. This is because *B. impatiens* and *O. lignaria* were not immobilized within 30 minutes, but time periods above 30 minutes resulted in high rates of *A. mellifera* and *M. rotundata* irritation and death.

Once the bees were immobilized I attached an RFID tag to the thorax of each bee using Elmer's glue and returned them to the refrigerator for 10 minutes to allow the glue to dry completely. I recorded the colony of each bee along with the unique RFID tag ID. I then transferred the bees to a dark cabinet and left them undisturbed for a 60 minutes period to allow for sufficient nutrient deprivation to stimulate hunger and encourage foraging. At the onset of an experiment I began the Arduino system and transferred the tagged bees to the enclosure. Information from each foraging trial was recorded for one hour.

16 individuals were utilized in all high-density experiments. For 2-species trials, 8 individuals were utilized from each species. For 3 species trials, five individuals of two species and six of the remaining species (rotating between the three species and changing each trial) were utilized. 8 individuals were utilized in single-species low-density trials. 31 single-species, high density *B. impatiens* trials were conducted by a doctoral student in the same laboratory for another body of research. These trials followed the exact same experimental methods.

Statistical Analysis

We analyzed the effects of interspecific and intraspecific competition on floral fidelity, complementarity, and energy uptake.

Floral Fidelity

Floral fidelity is the proportion of total flower transfers that are conspecific as opposed to heterospecific. Conspecific flower transfer is defined as movement from a flower to a flower of the same artificial flower type. Floral fidelity was analyzed for each individual species using a series of binomial errors generalized linear models (GLMs).

Complementarity

Complementarity was analyzed in terms of flower evenness. Flower evenness is defined as the relative proportion of flower visits to each flower reward type. Flower reward types were defined as "high-reward" flowers, which included only the highest-reward blue flowers, and "low-reward" flowers, which included the three remaining artificial flower types. Flower evenness was compared for all trial types using a series of chi-squared tests.

Energy Uptake

Energy uptake was measured in kilojoules per gram. The molarity of each flower type was used to calculate the g/L of sugar for each type. From there, the kilojoules of energy in each droplet of sucrose dispensed was calculated assuming a10uL volume of each droplet and a conversion rate of 17 kilojoules of energy per gram. The kilojoules of energy for each flower type was found to be 0.11628 for blue flowers, 0.08721 for white flowers, 0.05814 for yellow flowers, and 0.02907 for red flowers. Energy uptake for each species was averaged by trial. Total energy uptake and average energy uptake for each species was compared between treatments using two-sample t-tests.

Results

Overview

During these experiments I collected data from 102 trials including 36 single-species high density *B. impatiens* trials, 5 single-species low density *B. impatiens* trials, 6 single-species high density *O. lignaria* trials, 5 single-species low density *O. lignaria* trials, 5 2-species trials with *B. impatiens* and *O. lignaria*, 14 single-species *M. rotundata* trials, 11 single-species *A. mellifera* trials, and 20 3-species trials with *B. impatiens, M. rotundata,* and *A. mellifera*. Trials were conducted between August 2013 and March 2014. There were a total of 15,980 unique flower visits aggregated between all trials, with 890 total individual bees that made at least 2 flower transfers during foraging. The average number of flower visits for individuals who made at least 2 flower transfer while foraging was 16.13 for *B. impatiens* individuals*,* 10.12 for *O. lignaria* individuals, 4.97 for *A. mellifera* individuals*,* and 5.28 for *M. rotundata* individuals. Out of 890 total individuals who made at least 2 flower transfers while foraging, 636 were *B. impatiens* individuals, 121 were *O. lignaria* individuals, 32 were *A. mellifera* individuals, and 101 were *M. rotundata* individuals.

Floral Fidelity

Interspecific competition was found to have a significant effect on floral fidelity in *B. impatiens* and *O. lignaria* individuals. A positive effect on floral fidelity was found for species density (p=1.39e-05) (Figure 1). Intraspecific competition was also found to have a significant effect on floral fidelity in *B. impatiens* and *O. lignaria* individuals, with a positive relationship between floral fidelity and density (p=0.006890) (Figure 2). The species of the individual was also found to have an effect on floral fidelity (p=2e-16).

Floral fidelity was higher in *B. impatiens* individuals for trials with increased interspecific competition (2-species trials as compared to single-species trials). Floral fidelity was higher in *B. impatiens* individuals for trials with increased density as compared to trials with low density. In contrast, floral fidelity in *O. lignaria* individuals was found to decrease with increased interspecific competition. Floral fidelity was found to decrease with an increase in intraspecific competition.

