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Individual bee foragers are less-efficient transporters of pollen for plants from which they collect the most pollen in their scopae

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Abstract

Premise: Bees provision most of the pollen removed from anthers to their larvae and transport only a small proportion to stigmas, which can negatively affect plant fitness. Though most bee species collect pollen from multiple plant species, we know little about how the efficiency of bees' pollen transport varies among host plant species or how it relates to other aspects of generalist bee foraging behavior that benefit plant fitness, such as specialization on individual foraging bouts.

Methods: We compared the pollen collected and transported by three bee species for 46 co-occurring plant species. Specifically, we compared the relative abundance of pollen taxa in the individual bees' scopae, structures where bees store pollen to provision larvae, with the relative abundance of pollen taxa on the rest of bees' bodies, which is more likely to be transferred to stigmas.

Results: Bees carried five times more pollen grains in their scopae than elsewhere on their bodies. Within foraging bouts, bees were relatively specialized in their pollen collection, but transported proportionally less pollen for the host plants on which they specialized. Across foraging bouts, two bee species transported proportionally less pollen for some of their host plants than for others, though differences didn't consistently follow the same trend as at the foraging bout scale.

Conclusions: Our results suggest that foraging-bout specialization, which is known to reduce heterospecific pollen transfer, also results in less-efficient pollen transport. Thus, bee foragers that visit predominantly one plant species may have contrasting effects on that plant's fitness.

KEYWORDS

bees, floral constancy, heterospecific pollen transfer, mutualism, plant–pollinator networks, pollen consumption, pollen transport, pollination, pollination efficiency, specialization

The choices bees make on individual foraging trips affect their patterns of pollen transfer and ultimately their contributions to plant reproduction. For the most part, studies of bees' foraging behaviors and their consequences for pollen transfer have focused on individual plant species and their visitor taxa (Harder and Thomson, 1989; Irwin et al., 2001; Castellanos et al., 2003; Stanton, 2003; Larsson, 2005; Bronstein et al., 2006; Burkle et al., 2007; Sahli and Conner, 2007; Toju et al., 2017; but see Irwin and Maloof, 2002). Logistical constraints typically prevent measurement of bees' pollen removal and deposition for many co-occurring plant species (Jordano, 1987; Vázquez et al., 2005; Dormann et al., 2009; Knight et al., 2018). Thus, a continuing challenge is to understand how the effects of bees' foraging behaviors scale up to affect the reproduction and coevolution not just of a single host plant, but an entire community of interacting plant species (Stanton, 2003; Bronstein et al., 2006; Ashman et al., 2020; Thomson, 2021).

While foraging, bees frequently groom their bodies to remove pollen grains from the areas where it might be

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lost to pollination and sequester it in pollen-collecting structures (i.e., scopae) where it is less likely to come off (Thomson, 1986; Thorp, 2000). This behavior allows them to remove large quantities of pollen from plant populations, feed most of it to their larvae, and deposit only a small proportion of it onto stigmas (e.g., bees deposit only 3.7% of pollen produced by *Campanula rapunculus* on to stigmas) (Schlindwein et al., 2005; Danforth et al., 2019). Pollination biologists often refer to this proportion of pollen a bee removes from anthers and actually deposits onto stigmas as a bee's "pollination efficiency" (e.g., Castellanos et al., 2003; Koski et al., 2018). Frequent visitation by inefficient bee pollinators can contribute to pollen limitation in plant populations and appears to have played a major role in floral evolution, selecting for floral adaptations that prevent bee grooming of pollen into scopae, limit the rate of bee pollen removal, or exclude bees as pollinators entirely (Harder and Thomson, 1989; Castellanos et al., 2003; Harder and Barclay, 2008; Hargreaves et al., 2010; Li et al., 2014; Martínez del Río and Bullock, 2017; Koski et al., 2018; Parker et al., 2018). At present, though, most of what we know about pollination efficiency comes from studies of pollinators on individual plant species. Thus, we know little about the extent to which bee pollination efficiency varies among co-occurring host plant species, or how it relates to other components of bees' foraging behavior.

Another aspect of bees' foraging behavior may contribute to differences in their pollination efficiency on different host plants. Foraging bout specialization—a foraging behavior by which a bee collects pollen from only one or a few plant species per foraging bout—is generally thought to be beneficial for plant reproduction, as foragers that are relatively specialized transfer less heterospecific pollen to conspecific stigmas (Grant, 1950; Brosi, 2016). Such patterns of specialized foraging can arise when there are few rewarding species of plants in a bee's foraging path or when a bee chooses to specialize despite having access to multiple rewarding plant species. In either case, the bee will transfer less heterospecific pollen (Waser, 1978; Morales and Traveset, 2008). Even generalist bee species, which typically account for most of the plant–pollinator interactions in plant communities, often specialize on the scale of an individual foraging bout—the scale relevant to pollen transfer (Heinrich, 1976, 1979; Tur et al., 2014; Smith et al., 2019; Cullen et al., 2021).

An unexplored consequence of foraging-bout specialization, however, is lower pollination efficiency. Studies of individual plant species show that bee individuals removing more pollen per visit transfer a lower proportion of that pollen to stigmas of the same plant (Harder and Thomson, 1989; Parker et al., 2016). Specifically, the number of grains that bees deposit on stigmas increases as bees remove more grains in total from anthers, but in a saturating fashion (Harder and Thomson, 1989). Bees that are pollen specialists at the species level, i.e., oligolectic bee species, likewise have lower pollen-transfer efficiency than nonspecialist species foraging on the same host plant, due to the large amounts of pollen they sequester (Parker et al., 2016). Similarly, individuals of generalist bee species may be less-efficient pollinators of the plant species they specialize on during a given foraging bout. This last possibility has not been explored, however, presumably because it requires data on individual-level specialization and on pollination efficiency across multiple plant species.

Bees may be especially likely to engage in foraging-bout specialization on preferred or abundant resources—that is, on plants from which they collect the most pollen overall (Heinrich, 1976, 1979; Brosi, 2016; Cullen et al., 2021; but see Tur et al., 2014). Thus, generalist bee species may have lower heterospecific pollen transfer and pollination efficiency across foraging bouts for the plant species on which they rely the most for pollen. This dynamic could affect the trajectory of generalist bee species' relationships with their host plants: the important pollen host plants for the bees may experience greater selection pressure to improve pollination efficiency by mitigating bees' removal of pollen, while its less-important host plants may experience greater selection pressure to reduce heterospecific pollen transfer by incentivizing specialization. Whether foragers of the same bee species are more likely to exhibit foraging-bout specialization on relatively important pollen host plants, though, and how this specialization relates to pollination efficiency, have not been examined.

Here we compared pollen transport and pollen collection for three co-occurring native bee species and 46 co-occurring plant taxa in understory communities of deciduous forests. To obtain data on pollen transport and collection by bees, we collected bees foraging at 11 forest sites and used light microscopy to identify and count the pollen grains on foragers' bodies and in their scopae. We assume that the pollen grains on bees' bodies outside of scopae represent what they were likely to transport to stigmas, and pollen grains carried in their scopae were destined to be fed to bee larvae and were relatively unavailable for pollination (Thorp, 2000; Alarcón, 2010; Stavert et al., 2016). By comparing body and scopal pollen, we can assess what we call "pollen-transport efficiency"—the proportion of pollen grains that each bee removed from anthers that was available for transport to stigmas on its body at the time that we collected it (Figure 1). This approach does not provide a direct measure of pollination efficiency (because not all of the pollen on a bee's body is necessarily deposited on to stigmas), nor does it provide a measure of bees' contributions to seed production or pollen limitation (as could be obtained with single-visit and hand-pollination experiments). However, it does allow us to make the first empirical comparison of bees' pollen-transport efficiency for multiple co-occurring pollen host plants simultaneously and the first examination of how pollen-transport efficiency relates to foraging-bout specialization in generalist bee species.

