BEE FORAGING CHOICE AND IMPLICATIONS FOR PLANT COEXISTENCE

by

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ABSTRACT OF THE DISSERTATION

Bee foraging choice and implications for plant coexistence By ELIZABETH ANNE BRUNINGA SOCOLAR Dissertation director:

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Species interactions are essential to our understanding of community ecology, particularly when we think about how species persist in communities. Compared to competition and predation, the effect of mutualism on the population dynamics and coexistence of species is less well studied. Interactions between plants and pollinators are a model system for studying mutualism. In these interactions, both of the partner species benefit: the bee receives food, and the plant is able to reproduce because the bee moves its gametes to other plants of the same species. This sounds straightforward, but two points make this more complicated. First, most pollen is deposited within just a few flower visits of where it was picked up. From the perspective of the plant, then, successful reproduction hinges on the foraging choices of bees, particularly the sequences in which they visit plants. A second point complicating the plant-pollinator relationship is that many foraging pollinators have a tendency to preferentially visit whichever plant species is most common in a community. If pollinator visits are proportional to plant abundance, then we might expect that sequential visits would be proportional to the square of plant abundance and so it should be really difficult for rare plants to reproduce. In pollen-limited plant communities, the foraging behavior of pollinators might mediate coexistence and competitive exclusion by determining which plants receive conspecific

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pollen. A key question is whether realistic pollinator foraging behavior promotes coexistence or exclusion. My first two thesis chapters quantify realistic pollinator foraing behavior in response to relative abundances of flowering species, and the spatial arrangement of flowering plants. In my third chapter, I use a simulation model to understand how pollinator foraging behavior impacts the coexistence dynamics of pollenlimited plants. To determine whether pollinators are likely to provide a biologically important coexistence mechanism in nature, I compare my results to bee foraging data from the literature and from a novel experimental analysis.

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Included in the thesis is a published paper (Chapter I), which is my original work and is co-authored by R.W. and my external committee member, Elizabeth Crone, both in an advisory role.

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Also included in my thesis is a paper which has been reviewed for publication at *The American Naturalist* and "declined without prejudice." This paper is my original work and is co-authored by Jacob Socolar, Sabine Konzmann, and Klaus Lunau, all in an advisory role.

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INTRODUCTION

In order for bee-pollinated plants to reproduce, a bee must collect pollen at one plant and move it to another individual of the same species. However, in natural plant communities, multiple plants flower simultaneously, and bees deposit most pollen within just a few plant visits after picking it up (Richards et al. 2009). Therefore, sequential visits (or nearly sequential) to the same plant species are most likely to result in pollination, and the choices an individual bee makes while foraging (whether it visits a high proportion of individuals of the same species within foraging paths or switches among species) crucially affect plant reproduction. Despite the hypothetical importance of individual bee behavior to plant reproduction and coexistence, models of pollinator visitation to plants (e.g. Essenberg 2012) and pollinator-mediated coexistence (e.g. Levin & Anderson 1970) lump all bees within a single pollinator parameter and do not include explicit variation in bee foraging behavior. These simple observations motivate my thesis. I ask how a better understanding of pollinator foraging behavior can further our understanding of plant coexistence. In my three dissertation chapters, I explore various facets of the question: under what conditions do bees make sequential visits to the same plant species, and under what conditions do they switch plant species while foraging?

Several variables influence bee foraging choices, particularly the relative density or abundance of local plant species, and their spatial arrangement. Studies on the effect of the relative abundance of plant species on bee foraging behavior report a range of results, including a positive relationship between bee visits to a focal plant and the abundance of conspecifics (e.g. Kunin 1997), negative or no relationship between bee visits and the abundance of conspecifics (e.g. Campbell & Motten 1985), a positive relationship of heterospecific plant species abundance on bee visitation to a focal plant (e.g. Jakobsson et al. 2009), or a negative or no effect of heterospecific plant species abundance on bee visitation (e.g. Feldman 2008). Studies of the effect of plant spatial arrangement on bee foraging choices find that bees prefer to travel short distances between plants (e.g. Lihoreau et al. 2011), but are flexible in their response to distance depending on the floral environment (Lihoreau et al. 2012).

My dissertation contributes to the literature on bee foraging choice in three ways. Most importantly, I analyzed the foraging paths of individual bees. The majority of the literature analyzing the effect of environmental variables (e.g. relative plant abundances and spatial arrangement) on bee foraging behavior uses plant visitation data, where observers record the number of bee visits to focal plant individuals per unit time. To infer the effects of bee foraging choice on plant reproduction, data on the foraging paths of individual bees are required because analysis of foraging paths can 1) determine the effects of environmental covariates on the proportion of visits by a single bee to a focal plant species, and 2) describe the discrete choices made by bees as they select individual plants to visit. Second, I conducted my research in an unmanipulated, natural system characterized by annual fluctuations in the relative abundance of plant species within sites, creating a natural experiment of the effects of relative plant abundances on bee foraging behavior. My study design is in direct contrast to previous abundance studies that artificially manipulate plant species composition and/or abundance (e.g. Ghazoul

2006). My study design also contrasts with much of the spatial arrangement literature which analyzes bee foraging choice in the context of linear arrays of flowering plants, which may bias the foraging distances and directions chosen by bees (e.g. Morris 1993). Third, I include a solitary bee group. The literature on bee foraging choice to date focuses on the honeybee (*Apis mellifera*) and/or bumblebees (genus *Bombus*), which represent only a small fraction of bee diversity. In particular, the large size and sociality of these bees should result in different foraging behavior than solitary bee species.

My first two thesis chapters use my field system to describe the effect of relative plant species abundances and spatial arrangement on bee foraging choice, respectively. In Chapter 1, I explore whether the proportion of bee visits within foraging paths to a focal plant species is influenced by the abundances of co-flowering plant species. I also explore the relationship between the proportion of visits within foraging paths to the focal plant species and conspecific flowering plant abundance, and whether this relationship differs across bee groups. In Chapter 2, I ask how the spatial arrangement of plants and plant identity affect bee foraging choices, and whether those choices differ between bee groups. In the two data chapters, I find evidence of predictive relationships between environmental covariates and bee foraging choice that vary among different types of bees.

In Chapter 3, I build a simulation model to explore the effects of variation in bee foraging behavior on plant coexistence in a pollen-limited plant community. I show that pollinator-mediated plant coexistence requires high levels of foraging specialization

within foraging paths.

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CHAPTER I. THE ROLE OF FLORAL DENSITY IN DETERMINING BEE FORAGING BEHAVIOR: A NATURAL EXPERIMENT

Abstract

Animal-pollinated plants depend on sequential pollinator visits to conspecifics for successful reproduction. Therefore, in co-flowering plant communities, the proportion of visits to a focal plant species in individual pollinator foraging bouts determines reproductive outcomes for that species. We investigated the factors determining bee visits to the plant *Astragalus scaphoides* within foraging bouts in a natural multi-species community in the northern Rocky Mountains. We found that both conspecific and heterospecific floral density influenced the proportion of visits to *A. scaphoides* during foraging bouts, but these effects of floral density differed among two abundant bee groups. Our field observations reject the null expectation that bees visit plant species in direct proportion to their relative floral densities. *Bombus* consistently visited *A. scaphoides* more than expected, while solitary bees of the genera *Anthophora* and *Eucera* exhibited a nonlinear response to floral density.

Introduction

In natural plant communities multiple plant species flower at the same time. Most of these plant species are visited by multiple pollinator species, and most pollinators visit multiple plant species (Michener 2000; Bosch et al. 2009). Animal-mediated plant reproduction is contingent on sequential (or nearly so) visits by a pollinator to multiple individuals of the same plant species, because pollen collected at one plant individual is generally deposited within a very small number of subsequent plant visits (Thomson 1986; Cresswell et al. 1995). In a natural plant community in which multiple plant species co-flower, the choices an individual bee makes within a foraging bout thus affect plant reproduction. Whether the bee visits multiple individuals of the same species within a foraging bout or switches among species affects the deposition of conspecific pollen and thus plant reproduction.

Bees use a variety of visual and other cues to make foraging decisions, but special attention has been paid to floral density as a key variable determining bee foraging behavior. The effects of floral density are complex and operate on multiple scales (Essenberg 2012). For a single plant species, there is a positive relationship between its floral density and pollinator visitation at small scales (e.g. patch sizes < 400 m²) (Kunin 1993, 1997; Dauber et al. 2010). When multiple flowering plant species are considered, the effects of floral density on bee foraging behavior become more complicated. In a system with two co-flowering plant species, pollinator visits to the focal plant species increased with both conspecific and heterospecific floral density at very small scales (≤ 3

m) (Jakobsson et al. 2009), though in a different two-plant system at a larger scale (plots of $\sim 2600 \text{ m}^2$), only conspecific density had an effect on pollinator visitation (Feldman 2008). In a system with four co-flowering plant species in $\sim 13 \text{ m}^2$ plots (small scale), overall floral density had a positive effect on pollinator visitation to the focal plant species to a point, after which pollinator visitation decreased due to competition with one or more of the additional plant species (Ghazoul 2006). Such findings suggest that higher overall floral density causes more pollinators to visit a patch, but also may increase competition between individual plants since pollinators are shared by more plants in the patch, as predicted by theory (Rathcke 1983). In multi-species plant communities, increased competition at higher plant densities may be compounded by the presence of heterospecific plant species, as suggested by Ghazoul (2006) and Essenberg (2012). Additionally, four of these five studies were conducted in small patches of less than 400 m^2 (e.g. a patch size of 20 m x 20 m). However, even very small bees forage at distances of 100 meters or more (Greenleaf et al. 2007; Zurbuchen et al. 2010). Therefore, studies of the effects of floral density on bee behavior must consider larger spatial scales (Essenberg 2012). Measuring the relationships between pollinator visitation, competition versus facilitation among plant species, and floral density requires tracking the movements of individual bees among plant individuals across different relative densities of the plant species in the community (Kunin 1993) and at spatial scales large enough to encompass bees' true foraging mobility.

A final complicating factor of bee behavioral response to floral density is that we expect different bee groups to respond differently to floral density due to life history traits. For example, social bees and solitary bees differ in their foraging habits. The workers of social bee colonies often specialize individually on particular resources, e.g. a single plant species, pollen, or nectar, and individual bees are thus less likely to change their foraging behaviors within foraging bouts (Heinrich 1976; Williams and Tepedino 2003). Individual females of solitary bee species must obtain all resources necessary for provisioning larvae, both pollen and nectar, by themselves. Polylectic solitary bees, those that feed on multiple plant species, may thus be more likely to change their foraging behavior within foraging bouts based on resource availability (Tepedino and Parker 1982). In other words, solitary bees may need to visit multiple species within some foraging bouts in order to obtain both pollen and nectar, or a mixture of pollens with different nutritional properties (Eckhardt et al. 2014; Heinrich 1976; Bosch et al. 2009). Müller (1996) showed that polylectic solitary bees in the tribe Anthidiini (Hymenoptera, Megachilidae) visited 2.2 plant species on average in single foraging bouts. Oligolectic solitary bees, which specialize on single plant species or groups of related species (Michener 2000), are expected to exhibit much higher rates of floral constancy depending on their degree of specialization.

We used a natural co-flowering plant community to study the effects of multiple plant species' floral densities on bee foraging behavior. Our system focuses on a pollenlimited, biennially-flowering plant *Astragalus scaphoides* (Jones; bitterroot milkvetch), which provides a strong oscillation of floral density across years (Crone et al. 2009) while the densities of co-flowering plants remain roughly constant across years. We recorded bee foraging behavior by following individual flight paths (foraging bouts) within discrete communities of plants (patches in an otherwise arid habitat) ranging in size from 414 to 4,327 m². We focused on two abundant bee groups that are known to visit *A. scaphoides* in our patches: the social genus *Bombus* and the polylectic solitary genera *Anthophora* (Latreille) and *Eucera* (Scopoli), referred to as *Anthophora/Eucera* hereafter (Crone 2013). We asked two questions: 1) Do the densities of co-flowering plant species influence bee visitation to the focal plant, *A. scaphoides*? and 2) Does the relationship between *A. scaphoides* density (expressed as a proportion of total flowering plant density) and visits to *A. scaphoides* vary by bee group and across high and low densities of *A. scaphoides*?