The effect of intraspecific competition was not enough to explain the effect of intraspecific competition for *B. impatiens* and *O. lignaria* individuals. The confidence intervals for the effect of interspecific competition (0.220 – 0.582) do not overlap the confidence intervals for the effect of intraspecific competition (0.009 - 0.054) suggesting that that the observed changes in floral fidelity in the increased interspecific competition trials were not due to decreases in the abundance of the utilized species. Interspecific competition was also found to have a much larger effect on floral fidelity than intraspecific competition, based on the coefficients (0.40135 for interspecific competition and 0.03127 for intraspecific competition).

Both interspecific and intraspecific competition were not found to have a significant effect on floral fidelity in either *A. mellifera* or *M. rotundata* individuals. However, this was likely due to a lack of foraging behavior in both species. The effect of interspecific and intraspecific competition in *B. impatiens* individuals was not analyzed for 3-species trials due to the lack of foraging of the other utilized species.

Complementarity

No significant effect of interspecific competiton on complementarity was found. Neither flower evenness nor the proportion of visits to lower reward flowers showed a significant change in response to interspecific competition. Intraspecific competition was also not shown to have an effect on flower evenness. Flower evenness was not different for the system or for any individual species in high density and low density trials. These results are likely due to my analysis rather than a lack of an underlying pattern, as these results are not consistent with my conclusions about the effect of competition on floral fidelity.

Energy Uptake

No significant effect of intraspecific competition was found on total energy uptake in the system. The total energy uptake in the system was not significantly different in single species trials than in two-species trials. Additionally, the effect of interspecific competition on the average energy uptake by species was not found to be significant for the system nor for any individual species. Intraspecific competition was also not shown to have a significant effect on total energy uptake. Both total energy uptake and average energy uptake per species were not found to be different in high density and low density trials.

Discussion

Overview

In this study, I explored the relationship between interspecific competition and short-term specialization. I hypothesized that interspecific interactions between pollinator species would shape floral fidelity in *B. impatiens*, *A. mellifera*, *M. rotundata*, and *O. lignaria* bee species. Specifically, I predicted that increased interspecific competition between pollinator species would result in an increase in floral fidelity and a narrowing of diet breadth. Fluctuation of the diet breadth of pollinators has potentially serious consequences for plant biodiversity and ecosystem functioning. Specialization of plant-pollinator relationships is beneficial for plant biodiversity because it increases conspecific pollen transfer and successful plant reproduction. Decreased interspecific competition resulting from global bee decline may result in wider diet breadths, impacting plant reproduction and decreasing plant biodiversity.

I analyzed the effects of interspecific competition on floral fidelity, complementarity, and energy uptake within the plant-pollinator system. I also explored the effects of intraspecific competition on my response variables. My results were consistent with the hypothesis that pollinators experience phenotypic plasticity in the presence of interspecific competition. I show an effect of interspecific competition on floral fidelity. I show a positive relationship between interspecific competition and floral fidelity in *B. impatiens* individuals and, in contrast, a negative relationship in *O. lignaria* individuals. I also show an effect of intraspecific competition on floral fidelity, with a positive relationship between intraspecific competition and floral fidelity for *B. impatiens* individuals and a negatives relationship for *O. lignaria* individuals. The effects of intraspecific competition were not enough to explain the effects found in the interspecific competition trials, suggesting that the observed changes in floral fidelity were not due to decreases in the abundance of both species. I did not find significant results for the effect of interspecific or intraspecific competition on complementarity. I also did not find significant results for the effect of interspecific or intraspecific competition on energy uptake within the system. Additionally, significant results were not found for the effects of competition on floral fidelity in *A. mellifera* or *M. rotundata* individuals.

Species-specific Difficulties

The use of several species was limited by factors that impacted both my data collection and results. The effect of interspecific competition on floral fidelity in both *A. mellifera* and *M. rotundata* individuals was found to be insignificant. This is likely due to the lack of active foraging behavior that both species exhibited. Over the course of my study I completed 14 single-species *M. rotundata* trials, and 11 single-species *A. mellifera* trials. Individuals from both species were used in 20 3-species trials. Of the 890 total individuals who made at least 2 flower transfer while foraging, only 32 were *A. mellifera* individuals and 101 *M. rotundata* individuals.