With these data, we answer the following questions: (1) How do the pollen taxa carried on bees' bodies compare with those in their scopae and corbiculae? (2) Is pollen-transport efficiency by individual bees lower for the plants from which they collect more pollen on a given foraging

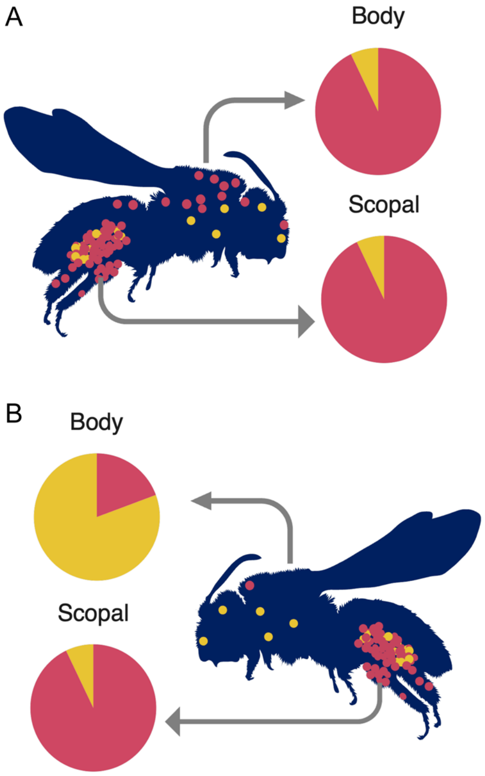

FIGURE 1 Comparing the relative abundance of pollen taxa on bees' bodies and in their scopae provides inference on the difference in their pollen-transport efficiency for different pollen host plants. In this cartoon example, two foraging female bees (A and B) collect more pollen from a plant species producing pink pollen than from a plant species producing yellow pollen. Both groom most of the pollen they remove from the anthers of both plant species into their scopae. (A) The first bee grooms the same proportion of pollen into her scopae for each plant species; thus, her pollen-transport efficiency is the same for both plant species, and even though the total quantity of pollen on her body is lower than the quantity of pollen in her scopae, the taxonomic composition of pollen is the same between her scopae and body. (B) The second bee grooms a higher proportion of the pink pollen into her scopae than yellow pollen; thus, her pollen-transport efficiency is lower for the plant producing the pink pollen, and the pink pollen is underrepresented on her body, relative to the percentage it comprises of the scopal load.

bout? (3) Is pollen-transport efficiency by a bee species lower, on average, for the pollen host plants from which it collects the most pollen overall?

MATERIALS AND METHODS

Study organisms

We analyzed pollen loads for three native co-occurring bee species: *Andrena erythronii*, *Andrena rugosa*, and *Bombus bimaculatus*. These species were among the most common at field sites and were present in samples from the most sites. *Andrena erythronii* and *A. rugosa* are solitary, ground-nesting bees that, like most other solitary bees, store pollen in collections of branched hairs on their hind legs called scopae. *Bombus bimaculatus*, like other bumblebees, is a social species in the family Apidae; foraging queens and workers store pollen in smooth surfaces on their hind legs known as pollen baskets or corbiculae. Hereafter, we will refer to all pollen stored in scopae or corbiculae as scopal pollen.

All three bee species are known to collect pollen from plants from disparate plant families but tend to collect more pollen from some plant species than from others. *Andrena erythronii* is thought to be a pollen specialist on spring ephemerals in the genus *Erythronium*, but is also known to collect pollen from other plant taxa, especially when its host plants are scarce (Michener and Retternmeyer, 1956; Smith et al., 2019). *Andrena rugosa* appears to collect mostly pollen from spring-blooming, entomophilous woody shrubs and trees such as maples and plants in the Rosaceae (Wood and Roberts, 2018). Queens of *Bombus bimaculatus*, the caste that is active in deciduous forests in the springtime, have an apparent preference for *Dicentra*, a genus of entomophilous spring-ephemeral species, and are important pollinators of wild populations of *Dicentra* (Macior, 1978).

Data collection

Study sites

We collected bee specimens in April, May, and June of 2018 and 2019 at 11 approximately 1-ha study sites in Laurentian-Acadian northern hardwood forests and other similar deciduous forest types (Hop et al., 2009, 2010, 2011). One site was located within the Moraine Nature Preserve in Indiana; the remaining 10 sites were located within three national parks in Indiana and Michigan: Indiana Dunes National Park, Sleeping Bear Dunes National Lakeshore, and Pictured Rocks National Lakeshore. Forest canopies at sites were dominated by beech, maples, yellow birch, and other deciduous hardwoods; understories were dominated by insect-pollinated, spring-ephemeral species. The ~300-km latitudinal distance between each pair of parks separates the phenology of each park by about 2 weeks (Robertson-Thompson, personal communication; L. R. Weinman, personal observations). We took advantage of this phenological lag time to match our sampling at each park with the bloom time of dominant understory ephemerals and maples.

Bee specimen collection

We only sampled on clear, bright days when the temperature was at least 13°C. We sampled sites at each park 2–4 times within 2 to 3 weeks. To sample a site, we began net-collecting bees in the morning as soon as the temperature reached 13°C or bee activity was observed until bee activity ceased. At each site, we used insect nets to opportunistically collect bees wherever we encountered them within the area of the study site, focusing on areas of the site with the highest bee activity. Most specimens (91%) were actively visiting a flower to forage either for nectar or pollen when they were collected; the remaining 9% were collected either while resting or in mid-flight. We transferred each bee specimen individually into a clean vial to prevent pollen contamination between specimens. To minimize bees' grooming activities and other movements that could disturb the distribution of pollen on their bodies and pollen-collecting structures, we then placed specimens on ice in a portable cooler while still in the field. To kill bee specimens, we froze them in a −20°C freezer overnight. All bee specimens were later identified to species by an experienced technician at Rutgers University and by coauthor Joel Gardner at the University of Manitoba. All bee specimens are curated in the Winfree lab collection at Rutgers University.

Pollen methods

To obtain the scopal pollen from each bee specimen, we removed the hind legs of each specimen and placed both legs in a microcentrifuge tube containing 95% v/v ethanol. To obtain the body pollen from each specimen, we also placed each bee specimen (sans its hind legs) into a microcentrifuge tube containing 95% ethanol. Microcentrifuge tubes containing bee legs and bee specimens, respectively, were then placed in an ultrasonic bath for 15 min to remove any pollen grains still sticking to bee hairs or corbiculae. To stain pollen samples and mount them onto microscope slides for identification, we first spun samples in a microcentrifuge at 1000 rpm for 2 min. For each sample, we then melted two cubes of fuchsin gel on a glass slide and pipetted two 5-μL subsamples of highly concentrated pollen solution directly into the molten gel.

To curate a pollen reference library for use in pollen identification, we collected freshly dehisced anthers from all plant species with open flowers at each site, surveying a ~3-ha area around the center of each site for plants with open flowers on every day that site was to be sampled for bees. We also collected dehisced anthers from woody plants common in the landscape that were not present within or near sites or whose flowers were inaccessible in the canopy, such as species in the genera *Salix*, *Quercus*, *Betula*, and *Acer*. All plants from which we collected anthers were identified to the species level in the field except for those in the genus *Salix*. For tree and shrub species that we knew to be present in the landscape, but for which we were unable to locate accessible individuals in the field, we collected pollen samples from herbarium specimens housed in the Rutgers Chrysler Herbarium. In total, we collected pollen reference samples from 127 plant taxa, which include the 16 plant species that we directly observed bees to visit as we collected them. To create the reference library, we mounted reference samples on to glass slides with molten fuchsin gel.