Methods

Study area

We conducted all fieldwork in the Beaverhead Valley of southwestern Montana and adjacent Lemhi River Valley of Idaho. The valley floor elevations range from 1500 m to 2000 m and are predominantly vegetated by semi-arid sagebrush steppe (Lesica and Cooper 1997). This shrubland ecosystem is dominated by wind-pollinated sagebrush (*Artemisia spp.* Linnaeus) with low densities of insect-pollinated flowering plants. Among these insect-pollinated plants is *Astragalus scaphoides* (Fabaceae), a regionally endemic perennial herb that grows in small, spatially discrete patches, generally less than one hectare in extent. Within patches, *A. scaphoides* is locally abundant, but patches are sparsely distributed over the immense sagebrush steppe. Three additional bee-attractive plants commonly co-occur with *A. scaphoides*, but typically in lower abundance: *Castilleja spp.* (Mutis; Orobanchaceae), *Lupinus spp.* (Linnaeus; Fabaceae), and *Penstemon albertinus* (Greene; Plantaginaceae).

Within each patch, A. scaphoides blooms synchronously approximately every other year in May and June. The mechanisms driving this biennial bloom pattern reflect resource costs of reproduction and do not affect the bloom frequency and magnitude of the coflowering species (Crone et al. 2009). Thus, the biennial bloom pattern of A. scaphoides provides within-site variation in A. scaphoides floral resource density that is decoupled from variation in floral densities of co-occurring species, which are relatively constant within sites and across years (E. Crone & B. Bruninga-Socolar, unpubl. data). Each patch, embedded in a vast arid matrix with few foraging opportunities for bees, provides a replicate natural experiment for examining the response of bee foraging bouts to variation in floral density. Due to the low herbaceous plant densities in this semi-arid environment and the low plant species richness at individual patches, this simple study system allows easy observation of bee behavior in a natural, multi-species plant community. Further, local bee abundance as measured by bees seen per unit time is low (approximately five bees encountered per hour on average across sites (Table S1)) so it is feasible to follow individual bees. Due to this low rate of encountering bees and the difficulty of identifying individual bees to species on the wing, we collected data on only the most common bees we observed, all of which fall into the social genus Bombus and the solitary group Anthophora/Eucera. Our voucher specimen collection of bees in A. scaphoides patches includes five species of Bombus: B. appositus, B. californicus, B.

fervidus, *B. huntii*, and *B. nevadensis*. *B. huntii* is most abundant at our sites, representing 68% of our specimens. We collected one species of *Anthophora*, *A. urbana*, and two species of *Eucera*, *E. frater* and *E. fulvitarsis*. All eight of these bee species are dietary generalists, using plants from four (*B. huntii*) to 33 plant families (*A. urbana*) (Koch et al. 2011; Ascher and Pickering 2015).

Data collection

We selected nine patches for sampling using surveys conducted in the 1980s, when *A*. *scaphoides* was being evaluated as an endangered species (P. Lesica, unpubl. data; see Lesica et al. 2006). All patches constitute spatially distinct clusters of *A. scaphoides* with at least one of the following co-flowering, bee-attractive plants: *Castilleja spp.*, *Lupinus spp.*, and *P. albertinus*. We refer to these four species collectively as our focal species. We defined the patch boundaries to include the contiguous area with at least one individual of one focal plant species per square-meter. Patches ranged in size from 414 to 4,372 m². We collected data in all patches in May-June 2014, and we resampled three of these patches in May-June 2015. We collected data at each patch on three to seven dates within each year (Table S1).

All bee observation data were collected on days that were sunny, partly cloudy, or bright overcast with wind $< 7 \text{ m s}^{-1}$ between the hours of 10:00 and 18:00 hours by the same observer (BBS) (Winfree et al. 2007). We used pin flags to delineate a 5x5 meter grid encompassing each *A. scaphoides* patch. On each sampling day, the observer began observations at a haphazardly chosen location within the patch and walked along the

established grid lines to systematize the search for bees. When a bee was spotted, the observer followed the bee's movements through the patch, recording the species identity of each plant visited. Each bee was followed until it either left the patch or switched to a non-foraging behavior.

Within four days of each bee foraging observation, we counted the total number of plants of each species in bloom (i.e. with open flowers) at each patch. Previous work has shown that bloom turns over on timescales of longer than one week in this system (B. Bruninga-Socolar, unpubl. data).

Analyses

To assess the effect of co-flowering plant densities on bee visits to *A. scaphoides*, we modeled the proportion of visits to *A. scaphoides* within a given foraging bout using a generalized linear model (GLM) framework. Initial attempts at fitting GLMs with binomial error resulted in high residual deviance in all candidate models indicating overdispersion, so we fit the model using quasibinomial error and a logit link. We began with a complex model including the following predictor variables: *A. scaphoides* density, *Lupinus spp.* density, *Castilleja spp.* density, and fixed effects of pollinator identity and patch identity. We also fit separate models that treated patch identity as a random effect; these did not affect our conclusions and are not shown. The density of *P. albertinus* was highly correlated with the density of *A. scaphoides* and was not included in our models. To obtain a parsimonious model, we used backward stepwise parameter selection in which the least significant parameter is dropped from the most complex model, and the

process is repeated for subsequent simpler models until a final model is obtained in which all parameters are significant and therefore retained (Zuur et al. 2007).

To assess the relationship between *A. scaphoides* density and visits to *A. scaphoides*, we asked whether the relationship between density and visits is a one-to-one relationship for each of our most abundant bee groups, *Bombus* and *Anthophora/Eucera*. If bees do not display floral preference, the null expectation is that bees will visit *A. scaphoides* in direct proportion to its density (a one-to-one relationship; Figure 1A). If bees show preference (or anti-preference) for *A. scaphoides*, then the proportion of visits should lie above (or below) the one-to-one line (Figure 1B). Lastly, if bees alter their preference depending on the density of *A. scaphoides*, then the proportion of visits should lie higher (or lower) above the one-to-one line at high *A. scaphoides* density than at low *A. scaphoides* density (Figure 1C).

To test these possibilities, we modeled the proportion of visits to *A. scaphoides* as a function of the proportion of *A. scaphoides* in the flowering plant community, fitting separate GLMs for *Bombus* and *Anthophora/Eucera* with quasibinomial error and a logit link. To visualize the results, we plotted the modeled expectation of the logit of the proportion of visits to *A. scaphoides* against the logit of the proportion of *A. scaphoides*. Thus, consistent floral preference will appear as a line parallel to the one-to-one line but with a significantly offset intercept (Figure 1E), while density-dependent floral preference will appear as a line with slope significantly different from one (Figure 1F).

All analyses were carried out in the program R version 3.1.3 (R Core Team 2014). All GLMs were fit using the R base package (R Core Team 2014) and parameter significances were estimated using the Anova function with an F-test (Crawley 2007) in package nnet (Venables and Ripley 2002). Inverse logits were calculated using the package boot (Canty and Ripley 2015), and confidence intervals were calculated using the package MASS (Venables and Ripley 2002).

Results

In general, 2014 was a high floral density year for *A. scaphoides* and 2015 was a low floral density year, although this pattern was reversed at one patch. The density of flowering *A. scaphoides* plants ranged from 0.01 to 2.07 plants per m^2 in 2014 and 0.4 to 0.7 plants per m^2 in 2015 (Table S1). The proportion of blooming *A. scaphoides* plants out of the total flowering plant community ranged from 0.24 to 0.86 in 2014 and 0.09 to 0.25 in 2015 (Table S1).

In total we observed 158 individual bee foraging bouts, mostly of bees in the genus *Bombus* (69 bouts) and the combined genera *Anthophora/Eucera* (67 bouts). Pollinator identity, patch identity, *A. scaphoides* density, and *Castilleja spp*. density all had significant effects on bee visits to *A. scaphoides* in the best model (Table 1). Visitation to *A. scaphoides* was positively associated with *A. scaphoides* density and negatively associated with *Castilleja spp*. density (Table 1).

The relationship between the proportion of visits to *A. scaphoides* and the proportion of *A. scaphoides* differed significantly from one-to-one (slope of one and intercept of zero on the logit-logit scale) for both *Bombus* and *Anthophora/Eucera*. The intercept for *Bombus* was significantly greater than zero, indicating an overall preference for *A. scaphoides* (Table 2). However, the slope for *Bombus* did not differ from one, suggesting that their visitation was approximately proportional to density across the range of *A. scaphoides* densities. Furthermore, the 95% confidence interval for the expected proportion of *Bombus* visits to *A. scaphoides* lies entirely above the one-to-one line across essentially the entire range of observed *A. scaphoides* densities, from proportions of 0.12 to 0.88 (the inverse logits of -2 and 2, respectively; Figure 2A).

The intercept for *Anthophora/Eucera*, by contrast, did not differ significantly from zero indicating no preference or lack of preference for *A. scaphoides* (Table 2). The slope was significantly lower than one indicating that the relationship between the proportion of visits to *A. scaphoides* per bee foraging bout and the proportion of *A. scaphoides* in the flowering plant community changes across different *A. scaphoides* densities for *Anthophora/Eucera* (Table 2, Figure 2B). The 95% confidence interval for the expected proportion of visits to *A. scaphoides* lies above the one-to-one line at low *A. scaphoides* densities, indicating that when *A. scaphoides* bloom is low (proportions of less than 0.18), *Anthophora/Eucera* preferentially seek out *A. scaphoides* (Figure 2B). However, the small slope indicates that this preference attenuates, and likely reverses when *A. scaphoides* bloom is high (Figure 2B). For both *Bombus* and *Anthophora/Eucera*, the

effects reported here manifest themselves at biologically realistic values for A.

scaphoides bloom: the sampled proportions of A. scaphoides range from 0.09 to 0.86.

Discussion

We found that the co-flowering plant community influences bee visitation to a focal plant species, *A. scaphoides*. Although we did not measure reproductive outcomes (e.g. pollen deposition or seed set) in this study, our method of following individual bees and recording the proportion of visits in each foraging bout to different plant species allows us to make inferences about whether plant species facilitated or competed with each other since visits to multiple conspecific individuals in a foraging bout are required for plant reproduction. In our system, the proportion of visits to *A. scaphoides* per foraging bout is not affected by the plant group in the same family, *Lupinus spp.* (Fabaceae), but is negatively affected by the genus *Castilleja* (Orobanchaceae; Table 1) and positively affected by itself. Thus, greater densities of *A. scaphoides* result in intra-specific pollination facilitation but *A. scaphoides* competes with *Castilleja spp.* for pollinators as *Castilleja spp.* density increases.

Flower morphology may play a role in determining whether the inter-specific relationships between *A. scaphoides*, *Lupinus spp.*, and *Castilleja spp.* are competitive or facilitative in this system. The flowers of both *A. scaphoides* and *Lupinus spp.* are complexly zygomorphic with reproductive parts that remain recessed in the folded lower petal until pressure from a visiting pollinator (or researcher) exposes them (Lesica 2012).

In contrast, the flowers of *Castilleja spp.* are simple tubes with protruding reproductive parts. Although beyond the scope of our study to test, the extra energy required to manipulate the flowers of the Fabaceae plants may instigate a switch to simpler flowers such as those of *Castilleja spp.* when they are available. Such a diet switch due to differences in handling time and energy cost at different flowers may be consistent with optimal foraging theory (Pyke 1978; Waddington & Holden 1979), although experimentation is required in this system to test this and elucidate the mechanism.

We found that the two most abundant bee groups, *Bombus* and *Anthophora/Eucera*, respond differently to the density of *A. scaphoides* as a proportion of the entire co-flowering plant community density. *Bombus* visited *A. scaphoides* more than expected based on the plant species' density across the entire range of *A. scaphoides* proportions in our study (Figure 2A). Our results indicate that as *A. scaphoides* density increases from zero, *Bombus* quickly increase their visits to *A. scaphoides* and use *A. scaphoides* nearly exclusively when it is common (Figures 1B & E; 2A). This rapid rise in use of *A. scaphoides* over the available co-flowering plant species. Pollen, nectar, and flower choice experiments could elucidate the proximate mechanisms that account for this preference.