The lack of foraging from both species is likely the result of a variety of problems. *Megachile rotundata* exhibited stationary foraging behavior and tended to stay in a single flower for the length of a trial. *Apis mellifera* individuals presented many difficulties. In early experiments, individuals experienced high rates of death when taken from the hive and given training time equivalent to other species. To counteract this problem I placed a heating pad underneath the chamber to mimic the temperature of the natural hive and reduced the time between collection and experimentation. However, this resulted in decreased training time. *Apis mellifera* also exhibited very low rates of foraging. Individuals were active in the enclosure but rarely foraged and only began when they detected another individual foraging. This behavior has been seen in bee species including *A. mellifera* individuals. Both species experienced a higher rate of death during the trials than *B. impatiens* or *O. lignaria*. The lack of data and significant results from both the *M. rotundata* and *A. mellifera* suggested that 2-species trials or low-density single-species trials utilizing these species would not provide any further conclusions or additional information.

While I was able to gather data for *B. impatiens* individuals for all trials types, I was only able to gather data for *O. lignaria* individuals for single-species and 2-species trials. *Osmia lignaria* individuals showed high levels of foraging in early single-species trials suggesting that they would be responsive to experimental manipulations. Unfortunately, my experiments including *O. lignaria* were restricted because *O. lignaria* are agricultural bees and are only shipped during certain seasons. The lack of additional trial types utilizing *O. lignaria* individuals is not prohibitive for my conclusions. It is unlikely that additional experimental manipulations would provide further information for two reasons: first, the low amount of foraging behavior exhibited by *M. rotundata* and *A. mellifera* individuals suggests that their presence would not greatly impact the behavior of *O. lignaria* individuals. It is unlikely that interactions between *O. lignaria* and *M. rotundata* and *A. mellifera* individuals would have shown more significant results for any species.

Floral Fidelity

Interspecific Competition

My results suggest that interspecific competition has an effect on floral fidelity. Floral fidelity in the system was found to have a positive relationship with interspecific competition. *B. impatiens* individuals showed a significant increase in floral fidelity between single-species and 2-species trials. In contrast, *O. lignaria* individuals showed a significant decrease in floral fidelity in trials with increased interspecific competition. These results are consistent with my hypothesis that interspecific interactions between pollinator species would shape short-term specialization. The observed changes in *B. impatiens* individuals are also consistent with my prediction that increased interspecific competition interactions would lead to an increase in floral fidelity.

The observed differences in the direction of the response in *B. impatiens* and *O. lignaria* individuals are consistent with the idea that competition can result in species-specific responses. Species have been shown to exhibit different responses in terms of niche expansion in the presence of competition (Bolnick et al. 2010). A possible explanation for an observed decrease in *O. lignaria* floral fidelity is the behavior of both *O. lignaria* and *B. impatiens* in the artificial flowers. *O. lignaria* individuals were observed entering a flower and staying in it for an extended period of time. During this time, an individual bee's RFID tag had the ability to trigger the RFID reader to record a flower visit every 30 seconds. This would result in many conspecific flower visits being recorded and an inflation of the estimate of floral fidelity. However, in interspecific competition trials, *B. impatiens* individuals were observed entering flowers that contained a static *O. lignaria* individual, forcing the *O. lignaria* individual to move to a new flower. This would explain both the decrease in floral fidelity of *O. lignaria* individuals in response to interspecific competition and the relatively high level of floral fidelity for *O. lignaria* individuals in all trial types. Future analysis should eliminate flower transfers to the same flower ID to counteract this possible inflation.

There is little previous research related to the effect of multi-species interactions on short-term specialization in pollinator species. My results are consistent with Brosi and Briggs (2013), a field study that showed that the loss of a single pollinator bee species in a natural community reduced the specialization of the remaining species and led to a decrease of conspecific pollen transfer during foraging. My research serves as a complement to the Brosi and Briggs (2013) field study because it confirms their conclusions in a controlled, laboratory setting. In this way I was able to isolate interspecific competition as the variable of interest and eliminate some of the uncertainties about the effects of unaccounted for variables that occur with field studies.

My results are also consistent with other studies that explore the relationship between interspecific competition and short-term foraging specialization in bee species. Bumblebee species have been shown to respond to competitive interactions by increasing specialization. Inouye (1978) showed that interspecific competition in bumblebee resulted in increased short-term specialization of the flower species that they visited. Bumblebees have also been shown to specialize within flowers and forage in specific sections of flowers in the presence of competition (Morse 1977). Increased specialization and phenotypic plasticity in response to interspecific competition has also been documented in a variety of non-bee species, including other pollinators (Pimm et al. 1985), aquatic species (Bolnick et al. 2010), and plants (Ashton et al. 2010, Burns & Strauss 2012).