Pollen identification

To ensure that we only included data from bees that were actively foraging for pollen and to minimize inclusion of pollen grains that have incidentally attached themselves to scopal hairs, we limited pollen identification to 325 bee specimens that had stored a minimum of 50 grains of pollen in their scopae or corbiculae.

We identified pollen in body and scopal pollen samples to the finest taxonomic resolution possible using light microscopy. To identify pollen grains, we compared the appearance of grains to the reference library of pollen samples at 400× magnification. We were not able to distinguish some plant species by their pollen, so in some cases, we grouped pollen by genus, family, or a higher rank (Appendix S1). Additionally, we used morphogroup identifications for types of pollen that were not in our pollen reference library and that we were not able to otherwise identify. These pollen morphogroups comprised 3.4% of pollen grains found in body and scopal samples combined. Hereafter, we refer to all unique types of pollen as pollen morphospecies. We estimated the precision of our identifications by identifying the grains in a subset of scopal and body pollen samples for 46 specimens twice and calculating the proportion of all grains for which our identifications differed between the two trials. Our error rate calculated in this way was 3.3%.

To estimate the percentage composition of each pollen morphospecies in body and scopal pollen samples, we identified a maximum of 100 grains of pollen per slide. To minimize the sampling bias potentially introduced by spatial clumping of pollen on the slides, we scanned the fuchsin-stained areas of the slide at regularly spaced intervals until we had either counted 100 grains of pollen or had covered the entire area of the slide that contained fuchsin-stained pollen, whichever came first. We counted 100 grains of pollen for 89% of pollen samples and between 50 and 100 grains for the remaining 11% for which we had scanned the entire area of the slide containing fuchsin. To minimize inclusion of pollen morphospecies that bees had picked up incidentally from the environment or that were present only by contamination, we omitted records of pollen morphospecies comprising 2% or less of each sample (Tur et al., 2014).

Analysis

Throughout our analysis, we assume that pollen stored in bees' scopae was destined to be fed to bee larvae and that the pollen on the rest of bees' bodies was available for transfer to stigmas (Thorp, 2000; Alarcón, 2010; Stavert et al., 2016; Koch et al., 2017; Cullen et al., 2021). Additionally, when a bee individual collected more grains of a given pollen morphospecies into its scopae than it did of others, we took assumed that that the bee was more specialized on that plant than on other plants during that foraging bout (Smith et al., 2019).

This measure of bee specialization is functional, rather than physiological or innate; different individuals of the same bee species may be more or less specialized in their foraging on a given host plant, and the same individual may be more or less specialized on a given host plant on different foraging bouts.

We approximated differences in pollen-transport efficiency between each of an individual bee's pollen host plants by comparing the percentage composition of pollen morphospecies in the pollen on bees' bodies versus the pollen in their scopal and corbiculate loads (Figure 1). If a bee sequestered pollen more efficiently into its scopae for some plant species than for others, then the pollen of those plants will be underrepresented in the pollen on the bee's body, relative to their percentage composition of the bee's scopal pollen. Thus, a difference in the percentage composition of pollen morphospecies between a bee's body and scopal load suggests that the bee sequestered a higher proportion of pollen into its scopae for some plants than for others and, therefore, that its pollen-transport efficiency was lower for those plants than it was for others,on that foraging bout. Ideally, to measure pollen-transport efficiency for different plant species, we would have counted all pollen grains in each body and scopal pollen sample, but that was not practical. Counting a subsample of pollen grains is typical for visual identification of pollen loads (eg. Tur et al., 2014; Wood and Roberts, 2018; but see Cullen et al., 2021).

In using differences in percentage composition as an indication of differences in bees' pollen transport efficiency, we made two additional assumptions. Firstly, we assumed all pollen that bees removed from anthers ended up in their pollen-collecting structures or elsewhere on their bodies. This assumption may be unrealistic; bees can displace pollen from anthers that falls to the ground or otherwise does not end up on their bodies. If pollen was displaced, then we are underestimating the total proportion of pollen that bees removed that they do not transfer to stigmas and overestimating the proportion of that pollen that they do transfer, and so our results should be conservative with respect to detecting low pollen transport efficiency. Secondly, we assumed that bees carried more pollen grains in total in their scopae than on the rest of their bodies. To check that this assumption is true of the bee specimens we collected, we estimated the total number of grains on bees' bodies and in their scopal loads for a subset of 46 specimens (Appendix S2).

Q1. How dissimilar is the composition of pollen taxa on bees' bodies from the pollen carried in bees' scopae and corbiculae?

To assess whether bees' pollen-transport efficiency tends to differ among the plants from which they collect pollen, we measured compositional differences between the pollen on bees' bodies and in their scopal loads. We measured those differences by computing the Bray–Curtis dissimilarity between body and scopal samples for each bee specimen, using the function vegdist in the R package vegan (Oksanen et al., 2022). Because Bray–Curtis dissimilarity is sensitive to differences between samples in sample size (in this case, the number of grains we counted on microscope slides) and we wanted to assess differences in the composition of pollen samples, rather than differences due to unequal sample sizes, we computed dissimilarities using the proportional abundance of pollen morphospecies in samples rather than the absolute number of grains that were observed. Thus, in this context, Bray–Curtis dissimilarity can be used to compare the percentage of grains of each pollen morphospecies in the scopal pollen with the percentage of grains of that pollen morphospecies in the body pollen. The index varies between 0 (the same pollen types are found in both body and scopal pollen, in the same relative abundance) and 1 (no grains of the same pollen type are found in both body and scopal pollen). Bray–Curtis dissimilarity should be relatively insensitive to differences between samples in the pollen morphospecies that are present in low relative abundance, which could differ for example due to subsampling effects (Barwell et al., 2015).

We examined the distribution of dissimilarities in body and scopal pollen composition across all bee specimens and for specimens of each bee species individually by plotting histograms of Bray–Curtis dissimilarity.

Q2. Is individual bees' pollen-transport efficiency lower for the plants from which they collect more pollen on a given foraging bout?

On a given foraging bout, bee individuals often engage in some degree of foraging-bout specialization, collecting more pollen from one or a few plant species than from others. To assess whether bees transport proportionally less pollen for the plants on which they specialize on a given foraging bout, we measured each bee specimen's relative pollen-transport efficiency for each of the pollen morphospecies it was carrying when we collected it. We then related relative pollen-transport efficiency to pollen morphospecies' rank percentage composition in that same specimen's scopal load.

To approximate relative pollen-transport efficiency for each occurrence of a morphospecies on a bee specimen, we subtracted its percentage composition of the specimen's scopal pollen sample from its percentage composition of the specimen's body pollen sample. A negative difference in percentage points indicates that the pollen morphospecies is underrepresented on the bee's body relative to its percentage composition of the bee's scopal load. Underrepresentation on a bee's body suggests that the bee's pollen-transport efficiency was lower for that pollen morphospecies than it was for other pollen morphospecies on that foraging bout.

We then plotted percentage point differences vs. morphospecies' rank abundance in bee specimens' scopal loads. If bees' pollen-transport efficiency tends to be lower for the plants from which they collect the most pollen on a given foraging bout, percentage point differences should fall below zero, on average, for the morphospecies with the highest rank abundance in scopal loads, and increase to fall above zero, on average, for morphospecies with lower rank abundance in scopal loads.

To describe and visualize trends, we modeled percentage point difference as a function of rank scopal abundance for each bee species. Models were fit with maximum likelihood using the function nls and the package aomisc in R version 4.2.3 (Onofri, 2020; R Core Team, 2022). Trends appeared nonlinear, so we applied both a general linear model and a nonlinear model with a logarithmic function, compared both to an intercept-only model, and retained the model with the lowest AIC. For all three bee species, we retained the nonlinear model (Appendix S3).