Anthophora/Eucera visit *A. scaphoides* more than expected when it is rare, but in proportion to its relative density in the co-flowering plant community when it is common (Figure 2B). This result is consistent with pollen mixing behaviors, i.e. collection of pollen from different plant species to balance nutritional requirements (Williams &

Tepedino 2003) or mitigate exposure to harmful secondary compounds (Eckhardt et al. 2014). In the case of *Anthophora/Eucera*, if *A. scaphoides* pollen contains an essential nutrient missing from other components of their diet, we would expect to see these bees seeking out *A. scaphoides* when it is rare.

The pattern of *Anthophora/Eucera* response to *A. scaphoides* density is consistent with the general model prediction of Essenberg (2012), which stated that the effects of floral density of a focal plant species on bee visitation would be positive at low densities and weaker or negative at higher densities. However, her model was based on the assumption that all flowers in a patch are identical (i.e. the same species) and should be rebuilt for a co-flowering plant community.

As expected, the social bee group, *Bombus*, responded differently to varying plant densities in a multi-species community than the solitary bee group, *Anthophora/Eucera*. *Bombus* visited *A. scaphoides* more than predicted by the null hypothesis (Figure 1A & D) across all proportions of *A. scaphoides* in the flowering plant community, consistent with an overall preference for this plant species (Figure 2A). However, despite the overall preference for *A. scaphoides*, 24.6% of *Bombus* foraging bouts contained no visits to *A. scaphoides* (data not shown), suggesting possible individual specialization. Larger sample sizes are required to test this. In contrast, the response of the solitary group *Anthophora/Eucera* to *A. scaphoides* density varied across proportions of *A. scaphoides* in the flowering plant community, suggesting changes in individual bee behavior in response to resource availability. Because individual female solitary bees need to collect all of the resources to provision each nest cell, individual *Anthophora/Eucera* may need a mix of *A. scaphoides* pollen with pollen and/or nectar from another species to provision each larva (Williams & Tepedino 2003). Testing the mechanism behind this observed pattern is outside the scope of this study but could be done by analysis of provision balls in *Anthophora/Eucera* nest cells and observation of pollen- and nectar-collecting behaviors in the field.

Previous work in this system has shown that *A. scaphoides* is pollen-limited at low floral densities (Crone et al. 2009). Our results show that, for this rare plant, heterospecific floral density affects bee visitation, with implications for pollen limitation and reproductive success. Alonso et al. (2010) conducted a meta-analysis across plant taxa and geographic regions showing that pollen limitation of endemic (range-restricted) species increases with regional species richness, but their study did not include a mechanism to explain this pattern. Our results suggest such a mechanism in an endemic plant. We did not quantify pollination limitation of *A. scaphoides* in this paper, but two past experiments in this system have demonstrated pollen limitation at low floral densities (Crone and Lesica 2006; Crone et al. 2009). Our results here suggest that the mechanism for density-dependent pollen limitation is competition for pollinators with co-flowering, common plant species. Further research should measure reproductive success of *A. scaphoides* as a function of relative floral densities.

For other rare plant species, past studies have suggested that co-flowering plant species may compete for pollinators with a target species. Baskett et al. (2011) found that pollinator visitation to a federally threatened species, Pitcher's thistle (*Cirsium pitcheri*), increased in plots where two invasive species were removed, reaching the visitation levels of thistle plants in naturally uninvaded plots. If our goal were to enhance reproduction of *A. scaphoides* only, it might be useful to remove co-flowering plants from existing populations, or target sites with few other co-flowering plants for reintroductions. More generally, our results reinforce the general notion that ecological communities are highly connected, and that changes in community composition can have far-reaching effects on other species.



Figure 1. Hypothetical relationships between the proportion of visits per foraging bout to *A. scaphoides* and the proportion of *A. scaphoides* in the flowering plant community. **a-c**) The dashed gray line represents the logit one-to-one relationship between these variables. The solid black line shows the expectation of the logit proportion of visits per foraging bout of *A. scaphoides*. a) a one-to-one relationship and thus no bee response to floral density; b) consistent positive floral preference; and c) density-dependent preference. **d-f**)

The same relationships as a-c) mapped back from the logit-logit scale to the identity scale.



Figure 2. Plot of the logit of the proportion of visits to *A. scaphoides* per foraging bout as a function of the logit of the proportion of blooming *A. scaphoides* in the flowering plant community for a) the bee genus *Bombus*, and b) the bee group *Anthophora/Eucera*. The points show the raw logit proportions for each foraging bout (proportions of zero and one are plotted at logit(0.025) and logit(0.975), respectively). The solid black line shows the predicted logit proportion of visits to *A. scaphoides* from the GLM output with 95% confidence intervals (dotted black lines). The gray dashed line shows the one-to-one relationship between the proportion of *A. scaphoides* and the proportion of visits to *A. scaphoides* on the logit-logit scale.

Table 1. Degrees of freedom and parameters included in the best model of visitation to *A*. *scaphoides* as a function of the densities of different plant species, with associated chi-square values and p-values. F and p-values were obtained from an ANOVA table using the F test (see Methods).

	d.f.	Pollinator identity	Patch identity	A. scaphoides density
Best model	144	+	+	+
estimates				1.51 ± 0.7
F		9.94	5.15	6.39
p-value		< 0.0001	< 0.0001	0.01

Table 2. Parameter estimates with confidence intervals from the GLMs describing the relationship between the proportion of visits to *A. scaphoides* per bee foraging bout and the logit of the proportion of *A. scaphoides* out of the total flowering plant community for *Bombus* and *Anthophora/Eucera* considered separately. Estimates in **bold** lie outside of the confidence interval and are thus different from zero (for the intercept) or one (for the slope).

	Estimate	2.5%	97.5%
Bombus			
Intercept	1.279	0.683	2.022
Proportion of A. scaphoides	1.215	0.711	1.87
Anthophora/Eucera			
Intercept	0.045	-0.451	0.546
Proportion of A. scaphoides	0.533	0.181	0.917

AC 2015 25 5. 6.5 3.8 0.07 0.18 0.02 HNC 2015 22 6 4.5 4.9 0.04 0.10 $n'a$ RC 2015 7 7 9 0.8 0.04 n/a $n'a$ RC 2014 15 4 2 7.5 0.04 0.09 0.04 AC 2014 11 4 2 7.5 0.10 0.01 0.01 AC-1 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.02 $n'a$ $n'a$ HDC 2014 19 4 2 5.5 0.02 $n'a$ $n'a$ HNC 2014 19 4 2.5 7.6 0.02 n'	Site	Year	No. bees followed	No. sampling days	No. sampling hours	Bees/hour	A. scaphoides density	Lupinus spp. density	Castilleja spp. density	P. albertimus density	Proportion of A. scaphoides
HNC 2015 22 6 4.5 4.9 0.04 0.10 n/a RC 2015 7 7 9 0.8 0.04 n/a n/a RC 2014 15 4 2 7.5 0.04 n/a n/a AC 2014 11 4 2 5.5 0.010 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 6 0.02 n/a n/a HDC 2014 19 4 2.5 7.6 0.02 n/a n/a MC 2014 12 3 1.5 3.5 0.02 n/a SCG 2014 12 3 1.5 2 0.01 n/a n/a </td <td>AC</td> <td>2015</td> <td>25</td> <td>\$</td> <td>6.5</td> <td>3.8</td> <td>0.07</td> <td>0.18</td> <td>0.02</td> <td>n/a</td> <td>0.25</td>	AC	2015	25	\$	6.5	3.8	0.07	0.18	0.02	n/a	0.25
RC 2015 7 7 9 0.8 0.04 n/a n/a AC 2014 15 4 2 7.5 0.04 0.09 0.04 AC 2014 15 4 2 7.5 0.04 0.09 0.04 AC-1 2014 11 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 19 4 2 8 0.02 n/a n/a HDC 2014 19 4 2.55 7.6 0.12 0.02 n/a MC 2014 12 3 1.5 3.5 0.03 0.02 n/a SCG 2014 12 3 1.5 2 0.01 n/a	HNC	2015	22	9	4.5	4.9	0.04	0.10	n/a	0.06	0.20
AC 2014 15 4 2 7.5 0.04 0.09 0.04 AC-1 2014 11 4 2 5.5 0.10 0.01 0.01 BC 2014 11 4 2 5.5 0.10 0.01 0.01 BC 2014 12 4 2 5.5 0.10 0.01 0.01 BC 2014 16 4 2 8 0.09 0.01 0.01 HDC 2014 19 4 2 4.5 0.02 n/a n/a HNC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 12 3 1.5 3.5 0.03 0.02 n/a SCG 2014 3 3 1.5 2 0.01 n/a	RC	2015	7	7	6	0.8	0.04	n/a	n/a	0.38	0.09
AC-1 2014 11 4 2 5.5 0.10 0.01 M/a m/a <thm a<="" th=""> <thm a<="" th=""> <thm a<="" td="" th="" th<=""><td>AC</td><td>2014</td><td>15</td><td>4</td><td>6</td><td>7.5</td><td>0.04</td><td>0.09</td><td>0.04</td><td>n/a</td><td>0.24</td></thm></thm></thm>	AC	2014	15	4	6	7.5	0.04	0.09	0.04	n/a	0.24
BC 2014 12 4 2 6 0.06 n/a n/a CSC 2014 16 4 2 8 0.09 0.01 0.01 HDC 2014 16 4 2 8 0.09 0.01 0.01 HDC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	AC-1	2014	Ξ	4	6	5.5	0.10	0.01	0.01	n/a	0.86
CSC 2014 16 4 2 8 0.09 0.01 0.01 HDC 2014 9 4 2 4.5 0.02 n/a n/a HDC 2014 9 4 2.5 7.6 0.12 0.02 n/a HNC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 7 4 2.5 3.5 0.03 0.02 n/a RC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	BC	2014	12	4	5	9	0.06	n/a	n/a	0.06	0.48
HDC 2014 9 4 2 4.5 0.02 n/a n/a HNC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 7 4 2.5 7.6 0.12 0.02 n/a MC 2014 7 4 2 3.5 0.03 0.02 n/a RC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	CSC	2014	16	4	5	8	0.09	0.01	0.01	0.01	0.73
HNC 2014 19 4 2.5 7.6 0.12 0.02 n/a MC 2014 7 4 2 3.5 0.03 0.02 n/a RC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	HDC	2014	6	4	6	4.5	0.02	n/a	n/a	0.03	0.35
MC 2014 7 4 2 3.5 0.03 0.02 n/a RC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	HNC	2014	19	4	2.5	7.6	0.12	0.02	n/a	n/a	0.85
RC 2014 12 3 1.5 8 2.07 n/a n/a SCG 2014 3 3 1.5 2 0.01 n/a n/a	MC	2014	7	4	7	3.5	0.03	0.02	n/a	n/a	0.61
SCG 2014 3 3 1.5 2 0.01 n/a n/a	RC	2014	12	3	1.5	8	2.07	n/a	n/a	4.41	0.32
	SCG	2014	3	3	1.5	2	0.01	n/a	n/a	0.01	0.44

 Table S1. Summary data across all sites and years.

Supplementary tables and figures

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CHAPTER II. NATIVE BEES FORAGE OPTIMALLY IN A NATURAL PLANT COMMUNITY

Introduction

The reproduction of most plant species relies on pollination by animal pollinators (Ollerton et al. 2011). Animal-mediated plant reproduction is contingent on sequential (or nearly so) visits by a pollinator to multiple individuals of the same plant species, because pollen collected at one plant individual is generally deposited within a very small number of subsequent plant visits (Richards et al. 2009). Pollination occurs as animal pollinators forage for plant resources for their own nutrition. Optimally foraging animals maximize their energy gained per unit time or effort (Schoener 1971; Pyke 1984). In the case of pollinators, travel between flowers is a key component of the time or effort denominator. Thus, the spatial arrangement of flowering plants should play an important role in determining bee foraging movements and plant reproduction.

Bees follow the predictions of optimal foraging theory by choosing the shortest routes between plants in most scenarios (Morris 1993; Cresswell et al. 1995; Lihoreau et al. 2011). Bees compromise between travel distance and floral reward quality, traveling greater distances for higher quality rewards (Lihoreau et al. 2011). In all cases, bees exhibit plastic foraging choice, optimizing the distance traveled depending on changes in the experimental array or reward value of flowers (Lihoreau et al. 2010; Lihoreau at el. 2011; Lihoreau et al. 2012). A bee flying through an array of plants and making brief floral visits should be able to keep track of the direction from which it arrives at flowers. Its movements should have some directional persistence, i.e. its steps should continue in the same general direction (Turchin 2015). Individual bees are known to move in a preferred direction of travel (Morris 1993; Cresswell et al. 1995), though they will deviate from their preferred direction when plants are spaced close together (Morris 1993). When plants are clumped, bees sometimes bypass the closest plant (Heinrich 1979; Cresswell 1997), presumably because all of the travel distances are so small that the tradeoffs in travel costs are minimal.