Intraspecific Competition

My results suggest that intraspecific competition also has an effect on floral fidelity. Intraspecific competition was found to increase floral fidelity within the system. *Bombus impatiens* individuals showed an increase in floral fidelity in high-density trials (16 individuals) as opposed to low-density trials (8 individuals). In contrast, *O. lignaria* individuals showed a decrease in floral fidelity in high-density trials as opposed to low-density trials.

The effect of pollinator abundance on diet breadth has been explored in previous studies. The results for the system and for *B. impatiens* individuals are inconsistent with the conclusion that a decrease in available resources due to increased competition should lead to an expansion of diet breadth. However, the results *for O. lignaria* individuals are consistent with this trend. This trend has been confirmed in previous studies that showed that increased intraspecific competition in bumblebee individuals resulted in increased generalization and an expansion of diet breadth (Fontaine et al. 2008).

These conclusions may be inconsistent with my results for *B. impatiens* individuals because of the variable of interest. My study explores the effect of competition on floral fidelity, or the proportion of conspecific flower visits. Previous studies analyze diet breadth in terms of flower visits (Fontaine et al. 2008), which is not as accurate of a predictor of successful plant pollination.

Furthermore, floral fidelity is an entirely individual measurement. Fontaine et al. (2008) analyzed diet breadth across all individuals and observed an increase in generalization with increased intraspecific competition. However, niche width across all individuals and niche width of single individuals have been shown to be decoupled (Bolnick et al. 2003, Bolnick et al. 2010). That is, individual niche width may become more specific in response to competition while the niche width across all individuals becomes more general. It follows then, that if floral fidelity is an individual measurement and Fontaine et al. (2008) measured specialization across all individuals, that our conclusions are not mutually exclusive.

Interspecific and Intraspecific Competition

The effect of intraspecific competition on floral fidelity is not enough to explain the observations in interspecific competition trials. Intraspecific competition is likely partially driving the results found in the 2-species trials. This is because the species present in the interspecific competition trials are present at a lower density than in the single-species trials. As shown by my intraspecific competition trials, a reduction in individuals has an effect on floral fidelity. However, the results found in the interspecific trials cannot be accounted for fully by the effect of intraspecific competition. The confidence intervals for the effects of interspecific competition and intraspecific competition do not overlap. This suggests that the effects of one variable are not enough to explain the effects of the other. Additionally, while the effects of both types of competition are significant, the magnitude of the effects of intraspecific competition is much smaller than the magnitude of the effects of interspecific competition (Figures 1 and 2). While intraspecific competition does have an effect on floral fidelity in interspecific trials, species number has an additional, larger effect.

Complementarity

I observed the effect of competition on complementarity in terms of flower evenness, a measure of the relative proportion of flower visits to each type of flower. Greater evenness of flower visits suggests complementarity relationships between species because it is evidence of larger niche coverage in the presence of competition. My results showed no significant effect of interspecific or intraspecific competition on complementarity. I observed no difference in flower evenness in trials with increase interspecific competition or in trials with increased density.

My observations are inconsistent with my expected results. It is unusual that I found significant effects of competition on floral fidelity and not flower evenness because we would expect to see changes in complementarity as a result of changes in floral fidelity. As diet breadth becomes less general, we would expect that some species would be forced to undergo niche shifts and forage on lesser reward flowers. In contrast, we would expect that individuals who are not exposed to competition would have less specific diet breadths and would visit a greater proportion of high reward flowers. This increases the pollination of lesser-reward flowers and results in a higher number of species being pollinated and greater biodiversity of plant species.

As a change in flower evenness is expected with a change in floral fidelity, the insignificant results that I found are likely due to problems with my analysis rather than to a lack of an underlying pattern. In order to analyze flower evenness I categorized every flower visit as being a high reward visit or a low reward visit and conducted a series of chi-squared tests to see if changes were observed between single-species and 2-species trials as well as between low and high density trials. However, this analysis proved to be unfitting because of inflated statistical power and issues with data aggregation. Aggregation of my data is complicated because the trial types do not have even sample sizes. This means that the effects of the species included in the trial, interspecific competition, and density are not evenly weighted. Aggregation of the data to find proportions in a simple way, then, gives an unevenly weighted result. In order to explore the relationship between species, interspecific competition, and intraspecific competition, then, I would have to analyze the data through a multinomial regression. This sort of random effects analysis would preserve all of the data and produce a result that shows accurate and comparable proportions for flower evenness. However, this type of analysis is extremely complicated and requires very careful handling of the data. Aggregation in incorrect ways could easily produce false results, as my over-simplified chi-squared model did. I am currently in the process of analyzing the complementarity data with this method, and I expect to find results that are consistent with my expectations and that complement my floral fidelity measurements.