One limitation of our analysis is that, because the independent and dependent variables are derived from the same data (i.e., the percentage composition of each pollen morphospecies in bees' scopal loads), it is not appropriate to assess statistical significance using P-values or to assess goodness of fit using R^2. Instead, we report the sign and magnitude of estimated parameters of each model and the difference in median percentage point difference between the pollen morphospecies that specimens collected the most of on each foraging bout and those they collected the least of.

The majority (94%) of bee specimens carried five or fewer distinct pollen morphospecies (only 3–10 specimens of each species carried more), resulting in very low sample sizes for the lowest rank abundances. To avoid allowing a few data points to have an outsized effect on fitted trend lines, we assessed trends for the top five pollen morphospecies in scopal loads of each bee species.

Q3. Is bee species' pollen-transport efficiency lower, on average, for the pollen host plants from which they collect the most pollen at the species level (across foraging bouts)?

At the bee species level (i.e., across foraging bouts), most generalist bee species collect more pollen from some plant species than from others and may be more likely to have a specialized foraging bout on these important pollen host plants than on other plants. If so, we should expect generalist bee species to transport proportionally less pollen, on average, for the plants from which they collect the most pollen overall.

To assess each bee species' relative collection of pollen from different host plants in their scopae, we calculated the average percentage of grains for each pollen morphospecies across all scopal loads of the bee species, across all specimens we collected across our 550-km study region, including those scopal loads in which it did not occur. For example, if a pollen morphospecies comprised 60% of the grains in one scopal load, 30% of the grains in another, and was not present in a third scopal load, then it comprised 30% of grains collected by those three specimens, on average.

We then assessed whether, on average, bee species transport proportionally less pollen for the plants from which they collect more pollen into their scopae on average. For this analysis, we plotted the distribution of percentage point differences for each pollen morphospecies on all specimens on which it occurred, ranking morphospecies by descending average percentage composition of bees' scopal samples. If pollen-transport efficiency is lower for plants from which a bee species collects more pollen overall, we expect the percentage point difference to fall below zero, on average, for the morphospecies that the bee species collected the most of into scopal loads and to increase above zero for the pollen morphospecies collected the least by the bee species.

To describe and visualize the trend for each bee species, we modeled percentage point difference as a function of morphospecies' rank average percentage of scopal loads. Models were fit with maximum likelihood using the function nls and the package aomisc in R (Onofri, 2020; R Core Team, 2022). We applied both a general linear model and a nonlinear model with a logarithmic function, compared both to an intercept-only model and retained the model with the lowest AIC. For *Andrena erythronii* and *Bombus bimaculatus*, we retained the nonlinear model, while for *Andrena rugosa*, the model with lowest AIC was the intercept-only model, so neither model was retained (Appendix S3). As for question 2, we report the sign and magnitude of estimated parameters of each model and the difference in median percentage point difference between the pollen morphospecies with the highest percentage of grains in scopal loads and the morphospecies with the lowest percentage.

For each bee species, many pollen morphospecies were collected infrequently, so we chose to group them for this analysis. Each bee species collected 10 to 35 pollen morphospecies that, respectively, comprised less than 5% of grains in scopal loads on average; 4 to 26 of these respectively comprised less than 1% (Appendix S1). The average percentage compositions of these morphospecies were all within 2 to 3 percentage points of each other, such that many comprise essentially the same, very small percentage of grains. Thus, differences in rank between these morphospecies carry little meaning, and different overall trends can be obtained with a number of different, equally valid rearrangements of their rank order. Instead of including data on each of these morphospecies separately, therefore, we grouped data on morphospecies that comprised less than 5% of grains on average.

RESULTS

Q1. How dissimilar is the composition of pollen taxa on bees' bodies from the pollen carried in bees' scopae and corbiculae?

We identified 46 distinct pollen morphospecies in the body and scopal loads of 325 bee specimens (Appendix S1); 100 specimens were *Andrena erythronii*, 102 were *Andrena* *rugosa*, and 123 were *Bombus bimaculatus*. Specimens carried a median of two morphospecies of pollen in their scopae or corbiculae (range: 1–8) and three morphospecies on their bodies (range: 1–7). Bees carried much more pollen in their scopae and corbiculae than on the rest of their bodies; for the 46 specimens for which we estimated the total number of grains of pollen in both body and scopal samples, we found 5 ± 1.5 (SE) times as many pollen grains in scopal and corbiculate samples, on average, than in body samples (Appendix S4).

Overall, Bray–Curtis dissimilarities of scopal and body pollen samples ranged from 0 to 1 and were right-skewed, with a median dissimilarity of 0.14 (Figure 2A). Bee species differed in Bray–Curtis dissimilarity on average, though the distribution of dissimilarities was right-skewed for all three species, indicating that the Bray–Curtis dissimilarity for most specimens was relatively low. For *Andrena erythronii*, the median dissimilarity was 0.14; for *Andrena rugosa*, it was 0.12; and for *Bombus bimaculatus*, it was 0.19. The tail of the distribution was fatter and longer for *Andrena rugosa* and *B. bimaculatus*, corresponding to about 21% of specimens for *A. rugosa* and 19% of specimens for *B. bimaculatus*.