Our knowledge of the distances and directions bees travel between plants comes almost exclusively from experiments in linear arrays of single plant species, or indoors with artificial flowers. These experiments use a few well-studied bee species: *Apis mellifera* and species in the genus *Bombus*. These bees are all large-bodied with social life histories, and show little variation among species in their response to the spatial arrangement of plants (Cresswell et al. 1995). In nature, plants occur in diverse communities where individuals are arranged without pattern, and hundreds of bee species can occur at a single location. Species of bees may respond differently to the spatial arrangement of plants for two reasons. First, foraging range is strongly correlated with bee body size (Greenleaf et al. 2007). Second, the social versus solitary life history strategy influences bee foraging behavior. Workers of social bee colonies often specialize individually on particular resources, e.g. a single plant species, genus, or family, or a resource type such as pollen or nectar (Heinrich 1976; Williams and Tepedino 2003). Among solitary bee species, individual females must obtain all resources necessary for provisioning larvae, both pollen and nectar, by themselves. Polylectic solitary bees, those that feed on multiple plant species, may thus be more likely to visit multiple plant species within a foraging path to collect a diversity of resources (Tepedino and Parker 1982). As a result of these life history and body size differences, social, large-bodied bees such as those in the genus *Bombus* may travel greater distances to reach their focal plants, whereas solitary, smaller bees may travel shorter distances on average as they collect a variety of resources by moving among closely-spaced plants of multiple species.

We use a natural, unmanipulated field system to quantify the effect of the spatial arrangement of plant resources on bee foraging choices. Specifically, we address three research questions: 1) How do the distance and direction of potential movements between individual plants affect bee foraging choice? 2) How do individual plant characteristics, e.g. species or genus identity, modify the effects of spatial arrangement on bee foraging choice? 3) Do bee responses to spatial arrangement and plant identity differ between major bee groups?

Methods

Study area

Our field system is located in the Lemhi River Valley of Idaho and Beaverhead River Valley of adjacent southwestern Montana. The valley floor elevations range from 1500 m

to 2000 m and are predominantly vegetated by semi-arid sagebrush steppe (Lesica and Cooper 1997). This ecosystem is dominated by wind-pollinated sagebrush (Artemisia *spp.* Linnaeus) with low densities of insect-pollinated flowering plants. Among these insect-pollinated plants is yellow-flowered Astragalus scaphoides (Jones; Bitterroot Milkvetch), a regionally endemic perennial herb that grows in small, spatially discrete patches, generally less than one hectare in extent. Within patches, A. scaphoides is locally abundant, but patches are sparsely distributed. Within each patch, A. scaphoides blooms synchronously in May/June approximately every other year. The mechanisms driving this biennial bloom pattern reflect the interplay between resource costs of reproduction, temporal precipitation patterns, and pollen limitation (Crone et al. 2009; Tenhumberg et al. 2018). Four syntopic bee-attractive plant species or species-groups have overlapping flowering periods with A. scaphoides: Castilleja spp. (Mutis; Orobanchaceae), Lupinus spp. (Linnaeus; Fabaceae), Penstemon albertinus (Greene; Plantaginaceae), and purpleflowered Astragalus spp. Due to the low herbaceous plant densities and the low plant species richness, this simple study system allows easy observation of bee behavior in a natural, multi-species plant community. Moreover, it is possible to follow individual bees in this system because the encounter rate (bees seen per unit time) is low.

Data collection

We collected data on only the most common bees observed, which are in the social genus *Bombus* and the genera *Anthophora Eucera*, which were indistinguishable on the wing in thi study. Voucher specimens collected in 2013 include five species of *Bombus*, one species of *Anthophora*, and two species of *Eucera* (Bruninga-Socolar et al. 2016). All

eight of these bee species are dietary generalists, using plants from 4-33 plant families (*A. urbana*) (Koch et al. 2011; Ascher and Pickering 2015).

We selected three patches with large populations of *A. scaphoides* based on previous work in the system (Crone & Lesica 2006; Bruninga-Socolar et al. 2016). All patches constitute spatially distinct clusters of *A. scaphoides* with at least one of the following co-flowering, bee-attractive plants: *Castilleja spp., Lupinus spp., P. albertinus*, and purple-flowered *Astragalus spp*. We refer to these five groups collectively as our focal species. We defined the patch boundaries to include the contiguous area with at least one individual of one focal plant species per square-meter. Small patches of focal plant species that were not contiguous with the main patch but were within 10 m were included (Figure 1). We collected data in all patches in May-June 2015 and 2016 on 2-6 days within each year.

At each patch, we mapped the location and species identity of each focal plant in bloom. We updated the map within three days of each bee observation. A single observer (BBS) collected all bee observation data during weather conducive to bee activity: sunny, partly cloudy, or bright overcast with wind $< 7 \text{ m s}^{-1}$ between the hours of 10:00 and 18:00 (Winfree et al. 2007). We used pin flags to delineate a grid of 1x1 meter squares encompassing each *A. scaphoides* patch. On each sampling day, we began observations at a haphazardly chosen location within the patch and walked along the established grid lines to systematize the search for bees. When a bee was spotted, we followed the bee's movements through the patch and marked each plant visited. Each bee was followed until it either left the patch or switched to a non-foraging behavior. Less than five percent of bees were lost prior to one of these endpoints. Immediately after each observation, we revisited the marked plants in order and referenced them against the site-map (Figure 1).

Analyses

We define the straight-line segments linking consecutive individual plants visited by each bee as steps in the bee foraging path (Turchin 2015). Thus, each step represents the selection, or use, of an individual plant from the total pool of flowering plants available at a site. Treating individual plants as habitat units selectable by bees, we modeled the probability of selection as a function of characteristics of these habitat units using discrete choice models. Discrete choice models use resource selection functions (RSFs), which give the relative probability of a given step being chosen given the population of available steps to choose from and covariate values for each possible step (Manly et al. 2002; Fortin et al. 2005). Each observed selected habitat unit is matched with a set of available habitat units within a predefined spatial and/or temporal range (Avgar et al. 2016; Arthur et al. 1996). The relative probability of a step being chosen is modeled by a linear combination of environmental variables ($x_{ij1}, x_{ij2}, ..., x_{ijp}$) that describe the resource units available to the animals (Manly et al. 2002; reviewed by Thurfjell et al. 2014):

$$w(x_{ij}) = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \dots + \beta_p x_{ijp})$$
Equation 1

When the population of available steps is exhaustively sampled, the probability p_{ij} that the jth resource unit is selected at the ith step is given by the RSF for the jth resource unit normalized by the sum of the RSFs for all resource units (Manly et al. 2002).

$$p_{ij} = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \dots + \beta_p x_{ijp}) / \sum_{k=1}^{n_i} \exp(\beta_1 x_{ik1} + \beta_2 x_{ik2} + \dots + \beta_p x_{ikp})$$

Equation 2

In standard applications of discrete choice models for habitat selection analyses, the available set of habitat units is generated randomly from the observed data (Avgar et al. 2016). In our analysis, the set of habitat units available to each bee at each step is directly measurable from our field data because habitat units are discrete plant individuals within a spatially limited plant community that is exhaustively sampled.

We characterized each step (the observed step and all available steps matched to each observed step) with two movement variables: step-length and cosine of the turning angle. The turning angle is the angular difference between the heading of the previous step and the heading of the next step. Taking the cosine ensures that angle values with the same magnitude but opposite signs have the same value and also that angles offset by 360 degrees have the same value (Turchin 2015; Figure 2). Because the turning angle can only be calculated after the first step, our analysis uses only the second through last steps of each foraging path.

We also characterized each step with four environmental covariates that characterize each plant resource: the identity of the selected and available plants, the interaction between plant identity and step length, the interaction between plant identity and the proportional abundance of plants of that type, and a sequentiality parameter. The sequentiality parameter describes whether two consecutive steps in a foraging path are more likely to visit the same plant type than the remaining covariates suggest. Thus, sequentiality is a binary covariate that takes a value of 1 when the selected plant in a step is the same identity as the plant selected in the previous step, and a value of 0 when the selected plant is a different identity than the plant selected in the previous step. The sequentiality parameter is best suited to capture foraging dynamics where the identity of the current plant influences the identity of the next plant visited. However, in our model this parameter also subsumes variation in the overall preferences of bees observed in different foraging bouts (this variation might exist among bee species within our identification groups, individuals within species, or even bouts within individuals; see Chapter 3). We are unaware of widely available implementations of RSF models that permit fitting random slopes, and even the simplest models that include a fixed interaction between foraging bout and plant ID failed to converge. Thus, the sequentiality parameter in our models is (at least in part) a computational trick to allow for bout-specific variation in preference, but it necessarily confounds this variation with any tendency that might exist for the plant identity of one step to exert causal influence on the plant identity of the next step. All covariates were included in a global model for the two data sets, one containing observations of bees in the genus Bombus and one containing observations of bees in the

combined genera *Anthophora* and *Eucera*. The global models were fit using the clogit() function in the package 'survival' (Therneau 2015).

We fit all nested models of the global model for each bee group and computed the Akaike Information Criterion (AIC) for each model using the dredge() function in the R package MuMIn (Bartoń 2017). All top-performing models contained distance, the cosine of the turning angle, and plant identity, so we interpret these parameters most heavily using model averaged coefficients generated using the mod.avg() function in the R package MuMIn. Plant identity is missing from only one of the top-performing models, which performs worse than the best model by 4.5 AICc units. The model averaged coefficients determine an RSF for each plant type. Using each RSF as the numerator in Equation 2, we calculated p_{ij}, or the relative probability of the jth resource unit of that plant type being selected out of the sum of the RSFs of all available plant types. Because we conceptualize environmental covariates as modifiers of an energy- or time-efficient foraging strategy, we graphically present the probabilities predicted by the RSFs as a function of the distances between plants we observed in the field. We used these RSFs to calculate the relative probability of bees in each group visiting each plant type.

All analyses were conducted in R version 3.4.2 (R Core Team 2017).

Results

All bees in our analysis responded negatively to distance and positively to the cosine of the turning angle in all top models (Table 1A, Table 2A). Thus, bees of both groups tend to select nearby plants in their continued direction of travel (Figure 2). *Anthophora/Eucera* respond more strongly to distance ($\beta = -0.55$; Table 1B) than *Bombus* ($\beta = -0.3$; Table 2B).

Plant identity was included in all but one of the top models for all bees (Table 1A; Table 2A; Figure S1). The model averaged coefficients for both bee groups show a different RSF for each plant type (the numerator in Equation 2; Table 1B, Table 2B), suggesting that plant identity plays an important role in step selection by modifying bees' response to other parameters, such as distance (Figure 3). Bees in each group travel farther for some plant types than for others (Figure 3; Figure S1). Based on the plant type-specific RSFs, *Anthophora/Eucera* have the highest relative probability of selecting *P. albertinus* plants, followed by the purple-flowered *Astragalus sp.* (Table 3). *Bombus* have the highest relative probability of selecting selections (Table 3). Sequentiality, i.e. visiting two plants of the same type in consecutive steps, is included in all top models for *Bombus* but only in three of the top five models for *Anthophora/Eucera* (Table 1A; Table 2A).

Proportional abundance of plant types was included in three of the top five models for *Anthophora/Eucera* and two of the top four models for *Bombus* (Table 1A; Table 2A). *Anthophora/Eucera* have an overall positive relationship with proportional plant

abundances, while *Bombus* have an overall negative relationship with proportional plant abundances (Table 1B; Table 2B).