Prior research directly supports the hypothesis that niche shifts resulting from interspecific competition act as a mechanism through which plant communities benefit from complementarity interactions. It has been shown that bee species foraged on novel resources and fill complementary niches when in the presence of interspecific competition, and that these niche shifts resulted in higher seed production and pollination success (Fründ et al. 2013). Pimm et al. (1985) showed that subordinate hummingbird species foraged on lesser-reward food patches in the presence of a more dominant species, increasing foraging coverage. Cardinale et al. (2003) showed that predator-prey niche shifts resulting from increased interspecific competition in pest species significantly increased crop yields in agricultural systems. This effect has also been shown in plant species in which productivity increases as a result of resource use phenotypic plasticity in response to competition (Burns & Strauss 2012).

Previous research has also explored the benefit of complementarity caused by interspecific and intraspecific competition on plant-pollinator communities through mechanisms other than niche shifts. Brittain et al. (2013) showed that the presence of non-Apis bees created a synergistic effect in pollination services of Apis-pollinated crops by changing the flight patterns of Apis individuals to allow for more conspecific pollen transfer. Greenleaf & Kremen (2006) showed that interspecific competition between wild bees and managed honeybee populations resulted in higher seed production due to an enhancement of pollination effectiveness caused by pollen deposition of wild bees.

The lack of complementarity found in the system does not mean that biodiversity ecosystem functioning relationships will not be affected by floral fidelity. Decreases in floral fidelity have been shown to decrease conspecific pollen transfer in natural systems

(Brosi & Briggs 2013), which has serious consequences for plant pollination (Flanagan et al. 2009, Arceo-Gomez & Ashman 2011, Morales & Traveset 2008). While an effect of competition on flower evenness would show a direct mechanism through which competition affects ecosystem functioning, the impact of floral fidelity on conspecific pollen transfer shows that interaction between pollinator bee species has direct effects on plant reproduction and biodiversity ecosystem functioning.

Energy Uptake

In addition to the effect of interspecific and intraspecific competition on floral fidelity and complementarity, I also explored the effect of competition on energy uptake. I found no significant results for the effect of interspecific competition on energy uptake in terms of total energy uptake or average uptake per species. I also found no significant results for the effect of intraspecific competition on total energy uptake or on the average energy uptake per species.

This result is surprising because previous research has shown that competition affects energy uptake in a wide variety of species. Interspecific competition in aquatic suspension feeders has been shown to cause changes in the abiotic environment that result in a higher uptake of resources for all species (Cardinale et al. 2002), and localized competition interactions in plants have been shown to cause shifts in the proportion of nutrient uptake to benefit more dominant species (Ashton et al. 2010). It is also surprising that I did not observe asymmetric shifts in nutrient uptake, as competition has been shown to cause this effect in many species, including pollinators (Pimm et al. 1985, Ashton et al. 2010).

It is possible that I found no observable trend because of the restrictiveness of the foraging enclosure. We would expect to find an increase in energy uptake with an increase in competition because of the efficiency of specialization. Foragers with narrower diet breadths spend less time searching for flowers and have more direct foraging paths. This allows for a higher amount of energy collection in relation to time spent foraging. However, the foraging enclosure may be too small to allow for this efficiency to develop. The time spent searching for flowers may already be decreased by the size of the chamber. A size limitation would mean that foraging paths are direct even without the effect of specialization, and would explain why I observed no change in energy uptake with a change in competition and resulting shifts in floral fidelity.

Additionally, the virtually infinite supply of sucrose solution to the artificial flowers in the system has the potential to alter the response in total energy uptake. In a natural system, an individual bee's choice to forage at a specific flower would consider the amount of resources that the flower contains. In a system without many competitors, we would expect that flowers would have a larger supply of nectar. In contrast, in a system with higher interspecific competition, we would expect that competitors would deplete resources of some flowers. The resource supply in the artificial system could not be depleted by competitors, which means that individuals were not making the same choices that they would and that the energy uptake does not accurately mimic a natural system.