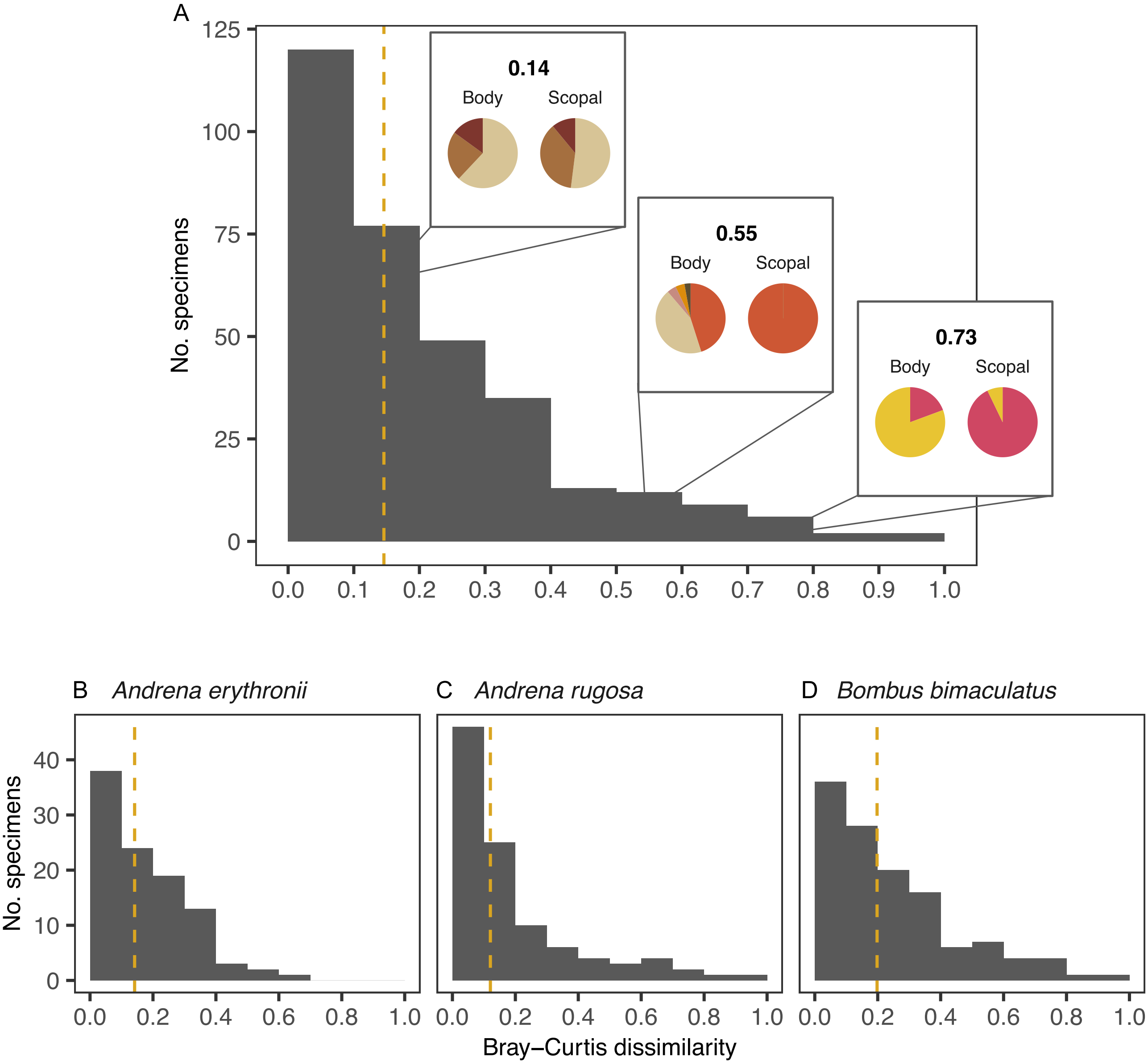

FIGURE 2 Histograms of pairwise Bray–Curtis dissimilarity between body and scopal and corbiculate pollen loads for all bee specimens (top) and for each bee species (bottom). Dissimilarities were calculated using the percentage compositional abundance of each pollen morphospecies on bees' bodies and in bees' scopal loads, respectively. Median dissimilarity values are indicated by vertical orange dashed lines. Pie charts display differences in composition for representative specimens with dissimilarity values of 0.14, 0.55, and 0.73. Different colors represent different pollen morphospecies.

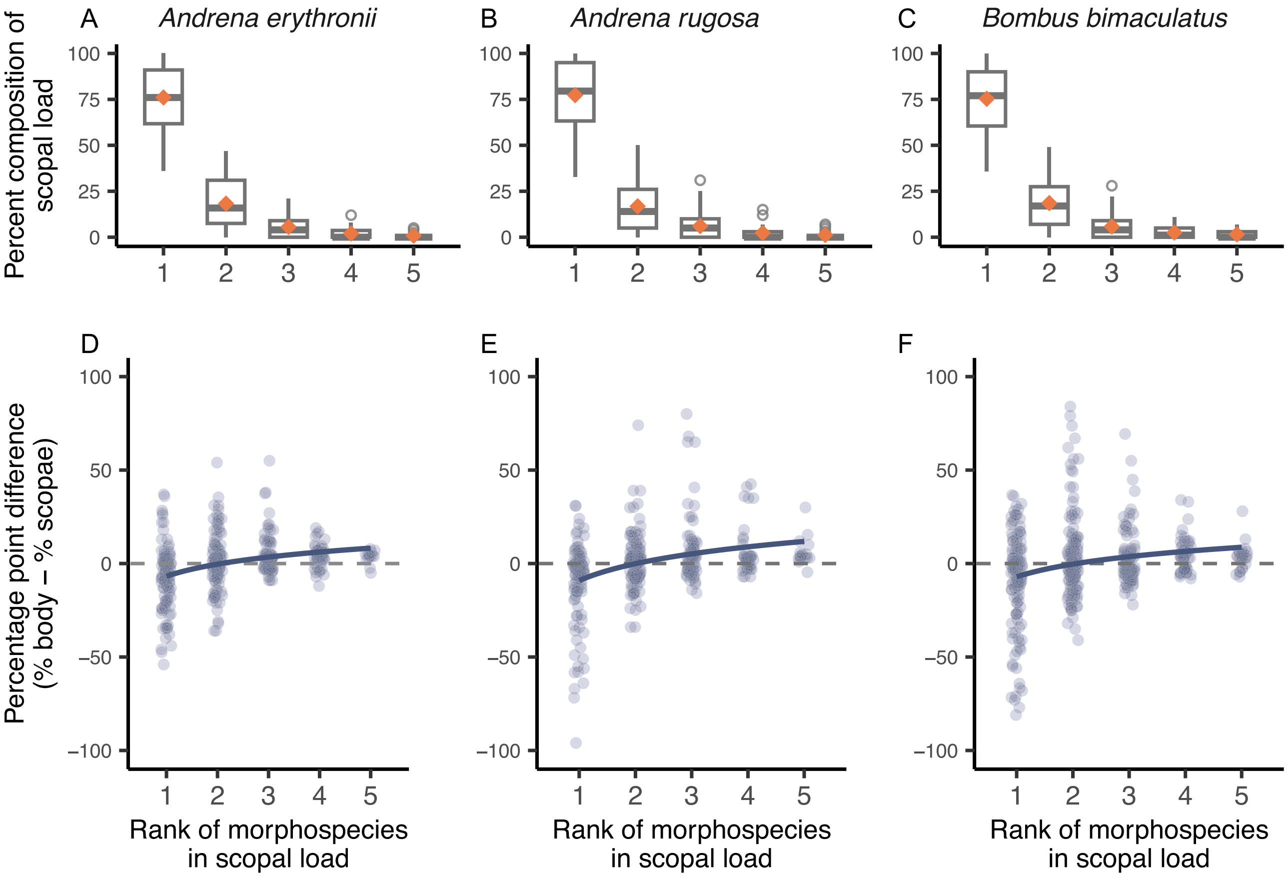

FIGURE 3 (A–C) Percentage composition of the highest to lowest ranking pollen morphospecies within each scopal sample, for each bee species. Means are indicated with orange diamonds. (D–F) Percentage point difference between percentage composition of body and scopal pollen for each of the highest to lowest ranking pollen morphospecies in the scopal loads of each bee specimen for each bee species. The number of data points decreases as rank decreases from one to five because data are included for all specimens that carried five or fewer pollen morphospecies in their scopal loads, including those that carried fewer than five pollen morphospecies. A negative difference indicates lower pollen-transport efficiency for that morphospecies on that foraging bout, while a positive difference indicates the reverse.

Q2. Is individual bees' pollen-transport efficiency lower for plants from which they collect more pollen on a given foraging bout?

Most scopal and corbiculate pollen samples were highly dominated by one or a few pollen morphospecies. On average, 2 ± 0.12 pollen morphospecies accounted for 80% of each scopal sample, and the percentage composition of the pollen morphospecies with the highest rank abundance in each sample accounted for 76 ± 2% of grains in the average sample, suggesting that most specimens engaged in some degree of foraging bout specialization (Figure 3A–C).

For all three bee species, the pollen morphospecies with the highest rank abundance in each scopal sample was underrepresented on average on specimens' bodies, relative to its percentage composition in the scopal sample. Median percentage point differences between body and scopal pollen were below zero on average for the pollen morphospecies with the highest rank abundance in each sample and above zero on average for pollen morphospecies of lower rank abundance (Table 1,

TABLE 1 Parameter estimates for the best-fitting models of percentage point difference as a function of the logarithm of pollen morphospecies' rank abundance in scopal loads, where pollen morphospecies were ranked by percentage composition within each scopal load. The intercept is interpretable as the predicted percentage point difference for the morphospecies with the highest rank abundance in a bee's scopal load. The slope gives the estimated change in percentage point difference with each change in the logarithm of rank abundance; a positive slope indicates that percentage point difference becomes more positive as rank decreases.