Discussion

As expected from optimal foraging theory, all bees in our study minimize the distance traveled between plants and exhibit directional persistence between steps in foraging paths (Table 1; Table 2). The relationship between step selection and distance is more strongly negative for solitary bees in the genera *Anthophora* and *Eucera*, perhaps because individuals are less likely to specialize on a particular plant type within foraging bouts, which may require moving greater distances to find more individuals of that plant type. Based on body size alone, we expect *Anthophora/Eucera* to have a more negative relationship with distance than the larger-bodied *Bombus*. Future work might consider the "clumpedness" of plant types within patches of flowering plants (Figure 1). We predict that *Anthophora/Eucera* (or other dietary-generalist solitary bee groups) would be less likely than predicted by their relationship with distance to stay within a single-species clump of a bee-attractive plant than *Bombus* individuals, which may specialize on that resource.

Plant identity is also an important covariate in bee step selection, appearing in the topperforming models for both bee groups (Table 1A; Table 2A). Bees in our models have strong preferences for some plant types. *Anthophora/Eucera* prefer *P. albertinus*, followed by the purple-flowered *Astragalus spp.* (Table 3). *Bombus* prefer *A. scaphoides*, followed by *P. albertinus* (Table 3).

Sequentiality occurs as a positive covariate in the four top-performing models for *Bombus*, and in the two top-performing models for *Anthophora/Eucera*. For both groups, the positive sequentiality estimate indicates a tendency for bees to select plants that share the same identity as the plant visited in the previous step. We are unable to disentangle whether this tendency is due to variation in bee preference (which could occur at any level from the level of the foraging path to be species) or due to constancy, where we define constancy simply as a causal link between the identities of the plants visited in sequential steps (Waser 1986). Interestingly, the estimate for sequentiality is the same for both bee groups: 1.177 for Anthophora/Eucera (Table 1B) and 1.186 for Bombus (Table 2B). Both bee groups have a similar increased tendency to visit the same plant species in sequence than the remaining covariates in the model suggest. This result is consistent with the literature that documents constancy in honeybees (Apis mellifera) and bumblebees (*Bombus*) (cite). We add to this literature by modeling sequentiality in a solitary bee group, with the caveat that our sequentiality parameter is unable to differentiate between constancy *sensu stricto* and variation in bee preference among foraging paths.

Anthophora/Eucera and *Bombus* responded differently to the interaction between plant identity and proportional abundance of each plant type, though for each bee group this covariate is not consistently in the top-performing models (Table 1A; Table 2A).

Anthophora/Eucera responded positively to this covariate, while *Bombus* responded negatively. A positive response captures either of two possible, non-exclusive patterns: 1) Non-specialized individual bees visit individual plants of types with high abundance with greater probability than the other covariates of those plants would suggest, consistent with prey-switching behavior (Murdoch 1969), and 2) Individual bees specializing on a plant type are more likely to visit individual plants of that type when abundant than expected due to an aggregative response. We hypothesize that the first pattern is more likely for *Anthophora/Eucera* because of their solitary life history.

The negative response of *Bombus* to the interaction between plant identity and proportional abundance of each plant type suggests that, conditioned on the remaining covariates, bees are less likely to visit individual plants that belong to a type that is locally abundant. This negative response is likely driven by *A. scaphoides* in particular, given that 65 percent of all *Bombus* visits in our dataset are to that species (Table 3). The negative interaction term suggests that *Bombus* are visiting *A. scaphoides* more than expected when it is rare. This result is at first glance surprising considering earlier work that showed an aggregative response of *Bombus* to *A. scaphoides* density, where focal plant individuals received more visits from *Bombus* with increasing *A. scaphoides* density (Crone 2013). In our study, the number of *Bombus* individuals may indeed have increased where and when *A. scaphoides* was highly abundant. However, individual *Bombus* did not increase the proportion of their visits within foraging paths to *A. scaphoides* as much as would be predicted by the other covariates in our models. In particular, it is worth noting that the aggregative response of *Bombus* to *Bombus* to high *A*.

scaphoides abundance does not appear to result in an aggregation of individuals or species with stronger preference for *A. scaphoides*. If that were the case, we would see a positive relationship between the probability of plant selection and the interaction between plant identity and plant proportional abundance.



Figure 1 Map of plant locations by species at the Agency Creek site in A) 2015 and B) 2016. The maps show the all plants that flowered in each season.



Figure 2. Diagram showing two possible bee step sequences and the turning angle between the steps in each sequence. The cosine of the turning angle is used in movement analyses because the cosine of 90° and the cosine of -90° are equal.

Table 1. A) The top discrete choice models within five AICc units of the top model for the bee group *Anthophora/Eucera*. + indicates that the factor covariate, "Plant ID", is included in the model. B) Model averaged estimates calculated from the models in Table 1A.

Model	Plant ID	Distance	Cos(turn)	Sequentiality	Plant ID*Proportional abundance	Plant ID*Distance	ΔAICc
1	+	-0.546	1.052	1.169			0
2	+	-0.54 <mark>6</mark>	1.061	1.108	2.74		1.45
3	+	-0.584	1.032				3.31
4	+	-0.582	1.058		3.277		3.85
5		-0.497	0.986	1.58	-3.585		4.55

B

A

	Plant ID	Distance	Cos(turn)	Sequentiality	Plant ID*Proportional abundance
A. scaphoides		-0.55	1.049	1.177	1.96
Castilleja	1.058	-0.55	1.049	1.177	1.96
Lupinus	-1.424	-0.55	1.049	1.177	1.96
P. albertinus	2.504	-0.55	1.049	1.177	1.96
purple Astragalus spp.	2.235	-0.55	1.049	1.177	1.96

Table 2. A) The top discrete choice models within five AICc units of the top model for the bee genus *Bombus*. + indicates that the factor covariates, "Plant ID" and the interaction between Plant ID and Distance, are included in the model. B) Model averaged estimates calculated from the models in Table 2A.

Model	Plant ID	Distance	Cos(turn)	Sequentiality	Plant ID*proportional abundance	Plant ID*Distance	AAICc
1	+	-0.316	0.939	1.167			0
2	.+.	-0.273	0.919	1.215		+	1.04
3	+	-0.316	0.939	1.17	-0.133		1.99
4	+	-0.272	0.916	1.222	-0.624	+	2.89

Α

B

	Plant ID	Distance	Cos(turn)	Sequentiality	Plant ID*proportional abundance	Plant ID*Distance
Astragalus		-0.3	0.931	1.186	-0.325	
Castilleja	-0.963	-0.3	0.931	1.186	-0.325	-0.102
Lupinus	-2.053	-0.3	0.931	1.186	-0.325	-0.389
Penstemon	-0.14	-0.3	0.931	1.186	-0.325	-0.142

Table 3. Relative probability of selection of each plant type by *Anthophora/Eucera* and *Bombus*. We calculated relative probability from Equation 2 using RSFs for each plant type. These values reflect the relationship between probability of selection and the range of distances in between plants in our data; all covariates other than distance and plant identity were held at zero.

Plant species/genus	Anthophora/Eucera	Bombus	
A. scaphoides	0.039	0.5	
Castilleja	0.112	0.15	
Lupinus	0.009	0.033	
P. albertinus	0.476	0.316	
purple Astragalus spp.	0.364		



Figure 3. Model averaged resource selection functions for A) the bee group *Anthophora/Eucera* and B) the bee genus *Bombus*.



Figure S1. Resource selection functions from each of the top-performing models for A) *Anthophora/Eucera* (Table 1A) and B) *Bombus* (Table 2A).

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CHAPTER III. POLLINATOR-MEDIATED PLANT COEXISTENCE REQUIRES HIGH LEVELS OF POLLINATOR SPECIALIZATION

Abstract

The role of mutualism in promoting species coexistence is relatively unexplored compared to that of competition or predation. In pollen-limited plant communities, the foraging behavior of pollinators might mediate coexistence and competitive exclusion by determining which plants receive conspecific pollen. A key question is whether realistic pollinator foraging behavior promotes coexistence or exclusion. We use a simulation model to understand how pollinator foraging behavior impacts the coexistence dynamics of pollen-limited plants. To determine whether pollinators are likely to provide a biologically important coexistence mechanism in nature, we compare our results to bee foraging data from the literature and from a novel experimental analysis. Model results indicate that strong specialization at the level of individual foraging bouts is required to promote coexistence. However, few empirical studies have robustly quantified withinbout specialization. Species-level data suggest that foraging behavior is sufficient to permit pollinator-mediated coexistence in species-poor plant communities and possibly in diverse communities where congeneric plants co-occur. Our experiments using bumblebees show that individual-level specialization does exist, but not at levels sufficient to substantially impact coexistence dynamics. The literature on specialization within natural foraging bouts suffers from key limitations, but overall suggests that pollinator-mediated coexistence should be rare in diverse plant communities.

Introduction

Competition and drift are expected to decrease community diversity in the absence of mechanisms promoting species coexistence. Modern coexistence theory focuses primarily on mechanisms that reduce resource-mediated interspecific competition (Chesson 2000, Adler et al. 2010, Chesson & Kuang 2010), mechanisms that reduce predator-mediated interspecific apparent competition (Holt 1977, Socolar & Washburne 2015), the distance-dependent action of Janzen-Connell agents (Janzen 1970, Connell 1971, Terborgh 2012), and the interactions between these processes (Paine 1966, Chesson & Kuang 2008). In contrast, we know relatively little about the role of positive interactions (i.e. mutualisms) in supporting species coexistence (Stachowicz 2001, Bruno et al. 2003). Mutualistic interactions are likely to influence coexistence in fundamentally different ways than consumer-resource interactions because the long-term effect of mutualistic interactions is the increase of resource pools (rather than their decrease), leading to runaway mutualism in which species grow exponentially without bounds in models without additional resource constraints (Gause & Witt 1935, May 1976). Thus, mutualism should lead to positive, not negative, frequency dependence and act against coexistence, as seen in the classic Lotka-Volterra model (Gause & Witt 1935). Yet, mutualisms are critically important to the population dynamics of a wide variety of taxa; for example, 87% of plants globally depend on animal pollinators for reproduction (Ollerton et al. 2011), and their pollinators universally depend on plant resources for growth and reproduction.

Runaway plant-pollinator mutualisms are kept in check by other limiting resources, such as plant nutrients or pollinator nest sites. If resources such as nutrients become limiting for the plants, then plant resources will eventually become limiting for the pollinators, leading to a classic consumer-resource system with donor control (pollinators deplete floral resources in the short term, but do not affect the total availability of the resource over the long term). However, if resources such as nest sites become limiting for the pollinators, then plant coexistence dynamics might depend substantially on the dynamics of plant competition for pollinators, and therefore on pollinator foraging behavior. In reality, the distinction between resource limitation versus pollen limitation is not blackand-white, because resource availability might affect a plant's allocation of resources towards pollinator attraction (Haig & Westoby 1988). Strict pollen limitation remains possible if resources are abundant but pollinators are limited by nest sites or other nonfloral resources. Studies of pollination services routinely assume that bees are not limited by floral resources (implicit in the assumption of no density compensation between pollinator species; Winfree & Kremen 2009). Even in the absence of nest-site limitation, pollen limitation should be possible in species-rich plant communities if pollinators fail to deliver sequential (or nearly sequential) visits to any particular species of plant. Numerous empirical studies (reviewed by Knight et al. 2005) have found evidence for pollen limitation beyond what is predicted by the Haig & Westoby equilibrium, although publication bias and other issues make it impossible to accurately estimate the true prevalence of pollen limitation (Knight et al. 2006).

Two properties of pollinator biology pose challenges to plant species coexistence. First, pollen is transferred quickly, so successful plant reproduction depends on sequential or nearly sequential visits to conspecific plants (Karron et al. 2009, Richards et al. 2009), i.e. flower constancy (Waser 1986). The sequence of plants visited will depend on the spatial arrangement of plants and pollinator preferences for the plant species in the local environment. In the context of dietary generalist pollinators, the frequency of pollination events to a particular plant species does not scale linearly with plant relative abundance (which would yield neutral dynamics). Instead, if pollinator visits are independent, then the probability that a pair of visits will be sequential to the same plant species is the square of the plant species' relative abundance. Thus, pollination by generalist pollinators should tend to exclude rare plants from the community via a positive feedback loop.