Biodiversity Ecosystem Functioning

Floral Fidelity and Conspecific Pollen Transfer

My conclusions have serious consequences for biodiversity ecosystem functioning relationships. My results show that interspecific competition causes short-term changes in floral fidelity. Specifically, my results are consistent with the prediction that increases in interspecific competition shape short-term specialization and result in greater floral fidelity in pollinator bee species.

Floral fidelity and specialization within plant-pollinator relationships is vital for the health of a functioning ecosystem. While it is beyond the scope of my study to directly measure ecosystem functioning, there is evidence to show that floral fidelity in pollinator species has profound effects on plant reproduction which is a component of ecosystem functioning. The specialization of plant-pollinator relationships is a mechanism for conspecific pollen transfer. Pollinators with higher floral fidelity exhibit a higher proportion of conspecific flower visits, which leads to an increase in conspecific pollen transfer. This increases successful plant reproduction and increases plant biodiversity.

Previous literature has explored the relationship between floral fidelity, conspecific pollen transfer, and ecosystem functioning. A decrease in interspecific competition increases heterospecific pollen transfer and decreases conspecific pollen transfer. This effect has caused direct reductions in seed production in experimentally manipulated systems (Brosi & Briggs 2013, Flanagan et al. 2009). Several mechanisms have been proposed to explain the relationship between interspecific competition and seed production in terms of conspecific pollen transfer. Two related factors have been proposed, (1) heterospecific pollen deposition, in which pollen from a competing species is deposited on an incompatible flower, and (2) conspecific pollen loss, in which compatible pollen is deposited on a competing species (Morales & Traveset 2008). The effects of both of these mechanisms are well documented, but the importance of each has been debated. The effect of conspecific pollen loss has been shown to be drastically greater than heterospecific pollen deposition in seed production in the native species *Mimulus* (Flanagan et al. 2009). However, other studies have shown heterospecific pollen deposition to be an important driver of reductions in seed production. This has been shown to increase with heterospecific pollen diversity (Arceo-Gomez & Ashman 2011).

My results show that floral fidelity is a flexible trait that has a positive relationship with competition. Floral fidelity has impacts on conspecific flower transfer, which has direct impacts on seed production, plant reproduction, and ecosystem functioning.

Interactions Between Species

My results suggest that interactions between species have serious consequences for biodiversity ecosystem functioning relationships. An ecosystems function is sometimes thought of as being comprised of its components. That is, the functioning of a component of the ecosystem can be understood by the impacts of that one component. Additionally, the impacts of the loss of any component of an ecosystem can be thought of in terms of the component itself. However, my results suggest that interactions between species have impacts outside of the impacts of each individual species. Interactions between species increase floral fidelity and thus increase the efficiency of pollination and of pollinator behavior.

The idea that interspecific interactions between pollinator bee species can increase biodiversity ecosystem functioning is an under-researched concept and has been studied in a limited capacity. The interactions between pollinator bee species are of particular importance in the light of recent pollinator declines (Potts et al. 2010, Wardell et al. 1998, Kearns et al. 2008). Reductions in bee species will change competition interactions in natural and managed communities. My research shows that reductions in interspecific interactions have serious consequences for plant-pollinator relationships and plant reproduction due to changes in short-term specialization.

The effects of interspecific interactions on biodiversity ecosystem functioning have large impacts on environmental policy and management. Traditional environmental management examines the impacts of a single species. However, my results suggest that the impacts of a single species are much more complex due to the interactions between species. Effective policy should evaluate the relationships between species and the impacts of their interactions.

Intraspecific competition interactions also have broad impacts for BDEF relationships. My results suggest that intraspecific competition affects floral fidelity in the same way that interspecific competition does. Changes in intraspecific competition in the form of reductions in species abundance thus should also be considered for effective environmental policy.

Limitations and Extensions

Limitations

This study had many limitations, primarily related to the difficulties of maintaining bee species in a laboratory setting. As discussed, some species did not forage at a rate that provided enough information to identify patterns and draw conclusions. Furthermore, this study is limited by the fact that it is an artificial system. While the controlled laboratory setting had benefits in terms of isolating the variables of interest, an artificial system may affect responses in a way that I did not account for.

It was difficult to satisfy the requirements of all utilized species. Each species has different optimal conditions in terms of temperature, light, wind, etc. The experimental and training conditions were designed to accommodate all species, but some species were in a more optimal environment than others. However, the differences in preferences that the species possess suggest that high bee diversity can increase complementarity. My study analyzed complementarity in terms of flower species preference, but complementarity of other niche types exists within pollinator systems. Complementarity of bee species has been shown to exist in a variety of ways including temperature and temporal niches. These niches have been shown to increase complementarity (Bartomeus et al. 2013) and pollination success (Fründ et al. 2013, Hoehn et al. 2008).