Bee species	Parameter	Coefficients
Andrena erythronii	Intercept	−6.80
	Slope	9.34
Andrena rugosa	Intercept	−9.10
	Slope	13.01
Bombus bimaculatus	Intercept	−7.10
	Slope	9.82

Figure 3D–F). For *Andrena erythronii*, the percentage point difference increased by 9 points, from −5 to 4; for *A. rugosa*, by 8 points, from −4 to 4; and for *Bombus bimaculatus*, by 7.7 points, from −5 to 3.7.

Q3. Is bee species' pollen-transport efficiency lower, on average, for the pollen host plants from which they collect the most pollen at the species level (across foraging bouts)?

Across all foraging bouts, bee species collected more pollen into scopae from some plant species than from others on average (Figure 4A–C). Five pollen morphospecies accounted for 80% of the pollen grains collected by foragers of *Andrena erythronii*, six accounted for 80% of the grains collected by foragers of *Andrena rugosa*, and five accounted for 80% of grains collected by *Bombus bimaculatus*. The pollen morphospecies most collected by each bee species made up 26–47% of grains in specimens' scopal loads on average (Figure 3A–C). However, for most pollen morphospecies, the percentage composition of scopal loads varied greatly across specimens, such that morphospecies that bees collected a lot of overall were present in both high and low quantities in the scopal loads of many specimens, and those that bees collected less of overall still dominated

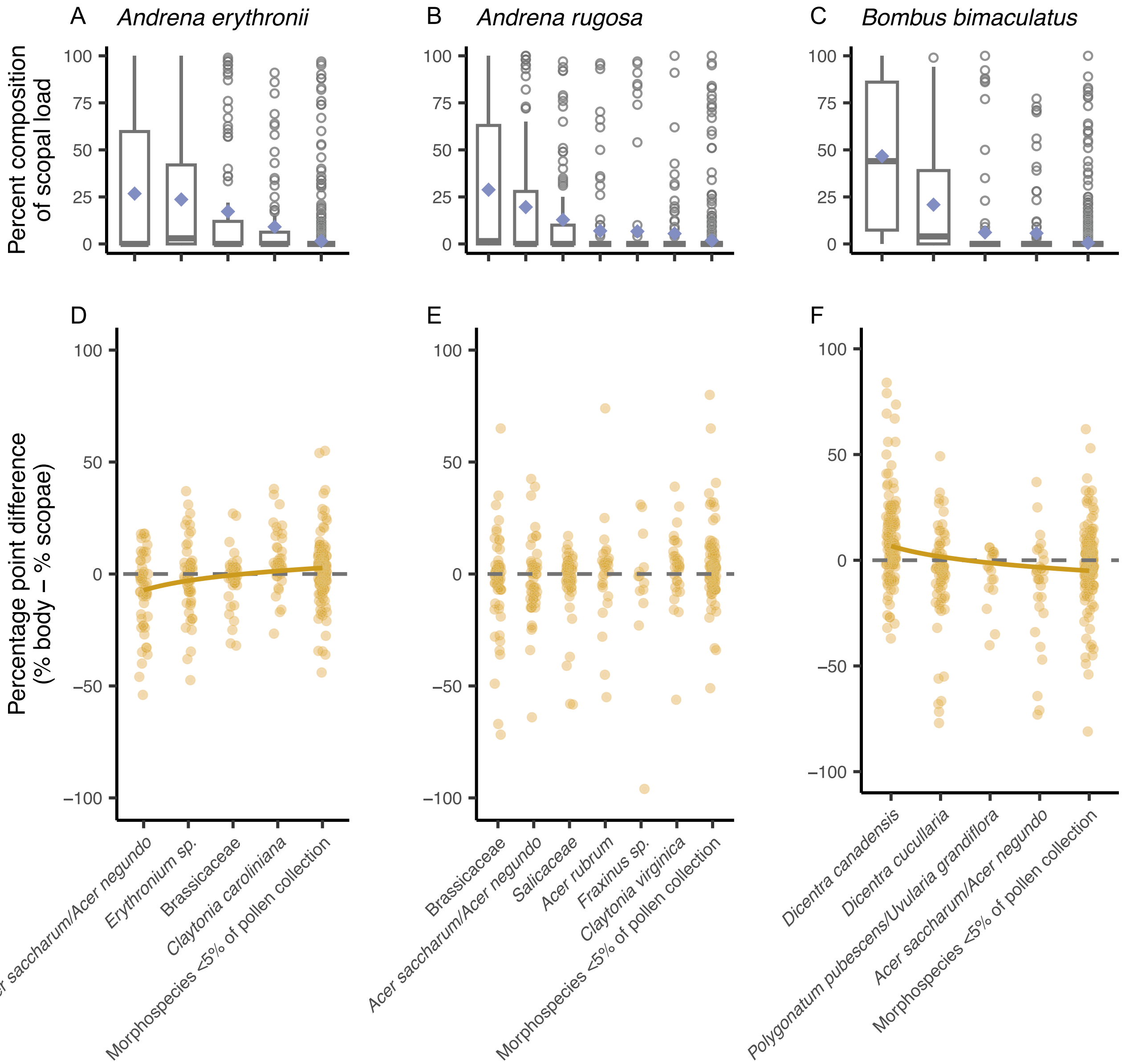

FIGURE 4 (A–C) Percentage composition of each pollen morphospecies in all scopal loads of each bee species, ranked by mean percentage composition. Means are indicated with purple diamonds. (D–F) Percentage point difference between percentage composition of body and scopal pollen for every occurrence of each pollen morphospecies on a bee specimen; as in (A–C), morphospecies are ranked by mean percentage composition in scopal loads across all specimens of the bee species. A negative difference indicates lower pollen-transport efficiency for that morphospecies on that foraging bout; a positive difference indicates the reverse.

TABLE 2 Parameter estimates for the best-fitting models of percentage point difference as a function of the logarithm of pollen morphospecies' rank average percentage composition in scopal loads. The intercept is the predicted percentage point difference for the morphospecies that bees collected the most of, on average, across foraging bouts. A positive slope indicates that the percentage point difference becomes more positive as the average percentage composition of a morphospecies in scopal loads decreases, while a negative slope indicates the reverse.

Bee species	Parameter	Coefficients
Andrena erythronii	Intercept	−7.28
	Slope	6.21
Bombus bimaculatus	Intercept	6.73
	Slope	−7.27

some of the scopal loads of the specimens that had collected them (Figure 4A–C).

For most pollen morphospecies, percentage point differences between body and scopal pollen composition were variable, suggesting that pollen-transport efficiency for any given plant species varied among the bee individuals transporting its pollen (Figure 4D–F). Despite this, percentage point differences followed a discernible trend for two of the three bee species (Table 2, Figure 4D–F; Appendix S3). For *Andrena erythronii*, the pollen morphospecies it collected the most of into scopal loads was a group comprised of *Acer saccharum* and *Acer negundo* pollen. This morphospecies was underrepresented on average on the bodies of *A. erythronii* specimens (median percentage point difference = −5), while the morphospecies *A. erythronii* collected the least of were overrepresented on average (median percentage point difference = 3; Table 2, Figure 3D). This difference in representation suggests that specimens of *A. erythronii* transported proportionally less pollen on average for *Acer saccharum* and *Acer negundo* compared to other plants. Conversely, for *B. bimaculatus*, the pollen morphospecies collected the most (*Dicentra canadensis*) was overrepresented on its body (median percentage point difference = 6), while the pollen morphospecies collected the least were underrepresented (median percentage point difference = −1; Table 2, Figure 4F). This difference in representation suggests that specimens of *B. bimaculatus* transported proportionally more pollen on average for *D. canadensis* than they did on average for other plants.