Second, foraging pollinators (i.e. bees) have a tendency to preferentially visit common plants (Levin & Anderson 1970, Augspurger 1980, Podolsky 1992, Kunin 1997a, Moeller 2004, Ghazoul 2006, Dauber et al. 2010, Bruninga-Socolar et al. 2016). This tendency coupled with the dependence of plant reproduction on sequential visits by bees suggests that successful pollination of rare plants should be infrequent, and pollen limitation should exclude rare plants from the community (Ferrière et al. 2004). Yet diverse communities of bee-pollinated plants are ubiquitous in nature, and some of these communities are pollen-limited at least some of the time (Ashman et al. 2004, Knight et al. 2005). How do rare plants find interaction partners and persist in such communities? Recent studies investigating pollinator-mediated plant coexistence do so in the context of strong effects of plant competition for resources other than pollinators (e.g. Benadi et al. 2012, Benadi et al. 2013, Valdovinos et al. 2013, Song & Feldman 2014). The fundamental question of how plants coexist when they are pollen-limited remains unanswered. Since successful plant reproduction requires sequential bee visits to conspecific plant individuals, one possibility to explain rare plant persistence is that the species-level foraging preferences of pollinators successfully deliver sequential visits to rare plant species in the community. Despite the observation that foraging pollinators generally prefer common plants, a segment of the pollinator community might nevertheless prefer rare plants enough to reliably pollinate them (Waser 1978, Goulson 1994, Kunin & Iwasa 1996, Benadi et al. 2012, Bruninga-Socolar et al. 2016).

For generalist pollinators, sequential visits to rare plant species may result from variation between conspecific individuals in short-term foraging behavior. Existing models of pollinator visitation to plants assume that all pollinators or all pollinators of the same species forage identically (e.g. Levin & Anderson 1970, Benadi et al. 2012, Essenberg 2012, Benadi et al. 2013). Yet Heinrich (1976) qualitatively demonstrated that individuallevel specialization exists in bumblebees. Individual-level variation in foraging behavior should be especially important for species coexistence when a small number of species dominates the pollinator community (i.e. the species abundance distribution ubiquitous in ecological communities; McGill et al. 2007, Song & Feldman 2014). However, to our knowledge, no studies have rigorously quantified variation among individual bees at the level of their foraging paths, where sequential visits to conspecific individuals of a rare plant species may occur, and few studies have investigated foraging behavior of individual pollinators as a mechanism for plant coexistence. Valdovinos et al. (2013) use simulations of an empirical plant-pollinator network to show that seasonal variation in foraging behavior among individual pollinators in response to the available resource environment (adaptive foraging) reduces extinctions in the network. Song & Feldman (2014) use coupled plant-pollinator population dynamics models to show that adaptive foraging promotes plant species coexistence. However, both studies show that plant competition for resources other than pollinators has a stronger effect on plant coexistence than competition for pollinators. Therefore, these results might fail to capture the dynamics of pollen-limited systems.

In this study, we model the effect of bee foraging behavior on plant coexistence in pollenlimited plant communities. We show that pollinator-mediated plant coexistence requires high levels of foraging specialization within foraging paths. We review the sparse existing literature on the degree of individual specialization in nature, and we present novel data investigating the possibility that individual-level foraging preferences across social bumblebee workers might help to maintain plant coexistence. We find that current understanding of pollinator foraging preference is incomplete, but available data suggests that typical bee preferences are sufficient to support pollinator-mediated coexistence in species-poor plant communities, particularly when each plant family or genus is represented by only a single species. However, our limited understanding of pollinator behavior suggests that realistic levels of pollinator specialization might not be sufficient to drive coexistence in species-rich plant communities. Thus, we suggest that pollination may be an important and overlooked coexistence mechanism in species-poor plant communities. We also formulate testable empirical predictions to be evaluated by future work:

- Where they exist, pollen-limited plant communities should interact with highly specialized pollinator communities (where specialization is quantifiable either at the level of the pollinator species, the individual pollinator, or the individual foraging bout).
- 2. Given that pollinator foraging is likely to lead to competitive exclusion in speciesrich pollen-limited communities, pollen limitation itself should be rare in speciesrich plant communities. We predict that pollen limitation in species-rich plant communities should coincide with ameliorating factors such as spatial or temporal clumping of conspecific flowering plants.

Methods

Simulation model

We wish to investigate the dynamics of a plant-pollinator community with two pollenlimited annual plant species that compete for shared pollinators. To do so, we use a Markov chain difference equation model to simulate the population size of both plant species through time under different bee foraging scenarios. This difference equation framework is well-suited to model a plant-pollinator system of annual plants and insects with annual life cycles.

Our modeling framework simulates the number of plants of each species in each successive generation based on the number of successful pollen transfers and the probability that a fertilized ovule recruits to the adult stage in the next generation. For this study, we treat the latter probability as fixed because we are most interested in exploring parameters related to bee foraging. The model allows the number of successful pollen transfers to depend on bee foraging preferences, plant abundances, and the decay of pollen transfer after bees visit intervening flowers (Richards et al. 2009). We assume that pollinator populations are not limited by plant populations (e.g. they are nest site limited), such that the number of flower visits per year is constant. This assumption allows us to model the effects of a particular pollination regime on plant coexistence without modeling changes in the bee community over time. The extent to which bees are limited by non-food resources such as nest sites is understudied (Roulston & Goodell 2011). However, a few studies document a positive relationship between nest site availability and bee abundance and species richness across nesting types (Potts et al.

2003, Potts et al. 2005) and demonstrate that neither floral nor nesting variables alone can explain bee population and community dynamics (Potts et al. 2005). For analytical simplicity and inferential clarity about pollinator-mediated plant coexistence, we conceptualize our system as a nest site-limited bee community. The model does not include a spatial component or other mechanisms of plant coexistence, such as competition for non-pollinator resources.

We further assume that the identity of the plant in the ith visit delivered by the jth bee is independent of the plant identity on the previous visit (conditioned on the bee's foraging preferences). Thus, our simulation computes the probability that any single bee visit will deliver conspecific pollen, samples binomially from this probability and the total number of visits delivered by a given bee, and then sums across all bees in the community. Our full model is given by

$$P_{1_{t+1}} \sim \text{binomial}(S_{1_t}, \rho_1)$$

$$S_{1_t} = \sum_i \sum_j V_{1_{ij}}$$

$$V_{1_{ij}} \sim \text{binomial}\left(\nu_{ij}, \sum_k \tau_k \left(\frac{(\alpha_{ij}P_{1_t})^\beta}{(\alpha_{ij}P_{1_t})^\beta + P_{2_t}^\beta}\right)^2\right)$$

$$P_{2_{t+1}} \sim \text{binomial}(S_{2_t}, \rho_2)$$

$$S_{2_t} = \sum_i \sum_j (V_{2_{ij}})$$

$$V_{2_{ij}} \sim \text{binomial}\left(\nu_{ij}, \sum_k \tau_k \left(1 - \frac{(\alpha_{ij}P_{1_t})^\beta}{(\alpha_{ij}P_{1_t})^\beta + P_{2_t}^\beta}\right)^2\right)$$

Equations 1-6

where P_{nt} is the population size of plant species n in year t, S_{nt} is the number of successful pollen transfers to plant species n in year t, and ρ_n is the probability (treated as constant) that a fertilized ovule of plant species n recruits to an adult in the next generation. S_{nt} is obtained by summing V_n , the per-bee number of successful pollen transfers to plant n, across all bee individuals j of all bee species i. To calculate V_{nij} for a given bee individual, we draw from a binomial distribution with number of trials v_{ii} equal to the total number of floral visits performed by the individual bee (treated as constant). The per-visit probability of successful pollen transfer is equal to the probability that sequential visits result in conspecific pollen transfer τ_k multiplied by the probability that visits are sequential. Note that τ_k is a vector whose first value is the probability of pollen transfer from immediately sequential visits, the second value is the probability of pollen transfer given one intervening visit to another plant species, and so on. We assume that a visit that simultaneously delivers pollen from multiple previous visits to conspecific plants results in more total reproduction than a bee visit delivering pollen from fewer conspecifics. The probability of sequential visits to plant n is a function of the foraging preference α_{ij} of the individual bee (constrained to take values greater than 0), the density of the plant species in year t, and a parameter β that controls whether the bee preferentially forages on common ($\beta > 1$) or rare ($\beta < 1$) plants. α_{ij} and β thus modify the true density of each plant species to an effective density determined by the bee's species- and individual-level preferences, and the probability that a given visit-pair involves plant species n on both visits is the square of this effective density.

Plant species 1 is preferred when α_{ij} is greater than 1, and plant species 2 is preferred when α_{ij} is less than 1. Each bee's α is sampled from a log-normal distribution specified by its species mean preference and standard deviation, which represents the intraspecific variation in preference around the mean:

Equation 7

where μ_i is the mean foraging preference of the ith bee species and σ_i is the standard deviation of the ith bee species. The mean and standard deviation are chosen *a priori* to span a wide range of possible values (Supplementary material Appendix B).

All simulations were run in program R (R Core Team 2017) for 100 plant generations. We ran simulations to explore the range of parameter space of the bee species means, standard deviations, and preference for rarity to determine how bee preferences stabilize or destabilize plant coexistence (Table 1). Parameters unrelated to bee foraging were held constant in most simulations (Table 2). We set the initial plant populations to very large values and allowed plant populations to equilibrate in the first time-step. In most simulations we initialized the plants at equal abundance (500,000 individuals each). We also explicitly investigated the ability of the pollinator community to support a rare plant species by systematically varying the initial abundance ratio of the two plants. The plant populations shared a constant population of 200 pollinators that each visited 25,000 plants per generation (Table 2; Supplementary material Appendix A). The number of plants visited per bee per generation was obtained from the literature (Ribbands 1949, Cane 1997). To determine whether our model results are sensitive to the values of bee abundance, pollen transfer probabilities, the probability of a fertilized ovule becoming an adult plant, or the number of visits per bee lifetime, we ran the entire simulation twelve additional times, varying one of these parameters in each model run (Table 2;

Supplementary material Appendix B). These sensitivity analyses do not qualitatively change our results (Supplementary material Appendix A, Figures A2-A13). We ran the model two additional times to determine the exact values of bee species mean preference required for coexistence for two specific cases, as described in the results: 1) where the plant species begin the simulation in equal abundance, and there is no intraspecific variation or preference for rare plants in bees, and 2) where the plant species begin the simulation abundance, and there is no intraspecific variation or preference for rare plants in bees, and 2) where the plant species begin the simulation or preference for rare plants in bees, and 2) where the plant species begin the simulation or preference for rare plants in bees, and 2) where the plant species begin the simulation or preference for rare plants in bees, and 2) where the plant species begin the simulation or preference for rare plants in bees, and 2) where the plant species begin the simulation with unequal abundance, and there is no intraspecific variation or preference for rare plants in bees (Supplementary material Appendix B).

Coexistence in our simulation context

Traditionally, ecological coexistence is analyzed based on the invasibility criterion: can a population increase when rare (Chesson 2000)? In pollinator-mediated coexistence, this criterion is difficult to meet because sequential visitation rates to a rare plant species should approach zero in the limit of low relative abundance. Instead, we hypothesized that coexistence will often be stable within a limited basin of attraction at intermediate relative abundance. Therefore, we measure the strength of coexistence as the fraction of communities with both plant species persisting after 100 generations. For each combination of parameter values, we run 100 simulations to calculate this fraction. Thus, our criterion for coexistence is not invasibility, but rather the requirement that neither plant is likely to leave the basin of attraction and go extinct over our 100-generation time window (Caswell 1978, Valdovinos et al. 2013, Socolar & Washburne 2015).

Experimental data on individual bee foraging

To quantify variation in individual bee foraging behavior, we observed foraging bumblebees (*Bombus terrestris*) in a laboratory setting, using a repeated measures design to test for statistical differences in individual foraging behavior. Marked B. terrestris workers foraged in an artificial meadow with 42 artificial flowers of two different types: 21 yellow flowers containing pollen rewards and 21 orange flowers containing nectar rewards (Supplementary material Appendix A, Figure A1). These two artificial flower types simulate two plant species from which bees get different rewards. We tested 41 B. terrestris workers in 199 individual trials across 20 combinations of pollen and nectar quantity and quality (Supplementary material Appendix A, Table A1). Each worker was not tested for all combinations of rewards. Each worker completed a mean of 4.85 ± 0.72 trials, and a maximum of 16 trials. For each trial, we recorded the number of flowers visited of each type. To be counted as a visit, the bee had to directly contact and collect the floral reward. After each trial, we calculated the amount of reward collected by measuring the sugar solution left in the nectar flowers and weighing the pollen collected by the bee. See [redacted] for additional details.