Extensions

There are many extensions of this study as well as related topics that would be interesting to explore further. My study only found significant results for two species, but natural plant-pollinator systems have a much more complex set of interactions. Finding solutions to the problems that I found with *M. rotundata* and *A. mellifera* individuals, as well testing my hypotheses with other species, could provide further insight. This study is unique in its ability to quantify energy consumption within a plant-pollinator system. However, this is a topic that has been very unexplored. Further research should be done on the effects of pollinator interspecific and intraspecific competition on energy consumption.

Complementarity through mechanisms other than flower evenness should be explored, especially in light of the lack of the significant results for the effect of competition on flower evenness. A field realistic setting may help eliminate the limitations that an artificial system presents. Experiments on the effect of interspecific competition have been conducted in the field (Brosi & Briggs 2013), and my results have shown effects in a laboratory setting. A greenhouse with natural flowers could act as an intermediate study system that has the control of a laboratory setting but does not contain artificial flowers or other artificial field components.

Conclusions

I have shown that interspecific competition has a positive relationship with floral fidelity. I have also shown that intraspecific competition has a positive relationship with floral fidelity, but it is not enough to explain the effects of interspecific competition in my observations. My conclusions are consistent with the hypothesis that pollinator species can exhibit phenotypic behavioral plasticity in response to competition. This is evidence that specialization in resource use and niche shifts can occur in ecological time. Phenotypic plasticity of foraging behavior in ecological time in bee species has implications for biodiversity ecosystem functioning relationships. Global trends of bee population declines will change the structure of competition networks between bee species and will likely reduce interspecific and intraspecific competition. My research shows that fluctuations in competition can result in changes in short-term specialization and diet breadth. This has profound impacts on plant reproduction and ecosystem functioning.

Tables and Figures

Color	Blue	White	Yellow	Red
Essential Oil	Clove	Wintergreen	Spearmint	Lemongrass
Molarity	2.0	1.5	1.0	0.5

Table 1. The effect of competition on bee species was explored using an artificial foraging system. The foraging chamber included four artificial flower species for bees to forage on. Chart showing four artificial flower species utilized in the experimental methods. Molarity refers to sugar concentration in sucrose solution. Sucrose solution consisted of water, sugar, and essential oil. Sucrose solution was dispensed to artificial flowers of the correct color in 10uL droplets.