DISCUSSION

Pollination biologists have long known that bees remove large quantities of pollen from plant populations, feed most of it to their larvae, and deposit only a tiny fraction onto stigmas (Schlindwein et al., 2005; Danforth et al., 2019). Consistent with this general consensus, the bee specimens in our study to carry five times more pollen in their scopae and corbiculae than on the rest of their bodies. Previous studies have not compared generalist bees' pollen-transport efficiency among their pollen host plants, however. Here we provided the first empirical evidence that generalist bee species' pollen-transport efficiency can differ among the plants from which they collect pollen on a given foraging bout. Specifically, we found that the composition of pollen morphospecies carried on bees' bodies (the pollen that is available for pollination) differed from the composition of morphospecies carried in scopal and corbiculate loads (the pollen the bee has harvested for her offspring) (Figure 2). Most visits to plant species in bee-plant communities are by foragers of generalist bee species (Waser et al., 1996). Our results suggest that accounting for variations in the pollination efficiency of generalist bee foragers on different host plants is likely important for understanding the effects of individual interactions on pollen transfer in bee-plant communities.

A previously unexplored mechanism of variation in pollination efficiency is foraging bout specialization, which is generally thought to be beneficial for plant reproduction due to its effects on heterospecific pollen transfer (Grant, 1950; Bronstein et al., 2006; Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; Brosi, 2016). Our results suggest that foraging bout specialization may also lower pollination efficiency. We found that most foragers were specialized, but that the dominant pollen morphospecies in each forager's pollen load was typically underrepresented on its body. Thus, at the level of the foraging bout, bees' pollen-transport efficiency was lower for the pollen host plants from which they collected the most pollen. This result suggests that specialization on the part of individual bees, even those belonging to generalist bee species, results in a trade-off from the plant's point of view. Visits from specialized individual foragers may result in less heterospecific pollen transfer, which can be good for fitness, but more pollen lost to bees' pollen consumption, which can be bad for fitness (Hargreaves et al., 2010; Parker et al., 2016; Koski et al., 2018). This lowered transport efficiency for more specialized bees has previously been shown for pollen specialist (oligolectic) bee species vs. nonspecialist bee species foraging on the same plant species (Parker et al., 2016). This study demonstrates for the first time that generalist bees can also cause these contrasting effects, but at the scale of the foraging bout, which is the scale at which pollen is transferred.

A trade-off between heterospecific pollen transfer and loss of pollen to bees' pollen consumption has implications for the selective pressures experienced by plants in generalized plant–pollinator communities. Though heterospecific pollen transfer can be a major contributor to pollen limitation, generalized flower morphologies, high overlap in flowering with other species, and other traits that allow for pollinator-sharing are common, suggesting that the fitness benefits of generalization often outweigh the fitness costs associated with heterospecific pollen transfer (Morales and Traveset, 2008;

Ashman and Arceo-Gómez, 2013; Brosi, 2016). It has been suggested that frequent foraging bout specialization by generalist bee species may contribute to the maintenance of floral generalization over evolutionary time by allowing its benefits to more easily outweigh costs (Brosi, 2016). Our results suggest that the extent to which foraging bout specialization can play this role will depend in part on the magnitude by which specialized foragers lower the fitness costs of heterospecific pollen transfer, relative to the magnitude by which they increase the fitness cost of bees' pollen consumption. While the drivers and consequences of heterospecific pollen transfer have been studied in community contexts, neither has been studied in conjunction with the effects of bees' pollen consumption. Future studies that measure the relative effects of heterospecific pollen transfer and bees' pollen consumption on seed set and pollen limitation are an important next step for understanding the evolutionary implications of generalization in plant–pollinator communities.

At the species level, i.e., across individual bees' foraging bouts, bee species collected more pollen from some host plant species than others, and two of the three bee species were less-efficient transporters of pollen for some of their host plant species than for others. However, the effects of foraging-bout specialization on pollen-transport efficiency did not scale up to the species level in a consistent way. The inconsistency of trends was likely due in part to bees of the same species engaging in foraging bout specialization on different plant species in different places; each pollen morphospecies in turn tended to dominate scopal loads at some sites and dates, but was collected by bees in lesser amounts at other places and times. Geographic variation in bees' foraging choices is not unusual; generalist bees are known to forage on different plant species in different places in response to contextual factors that vary in space and time, such as the relative abundance of host plant species and competition with other pollinators. This result does highlight, though, that bee species' pollination efficiency for any given plant species likely varies geographically and temporally. Variation in pollination efficiency across plant populations has been shown in some cases to be driven by spatial variation in pollinator community composition because pollinator taxa can differ in their pollination efficiency (e.g., Koski et al., 2018; Parker et al., 2018). Such context dependency is thought to play a major role in the trajectory of coevolution between plants and their pollinators (Thomson, 2003; Guimarães et al., 2011). Our results point to an additional layer of context dependency: The same bee species may impose different pressures on the same plant species in different places, according to its reliance on that plant as a pollen resource in those places.

CONCLUSIONS

We showed that individual bees frequently transport proportionally less pollen for the host plants on which they specialize during each foraging trip, suggesting that plants visited by specialized foragers trade less heterospecific pollen deposition for greater loss of pollen to bees' pollen consumption. A next step for future research is to assess how variation in bees' pollen-transport efficiency affects their contributions to pollen limitation and seed set, especially in relation to the effects of heterospecific pollen transfer. In general, we feel that more case studies of smaller numbers of interacting species, for which careful measurements of pollen transport, pollen export and pollen deposition are more feasible, are needed as a complement to community wide approaches, to link patterns at community scales with behavior and patterns of pollen transfer.

AUTHOR CONTRIBUTIONS

L.W. and R.W. conceived the study. L.W. collected and analyzed data and drafted the manuscript. T.R. and L.W. identified pollen. J.G. identified bee specimens. R.W. and L.W. revised the manuscript, with comments from T.R. and J.G.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2547d7wwg (Weinman et al., 2023).

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REFERENCES

Alarcón, R. 2010. Congruence between visitation and pollen-transport networks in a California plant-pollinator community. *Oikos* 119: 35–44.

Ashman, T. L., C. Alonso, V. Parra-Tabla, and G. Arceo-Gómez. 2020. Pollen on stigmas as proxies of pollinator competition and facilitation: complexities, caveats and future directions. *Annals of Botany* 125: 1003–1012.

Ashman, T. L., and G. Arceo-Gómez. 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany* 100: 1061–1070.

Barwell, L. J., N. J. B. Isaac, and W. E. Kunin. 2015. Measuring β-diversity with species abundance data. *Journal of Animal Ecology* 84: 1112–1122.

Bronstein, J. L., R. Alarcón, and M. Geber. 2006. The evolution of plant–insect mutualisms. *New Phytologist* 172: 412–428.

Brosi, B. J. 2016. Pollinator specialization: from the individual to the community. *New Phytologist* 210: 1190–1194.

Burkle, L. A., R. E. Irwin, and D. A. Newman. 2007. Predicting the effects of nectar robbing on plant reproduction: implications of pollen limitation and plant mating system. *American Journal of Botany* 94: 1935–1943.

Castellanos, M. C., P. Wilson, and J. D. Thomson. 2003. Pollen transfer by hummingbirds and bumblebees, and the divergence of pollination modes in *Penstemon*. *Evolution* 57: 2742–2752.

Cullen, N., J. Xia, N. Wei, R. Kaczorowski, G. Arceo-Gómez, E. O'Neill, R. Hayes, and T. L. Ashman. 2021. Diversity and composition of pollen loads carried by pollinators are primarily driven by insect traits, not floral community characteristics. *Oecologia* 196: 131–143.

Danforth, B. N., R. L. Minckley, J. L. Neff, and F. Fawcett. 2019. The solitary bees: biology, evolution, conservation. Princeton University Press, Princeton, NJ, USA.