Data analysis

To assess whether individual bees differed in their foraging preferences, we modeled individual bee foraging decisions (probability of visiting pollen vs. nectar flowers) as a function of the quality and quantity of pollen and nectar rewards as well as a random effect of individual bee. If all bees are identical in preference, then the random effect variance should be indistinguishable from zero and including the random effect should not substantially improve the model fit. Therefore, we sought direct inference on the
random effect variance to examine whether the data rule out near-zero variance, where random effect variance indistinguishable from zero would indicate no differences between individual bees. Because frequentist model fits may underestimate the uncertainty in variance parameters (Kéry 2010), we fit the model under a Bayesian mode of inference using vague priors (Supplementary material Appendix C). This analysis was done in JAGS (Plummer 2003) via the R package 'rjags' (Plummer 2016). We compared prior and posterior distributions for the standard deviation to assess whether the data constrain the standard deviation away from zero. To confirm whether the random effect of individual variation should be in the best fit model, we compared the models with and without individual variation using both a frequentist likelihood ratio test and a Bayesian indicator variable analysis (Supplementary material Appendix A, Appendix C). All analyses were done in the program R (R Core Team 2017).

Results

Effects of variation in bee foraging preferences on plant coexistence

Our simulation model of individual bee foragers requires strong bee specialization for plant coexistence. Bee specialization in the model is a result of density-dependent preference for rare plants and/or strong variation in bee preference, such that different individuals strongly prefer different plant species. In our model, this variation could arise either from differential species-specific mean preferences or high levels of individual variation around the means. Differences in the mean preferences of bee species have a large effect on plant coexistence in our model, i.e. one bee species has a positive mean preference value and the other has a negative mean preference value, where positive values indicate preference for plant species 1 and negative values indicate preference for plant species 2 (Figure 2). Differences in mean preference can promote plant coexistence even when densitydependent preference for rare plants is weak (Figure 2B) or non-existent (Figure 2C, D), i.e. pollinators prefer to visit common plants. Plant communities always persist when bee species have strongly opposing mean preferences (Figure 2). When initial plant population sizes vary such that one plant species starts out as rare, stronger bee specialization is required for coexistence in our model (Figure 3). With a strongly skewed ratio of initial plant population sizes (e.g. 625:1) extremely high levels of specialization are required for coexistence (Figure 3). When the initial plant population sizes are equal, smaller differences between the bee species' means maintain coexistence (Figure 2).

To provide a numerical example of the strength of pollinator specialization from our model, we calculated the percentage of visits to each plant species in a bee foraging path using the minimum parameter values required for coexistence. We assume the starting conditions of the model (Table 1; equal populations of the two plants), no variation around each bee species mean, and mean values of 1.3 and -1.3 for bee species 1 and 2, respectively (Figure 2C). An individual bee's preference is drawn from a log-normal distribution with a mean of 1.3 or -1.3, depending on its species identity, and no standard deviation (Equation 7). The resulting value from this distribution (3.67 from a mean of 1.3; 0.27 from a mean of -1.3) is α in Equation 3. For the purposes of this example, we

assume that $\beta = 1$ (no preference for rarity) and the effective density of plant species 1 thus becomes $(\alpha^*P_{1t}) / ((\alpha^*P_{1t}) + P_{2t})$ (Equation 8). For a bee species mean of 1.3, the effective density of plant species 1 is 0.79, an increase from its "true" density of 0.5. Thus, 79% of the individual bee's visits go to plant species 1. For a bee species mean of -1.3, 79% of the individual bee's visits go to plant species 2. Our model requires high levels of individual pollinator specialization within foraging paths for plant coexistence; that is, the vast majority of visits within a single foraging trip must be to a single plant species.

For the case where the initial population sizes of the plant species are unequal, for example with a ratio of 25:1, the bee species means must differ in magnitude by 4.4 for coexistence to occur, i.e. the mean preference of bee species 1 is 2.2 and the mean preference of bee species 2 is -2.2 (Figure 3). Repeating our calculation above assuming that $\beta = 1$ and there is no intraspecific variation in bee foraging behavior, the α values for bee species 1 and bee species 2 are 9.03 and 0.11, respectively (Equation 7). Using Equation 8, approximately 99.6% of the visits of an individual bee of species 1 go to plant species 1 (the common plant), and 0.04% of visits of an individual bee of species 1 go to plant species 2 (the rare plant). Approximately 73% of the visits of an individual bee of species 2 go to plant species 1, and 27% of visits of an individual bee of species 2 go to plant species 2. Thus, with mean preference values of 2.2 and -2.2 for bee species 1 and bee species 2, respectively, the rarer plant species 2 receives a non-trivial percentage (27%) of visits from one of the bee species. When bee species have strongly diverging mean preferences such that one species prefers the rare plant, pollinator visits to the rare plant occur. If we use these same preference values (+/-2.2) to calculate bee preference when the plant species are in equal mixture for comparison to our first example, we find that 90% of visits in a foraging path of each bee species must go to their preferred plant species, compared to 79% with preference values of +/-1.3.

When bees have a strong density-dependent preference for rare plants, coexistence is achieved for all parameter combinations except where both bee species have a strong mean preference for the same plant species (Figure 2A). As density-dependent preference for rare plants decreases (Figure 2B-D), fewer of the modeled plant communities coexist, although this decrease is attenuated by the effects of the bee species' mean preferences and the standard deviation around those preferences.

In our model, high standard deviation around the mean bee species preference allows individual foragers to differ from their species means. High standard deviation increases coexistence slightly in our model communities (Figure 2A-D; compare bottom left plot of all panels to upper right plot). Interestingly, the effect of intraspecific variation is more noticeable when there is some preference for rare plants (Figure 2B; compare bottom left plot to upper right plot). In this case, intraspecific variation in bee preference of both species, as indicated by standard deviations of 3 (upper right plot), maintains plant coexistence even when the species' mean preference is for the same plant species, i.e. each bee species has a positive mean preference.

Experimental data on individual bee foraging

The posterior distribution of the standard deviation of the random effect was constrained away from zero (Figure 1), indicating that variation in the random effect, attributable to variation among individual bees, is included in the best model. The standard deviation of the random effect is mathematically equivalent to the standard deviation of bee species preferences in our simulation model. In our data analysis, the standard deviation (sigma) takes a value close to 1. In our simulation model, increasing the standard deviation from 0 to 1 in agreement with our experimental result had a very minor effect on plant species coexistence when there was no preference for rare plants (Figure 2C), but improved coexistence slightly when there was moderate preference for rare plants (Figure 2B). When there is no interspecific variation, intraspecific variation only improves coexistence when the standard deviation of at least one species is 3, a level much higher than our experimental result (Figure 2). The likelihood ratio test and Bayesian indicator variable analysis confirmed that individual variation is included in the best fit model (Supplementary material Appendix A).

Discussion

Our simulations show that only highly specialized pollinators permit coexistence in pollen-limited plant communities. Therefore, we predict that where they exist, pollenlimited plant communities should interact with specialized pollinator communities, where specialization is quantifiable at the pollinator species level and/or the level of the individual forager. A key question is whether the levels of pollinator specialization that drive pollinator-mediated coexistence in our model are widespread in nature. We consider four mechanisms that might deliver sufficiently specialized within-bout foraging dynamics: species-level specialization, individual- or bout-level specialization, densitydependent preference for rare plants, and spatial or temporal clumping of flowers.

Species-level specialization

Most bees are not dietary specialists, and very few bee species are monolectic (specialized on a single plant species) (Michener 2000). However, oligolecty (specialization on one or a few plant taxa) is not uncommon (Michener 2000). For example, 43% of bee species in the tribe Anthidiini are oligolectic at the level of plant family, subfamily, or tribe (Muller 1996), and 30% of bee species in a region of subtropical Brazil are oligolectic (Schlindwein 1998). Thus, in species-poor systems with a single plant per family, oligolectic bees might provide a powerful mechanism for plant species coexistence. Note that competition between two species of congeneric plants for oligolectic pollinators is precisely analogous to the two-plant scenario for generalist pollinators in our model.

Documented cases of strongly monolectic pollinators are rare and often involve unusual examples of coevolution, such as orchids that mimic species-specific insect pheromones (e.g. Schiestl et al. 1999). In such specialized cases where bees and plants have a strong reciprocal preference, pollinators might easily mediate persistence of the plant in arbitrarily species-rich systems, and the selective forces that guided the evolution of such elaborate signaling seem likely to involve pollen limitation (Kiester et al. 1984). However, we expect that these extraordinary cases account for the persistence of only a small minority of plant species.

Individual- or bout-level specialization

Our simulation model provides quantitative benchmarks for the within-foraging-bout visitation frequency to each plant species in order to support coexistence. To maintain coexistence of two plants with equal initial abundance, our model requires that at least some individual foraging paths must visit each plant species approximately 79% of the time. Preferences must be even stronger to buffer against unequal initial population sizes. For example, if plant species abundance ratios start at 25:1, coexistence emerges only when some bees have preferences of α equal to +/- 2.2 (Figure 3), which corresponds to delivering over 90% of visits to one plant when the plants are in equal mixture.

Evidence of high individual bee specialization in nature is limited. While multiple studies report the frequency of visits to a given plant species within a foraging bout, these studies generally are not accompanied by data on the relative abundance of that plant within the community. Thus, it is possible (and in our view likely) that reported cases of high apparent specialization simply reflect preferential visitation to common plant species (or the commonest plant among the family preferred by an oligolectic bee). Nevertheless, we note that many reported foraging paths are entirely restricted to a single plant species, which suggests that pollinator-mediated coexistence might be possible. In an alpine system, 77% of individual bumblebees visited only one plant species within a foraging bout (Brosi & Briggs 2013), and in an Australian garden, 88% of foraging trips of a stingless bee consisted of visits to only one plant species (White et al. 2001). However, only 35% of bumblebee foraging paths in a German meadow visited exclusively one

plant species, and 37% of foraging paths included visits to at least three plant species (Raine & Chittka 2007). In an agricultural system in Uruguay, approximately 80% of individuals of two bumblebee species collected only one type of pollen in corbicular pollen loads (Rossi et al. 2015). However, only 60% of individuals carried one type of pollen in nectar expressed from the abdomen, including most of the bees whose corbicular pollen loads were also tested (Rossi et al. 2015). Thus, studies that only examine corbicular pollen loads as a test of constancy may underestimate the diversity of plants visited within foraging paths. Among solitary bees, three species in the genus *Osmia* collected only one plant family in 44-58% of pollen loads (each pollen load corresponds to one foraging path, subject to the caveat above; Eckhardt et al. 2014). However, two additional *Osmia* species showed no specialization within foraging paths at all (Cane 2011).

One way to circumvent the need for data on the relative abundance of plants is to use Thomson's interview method of assessing bee preference, in which individual foragers are experimentally confronted with a choice of flowers of different plant species (Thomson 1981). Two studies use this method to document high specialization of bumblebee foragers on either of two congeneric plant species (Raine & Chittka 2005, Wilson & Stine 1996). In a mixed field of white and red clover (*Trifolium repens* L. and *T. pratense* L., respectively), Wilson and Stine (1996) show that 68% of *Bombus vagans* workers chose white clover when interviewed if the previous flower they had visited was also white clover. 88% of workers chose red clover (Wilson & Stine 1996). Raine and Chittka (2005) calculate a bee species-specific constancy index that compares the number of visits to the same plant species as the previous flower visited to the number of visits to a different plant species than the previous flower visited. They calculated constancy indices for three bumblebee species and found that the constancy indices for these species ranged from partial constancy to complete constancy (Raine & Chittka 2005). These results suggest that bout-level specialization in bumblebees might be sufficient to promote coexistence even of congeneric plants. The 79% sequential visitation rate required by our model sits between the 88% and 68% sequential visitation rates to red and white clover, respectively, documented by Wilson and Stine (1996).