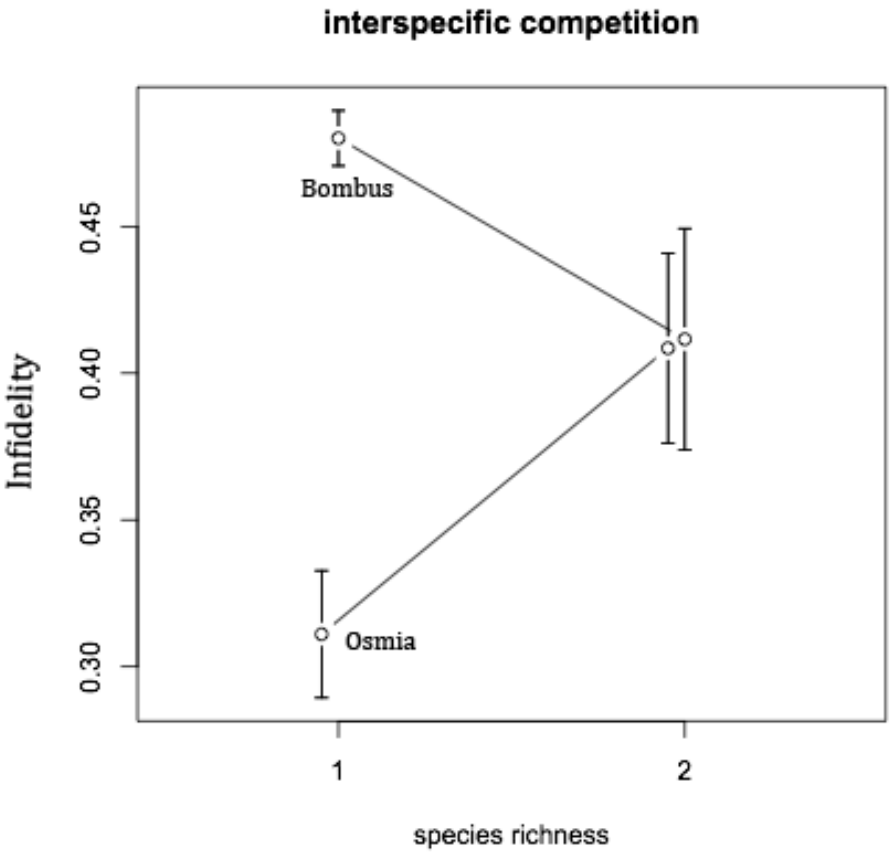

Figure 1. The effect of interspecific competition on infidelity in *B. impatiens* and *O. lignaria* individuals. The x axis shows the number of species and the y axis shows infidelity, or the proportion of heterospecific flower transfers. The top line shows the effect of interspecific competition for *O. lignaria* and the bottom line shows the effect of interspecific competition on *B. impatiens. B. impatiens* show a decrease in infidelity (and thus an increase in fidelity) in response to increased interspecific competition while *O. lignaria* show the opposite response. Figure created using R.

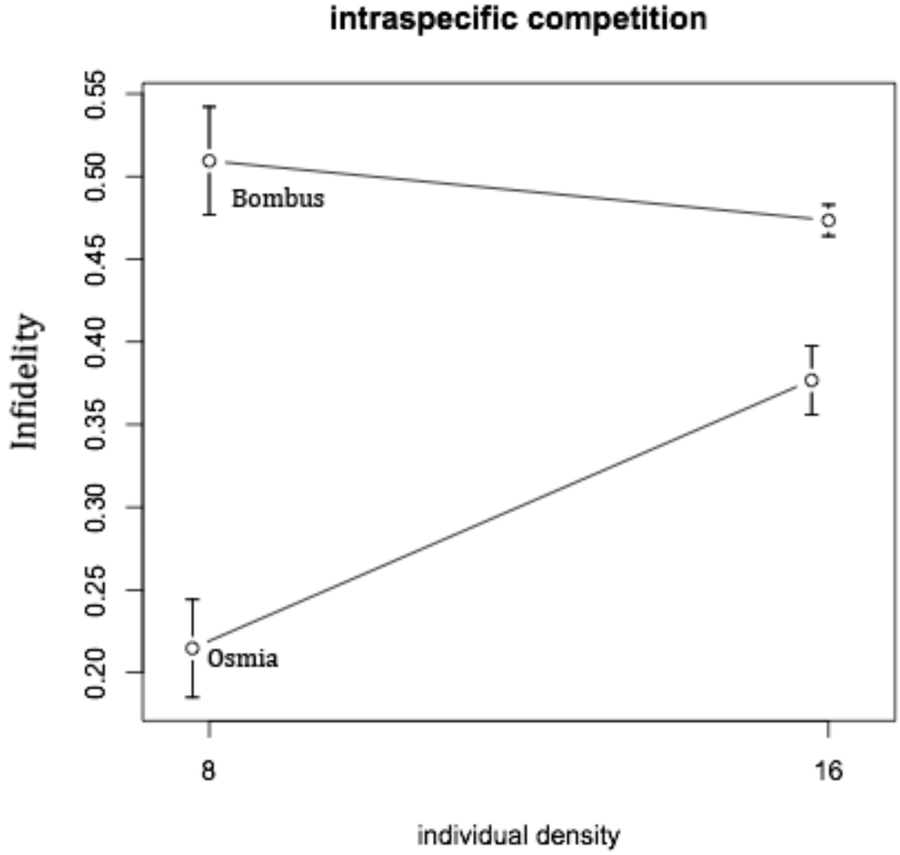

Figure 2. The effect of intraspecific competition on floral fidelity in *B. impatiens* and *O. lignaria* individuals. The x axis shows the number of individuals (high and low density) and the y axis shows infidelity, or the proportion of heterospecific flower transfers. The top line shows the effect of interspecific competition for *B. impatiens* and the bottom line shows the effect of interspecific competition on *O. lignaria. B. impatiens* show a decrease in infidelity (and thus an increase in floral fidelity) with an increase in density. *O. lignaria*

show the opposite of this with an increase in infidelity with increased density. Figure created using R.

Acknowledgements

Thank you to my advisor, Berry Brosi. Thank you to my committee members Christopher Beck and Thomas Gillespie. Thank you to everyone in the lab, especially to Emily Dobbs, Carolyn Ayers, and Travis Dynes. Lastly, thank you to Emory University and the entirety of the Environmental Science department.

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