Dormann, C. F., J. Frund, N. Bluthgen, and B. Gruber. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal* 2: 7–24.

Grant, V. 1950. The flower constancy of bees. *Botanical Review* 16: 379–398.

Guimarães, P. R., P. Jordano, and J. N. Thompson. 2011. Evolution and coevolution in mutualistic networks. *Ecology Letters* 14: 877–885.

Harder, L. D., and R. M. D. Barclay. 2008. The functional significance of poricidal anthers and buzz pollination: controlled pollen removal from dodecatheon. *Functional Ecology* 8: 509–517.

Harder, L. D., and J. D. Thomson. 1989. Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *American Naturalist* 133: 323–344.

Hargreaves, A. L., L. D. Harder, and S. D. Johnson. 2010. Native pollen thieves reduce the reproductive success of a hermaphroditic plant, *Aloe maculata*. *Ecology* 91: 1693–1703.

Heinrich, B. 1976. The foraging specializations of individual bumblebees. *Ecological Monographs* 46: 105–128.

Heinrich, B. 1979. 'Majoring' and 'minoring' by foraging bumblebees, *Bombus vagans*: an experimental analysis. *Ecology* 60: 245–255.

Hop, K. D., S. Lubinski, J. Dieck, J. Drake, and S. Menard. 2009. National Park Service Vegetation Inventory Program: Indiana Dunes National Lakeshore, Indiana. National Park Service, Natural Resource Stewardship and Science, Fort Collins, CO, USA.

Hop, K., S. Lubinski, J. Dieck, J. Drake, and S. Menard. 2010. National Park Service Vegetation Inventory Program: Pictured Rocks National Lakeshore, Michigan. National Park Service, Natural Resource Stewardship and Science, Fort Collins, CO, USA.

Hop, K. D., S. Lubinski, J. Dieck, J. Drake, and S. Menard. 2011. National Park Service Vegetation Inventory Program: Sleeping Bear Dunes National Lakeshore, Michigan. Natural Resource Report NPS/GLKN/NRR—011/395. National Park Service, Natural Resource Stewardship and Science, Fort Collins, CO, USA.

Irwin, R. E., A. K. Brody, and N. M. Waser. 2001. The impact of floral larceny on individuals, populations, and communities. *Oecologia* 129: 161–168.

Irwin, R. E., and J. E. Maloof. 2002. Variation in nectar robbing over time, space, and species. *Oecologia* 133: 525–533.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance dependence asymmetries, and coevolution. *American Naturalist* 129: 657–677.

Knight, T. M., T. L. Ashman, J. M. Bennett, J. H. Burns, S. Passonneau, and J. A. Steets. 2018. Reflections on, and visions for, the changing field of pollination ecology. *Ecology Letters* 21: 1282–1295.

Koch, L., K. Lunau, and P. Wester. 2017. To be on the safe site – Ungroomed spots on the bee's body and their importance for pollination. *PLoS One* 12: 1–16.

Koski, M. H., J. L. Ison, A. Padilla, A. Q. Pham, and L. F. Galloway. 2018. Linking pollinator efficiency to patterns of pollen limitation: Small bees exploit the plant–pollinator mutualism. *Proceedings of the Royal Society, B, Biological Sciences* 285: 20180.

Larsson, M. 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia* 146: 394–403.

Li, X. X., H. Wang, R. W. Gituru, Y. H. Guo, and C. F. Yang. 2014. Pollen packaging and dispensing: adaption of patterns of anther dehiscence and flowering traits to pollination in three *Epimedium* species. *Plant Biology* 16: 227–233.

Macior, L. W. 1978. Pollination interactions in sympatric *Dicentra* species. *American Journal of Botany* 65: 57–62.

Martínez del Río, C., and S. H. Bullock. 2017. Parasitismo floral por abejas sociales (Meliponinae; Apidae) en el árbol quiropterófilo Crescentia alata (Bignoniaceae). *Botanical Sciences* 199: 69.

Michener, C. D., and C. W. Retternmeyer. 1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymentoptera, Andrenidae). *University of Kansas Science Bulletin* 35: 1351–1523.

Morales, C. L., and A. Traveset. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences* 27: 221–238.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, et al. 2022. vegan: Community ecology package. Website: https://cran.r-project.org/web/packages/vegan/index.html

Onofri, A. 2020. The broken bridge between biologists and statisticians: a blog and R package. Website: https://www.statforbiology.com

Parker, A. J., N. M. Williams, and J. D. Thomson. 2016. Specialist pollinators deplete pollen in the spring ephemeral wildflower *Claytonia virginica*. *Ecology and Evolution* 6: 5169–5177.

Parker, A. J., N. M. Williams, and J. D. Thomson. 2018. Geographic patterns and pollination ecotypes in *Claytonia virginica*. *Evolution* 72: 202–210.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website: https://www.r-project.org

Sahli, H. F., and J. K. Conner. 2007. Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). *American Journal of Botany* 94: 203–209.

Schlindwein, C., D. Wittmann, C. F. Martins, A. Hamm, J. A. Siqueira, D. Schiffler, and I. C. MacHado. 2005. Pollination of *Campanula rapunculus* L. (Campanulaceae): How much pollen flows into pollination and into reproduction of oligolectic pollinators? *Plant Systematics and Evolution* 250: 147–156.

Smith, C., L. R. Weinman, J. Gibbs, and R. Winfree. 2019. Specialist foragers in forest bee communities are small, social or emerge early. *Journal of Animal Ecology* 88: 1158–1167.

Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualisms. *American Naturalist* 162(Suppl 4): S10-S23.

Stavert, J. R., G. Liñán-Cembrano, J. R. Beggs, B. G. Howlett, D. E. Pattemore, and I. Bartomeus. 2016. Hairiness: the missing link between pollinators and pollination. *PeerJ* 2016: 1–18.

Thomson, J. D. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *Journal of Ecology* 74: 329–341.

Thomson, J. D. 2021. Editorial: How worthwhile are pollination networks? *Journal of Pollination Ecology* 28: I–VI.

Thomson, J. 2003. When is it mutualism? (An American Society of Naturalists presidential address). *American Naturalist* 162(Suppl 4): S1–S9.

Thorp, R. W. 2000. The collection of pollen by bees. *Plant Systematics and Evolution* 222: 211–223.

Toju, H., M. Yamamichi, P. R. Guimarães, J. M. Olesen, A. Mougi, T. Yoshida, and J. N. Thompson. 2017. Species-rich networks and eco-evolutionary synthesis at the metacommunity level. *Nature Ecology and Evolution* 1: 1–11.

Tur, C., B. Vigalondo, K. Trøjelsgaard, J. M. Olesen, and A. Traveset. 2014. Downscaling pollen-transport networks to the level of individuals. *Journal of Animal Ecology* 83: 306–317.

Vázquez, D. P., W. F. Morris, and P. Jordano. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters* 8: 1088–1094.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59: 934–944.

Waser, N. M., L. Chittka, M. V. Price, and N. M. Williams. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.

Weinman, L., T. Ress, and J. Gardner. 2023. Individual bee foragers are less efficient transporters of pollen for the plants from which they collect the most pollen into their scopae. *Dryad, Dataset*. https://doi.org/10.5061/dryad.2547d7wwg

Wood, T. J., and S. P. M. Roberts. 2018. Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. *Biological Journal of the Linnean Society* 124: 732–746.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

APPENDIX S1. Pollen morphospecies identified in body, scopal, and corbiculate pollen samples.

APPENDIX S2. Methods for estimating the factor difference between the number of pollen grains stored in bees' scopae and on their bodies.

APPENDIX S3. AIC model selection tables.

APPENDIX S4. Factor difference between the number of pollen grains stored in bees' scopae and on their bodies.

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