Our experimental results using bumblebees likewise reveal individual-level specialization (i.e. intraspecific variation; Figure 1). However, the level of observed variation (standard deviation = 1) does not appreciably affect plant coexistence in our model when there is no preference for rare plants (Figure 2C), but did improve coexistence slightly when there was moderate preference for rare plants (Figure 2B). Other studies have analyzed floral choice among bumblebee and honeybee workers, but did not calculate means of individual behavior for quantitative comparison (Heinrich 1976, Heinrich 1979, Grüter et al. 2011). Further work in natural systems is needed to quantify variation in individual bee foraging behavior and describe under what conditions such variation occurs. In particular, studies that record plant visit sequences within bee foraging paths and quantify the relative rarity vs. commonness of available plant species are necessary (Thomson 1981, Waser 1986).

Density-dependent preference for rare plants

Density-dependent preference for rare plants is under-explored and further empirical work in natural systems is needed. We expect that bee preference for rare plant species may occur in nature when generalist bees require a certain resource that only a specific plant species can provide, and that plant species happens to be rare in the community (Williams & Tepedino 2003). Rare plants may also offer respite to generalist pollinators from harmful secondary compounds present in common plants (Eckhardt et al. 2014, Bukovinsky et al. 2017), or allow generalist pollinators to balance collection of multiple necessary nutrients, e.g. essential amino acids (Cook et al. 2003, Hendriksma & Shafir 2016). Pollinators are able to detect the nutritional properties of pollen of different plant species, suggesting that such fine-scale adaptive foraging is possible (Vaudo et al. 2016). Indeed, several studies show that pollinator species exhibit temporal or spatial variation in foraging preference due to resource-switching determined by plant species frequency (Campbell & Motten 1985, Kunin 1993, Kunin 1997b, Totland & Matthews 1998, Ghazoul 2006, Feldman 2008, Essenberg 2012, Valdovinos et al. 2013, Bruninga-Socolar et al. 2016), but whether rare plants are visited sequentially within foraging paths has yet to be demonstrated empirically. In some systems, rare plants mimic more common cooccurring species in floral morphology and color, suggesting that these plants do not rely on density-dependent rare-species advantage for pollination (Juillet et al. 2007, Jersáková et al. 2016, Lunau & Wester 2017).

Spatial or temporal clumping

Because of the high levels of individual bee specialization required by our simulation model for plant coexistence, we predict that in species-rich, pollen-limited plant communities, rare plant species should occur in clumps of high local abundance. Optimally foraging animals maximize energy gained per unit of time or effort (Schoener 1971). In the case of pollinators, transit between flowers is a key component of the time/effort denominator, and so spatial or temporal clumping of a rare plant species yields a higher probability of optimally foraging pollinators delivering sequential visits to conspecific plant individuals. If congeneric plants are clumped such that different species represent over 80% of flowering individuals in different spatial regions or time periods, then even neutrally foraging generalist pollinators could maintain coexistence and simultaneously reinforce the spatial clumping (if seed dispersal generally occurs over short distances) or temporal clumping. Interestingly, spatial clumping and/or mass flowering (temporal clumping) have been documented in plant species known to be pollen-limited (e.g. Crone & Lesica 2006). More broadly, in many systems, certain plants or plant communities flower during short periods of the year, e.g. spring ephemerals (Kudo et al. 2008).

Conclusions

The role of pollinators in mediating plant coexistence is of major interest both as a potentially important aspect of modern coexistence theory and for its basic and applied implications for pollen limitation: as a rule, diverse plant communities should not be severely pollen-limited unless their pollinators tend to promote coexistence rather than exclusion. Our results suggest that strong pollinator specialization is necessary for

coexistence of pollen-limited plants. Species-level specialization among bees is variable in nature, but may rarely be sufficient to promote coexistence among congeneric coflowering plants. Individual- and bout-level foraging specialization, coupled with spatial clumping of rare plants, might be sufficient to provide a more general coexistence mechanism. We provide empirical evidence of intraspecific variation among bumblebee workers, but at a level insufficient to contribute strongly to plant coexistence in our simulation model. In the existing literature on bee foraging preference, we find that few studies permit rigorous quantification of bee foraging specialization, which requires quantitative data on the relative abundance of local plant species. However, a handful of studies using Thomson's interview method suggest that bumblebees might conceivably promote coexistence even among pollen-limited congeners. We conclude that pollinator specialization should be included in models of plant coexistence and propose that future empirical work in pollen-limited plant communities investigate the role of pollinator specialization in the persistence of those communities, particularly the persistence of rare plant species.

Tables and figures

Table 1. Ranges of values of parameters describing bee foraging in the simulation model.

Parameter	Values
Bee species 1 mean preference, μ_1	0, 2, 4, 6, 10
Bee species 1 standard deviation, σ_1	0, 1, 3
Bee species 2 mean preference, μ_2	-10, -6, -4, -2, 0, 2, 4, 6, 10
Bee species 2 standard deviation, σ_1	0, 1, 3
Preference for rarity, β	0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5, 1.7, 1.9

Table 2. Values for parameters unrelated to bee foraging behavior in our simulation

 model. Parameter values are also provided for 12 model runs assessing the sensitivity of

 our results to the values of these parameters.

Parameter	Value	Values in sensitivity analyses
Bee abundance, A_i	100 per bee species	Both elevated: 150 bees
	(Supplementary material	(Supplementary material Appendix A,
	Appendix A)	Figure A2)
		Both lowered: 50 bees (Figure A3)
		Asymmetric elevated: 100 species 1,
		150 species 2 (Figure A4)
		Asymmetric lowered: 100 species 1,
		50 species 2 (Figure A5)
Initial plant population sizes	500,000 per plant species	
Pollen transfer probabilities,	Sequentially for each visit in a	Lowered: 0.7, 0.7, 0.7, 0.7, 0.49, 0.35,
$ au_k$	bee foraging path: 1, 1, 1, 1, 1,	0.14 (Figure A6)
	0.7, 0.5, 0.2 (Richards et al.	Faster decay: 1, 0.9, 0.7, 0.5, 0.3, 0.2,
	2009)	0.1 (Figure A7)
Probability of pollen	0.04 for both plant species	Both elevated: 0.2 (Figure A8)
becoming an adult plant, ρ_1	(Supplementary material	Both lowered: 0.01 (Figure A9)
	Appendix A)	Asymmetric elevated: 0.04 species 1,
		0.05 species 2 (Figure A10)
		Asymmetric lowered: 0.04 species 1,
		0.03 species 2 (Figure A11)
Visits per bee lifetime, υ_{ij}	25,000 per individual for each	Both elevated: 30,000 visits (Figure
	bee species (Cane 1997;	A12)
	Ribbands 1949)	Both lowered: 20,000 visits (Figure
		A13)









Figure 2. With strong bee preference for rare plants (Figure 2A), the two plant species coexist across most values of the bee species' mean preferences (orange regions of all plots), where positive mean values indicate preference for plant species 1 and negative mean values indicate preference for plant species 2. The two plant species do not coexist where both bee species have a strong preference for the same plant species, indicated by high positive values of both means (blue regions of all plots). When the bee species prefer different plant species, as indicated by one positive mean and one negative mean, plant species coexistence is supported (left side of all plots). High levels of individual

variation around both bee species means increase coexistence. The greatest coexistence is obtained when there are high levels of variation around both bee species' means (upper right plot of all panels). When only one bee species' standard deviation is high, coexistence occurs less than in the previous case but more than when variation is low for both species (bottom left plot of all panels). When bees prefer common plants (Figure 2D), even high levels of intraspecific variation among individuals, as indicated by high values of each bee species' standard deviation, cannot substantially increase coexistence.



Figure 3. With no preference for rare vs. common plants ($\beta = 1$) and no intraspecific bee variation ($\sigma = 0$), the two plant species coexist (orange regions of graph) with large differences between the mean bee species' preferences. Coexistence is more difficult as the ratio of the initial plant population sizes increases, i.e. if one plant species starts out as rare compared to the second plant species. When the initial plant population sizes are equal, coexistence is obtained at smaller differences between the mean bee species' preferences.

Supplementary information, tables, and figures

Simulation model

We selected biologically reasonable parameters based on the study system with which we're most familiar (Bruninga-Socolar et al. 2016), where we estimate that roughly 200 bees may pollinate a patch of flowers and roughly 500,000 flowers may populate a patch. We determined the probability that a fertilized ovule recruits to the adult stage in the next generation based on the values we chose for the parameters in Table 2.

Likelihood ratio test and indicator variable analysis

When comparing a random effects model with one without the random effect, standard AIC-based approaches to model selection are difficult to implement because estimation of the number of effective degrees of freedom associated with the random effect is challenging (Kéry 2010). Instead, we applied two alternative approaches to assess the strength of evidence for the inclusion of the random effect. First, we fit models with and without the random effect in the R package lme4, and we compared their fits using a likelihood ratio test (Supplementary material Appendix C). The likelihood ratio test between the models with and without the random effect representing variation among individual bees was significant ($\chi^2 = 125.67$, p < 0.0001).

Second, we performed fully parametric Bayesian model selection using indicator variables (Hooten & Hobbs 2015) to perform direct inference on whether the random effect should be included in the model. To do so, we modified the random effects model by multiplying the random effect variance by a Bernoulli indicator variable

(Supplementary material Appendix C). When the indicator variable takes value zero, the random effect is excluded from the model, and when the variable takes value one, the random effect is included. The posterior distribution of the indicator variable is directly interpretable as the Bayesian posterior probability that the model including the random effect is the correct model. Our indicator variable analysis confirmed that the random effect is included in the best-fit model (indicator variable V = 1 in 25,000 model runs).

References

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Figure A1. Artificial flowers containing pollen rewards (left) and nectar rewards (right).See Konzmann & Lunau (2014) for additional details.

Table A1. Combinations of rewards used in 20 tests of *B. terrestris* foraging behavior. For example, in each of five tests, bees were presented with a different value for nectar quantity while nectar quality, pollen quantity, and pollen quality were held constant. In the next series of five tests, bees were presented with a different value for nectar quality while nectar quantity, pollen quantity, and pollen quality were held constant, and so on for all 20 tests. See Konzmann & Lunau (2014) for additional details.

	Varied reward	Standardized reward
Nectar quantity	210 µl, 105 µl, 52.5 µl, 21 µl, 0 µl sugar solution (45%)	1 ml 100% pollen
Nectar quality	60%, 45%, 30%, 15%, 0% sugar solution (210 μl)	1 ml 100% pollen
Pollen quantity	1 ml, 0.5 ml, 0.25 ml, 0.1 ml, 0 ml pollen (100%)	210 µl 45% sugar solution
Pollen quality	100%, 75%, 50%, 25%, 0% pollen (1 ml)	210 µl 45% sugar solution



Figure A2. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for bee abundance of each species are both elevated to 150 bees compared to abundances of 100 for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A3. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for bee abundance of each species are both lowered to 50 bees compared to abundances of 100 for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A4. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for bee abundance are asymmetric with species 1 set to 100 individuals and species 2 set to 150 individuals compared to abundances of 100 each for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A5. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for bee abundance are asymmetric with species 1 set to 100 individuals and species 2 set to 50 individuals compared to abundances of 100 each for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A6. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for the probability of conspecific pollen transfer are all lowered (0.7, 0.7, 0.7, 0.7, 0.49, 0.35, 0.14) compared to the set for our main model results (1, 1, 1, 1, 0.7, 0.5, 0.2; Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A7. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the values for the probability of conspecific pollen transfer decay faster (1, 0.9, 0.7, 0.5, 0.3, 0.2, 0.1) than the set for our main model results (1, 1, 1, 1, 0.7, 0.5, 0.2; Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A8. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the probabilities of pollen becoming an adult plant of each species are both elevated to 0.2 compared to the value 0.04 used for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A9. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the probabilities of pollen becoming an adult plant of each species are both lowered to 0.01 compared to the value 0.04 used for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.





sd preference; bee sp. 1

sd preference; bee sp. 1



Figure A11. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the probabilities of pollen becoming an adult plant of each species are asymmetric with species 1 set to 0.04 and species 2 set to 0.03 compared to 0.04 for both species for our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A12. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the lifetime visits per bee individual are set to 30,000 for each bee species compared to 25,000 used in our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.



Figure A13. We ran the model twelve times to test the sensitivity of our results to the parameters listed in Table 2 (Supplementary material Appendix B). Here, the lifetime visits per bee individual are set to 20,000 for each bee species compared to 25,000 used in our main model results (Figure 2). All other parameters in Table 2 stayed the same. All parameters given in Table 1 stayed the same.

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