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Pollen carryover, pollinator movement, and spatial context impact the delivery of pollination services in apple orchards

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Abstract

Assessing the relative contributions of different pollinator taxa to pollination services is a central task in both basic eco-evolutionary research and applied conservation and agriculture. To that end, many studies have quantified single-visit pollen deposition and visitation frequency, which together determine a pollinator species' rate of conspecific pollen delivery. However, for plant species that require or benefit from outcrossing, pollination service quality further depends upon the ratio of outcross to self-pollen deposited, which is determined by two additional pollinator traits: pollen carryover and movement patterns among genetically compatible plant individuals. Here, we compare the pollination capacities of managed honey bees, native bumble bees, and native mining bees in apple—a varietally self-incompatible commercial crop—when pollen carryover and pollinator movement patterns are considered. We constructed simulation models of outcross pollen deposition parameterized using empirically measured single-visit pollen deposition, visitation frequency, and probabilities of intertree movement exhibited by each pollinator type, as well as pollen carryover patterns simulated based on parameters reported in the literature. In these models, we also explicitly specified the spatial relationships among cross-compatible trees based on field-realistic orchard layout schemes. We found that estimated pollination service delivery was considerably reduced for all pollinator types when pollen carryover and pollinator movement patterns were considered, as compared to when only single-visit pollen deposition and visitation frequency were considered. We also found that the performance of different pollinator types varied greatly across simulated orchard layout schemes and pollen carryover scenarios, including one instance where bumble and mining bees reversed their relative rankings. In all simulations, native bumble and mining bees outperformed managed honey bees in terms of both outcross pollen delivery per unit time and per flower visited, with disparities being greatest under scenarios of low pollen carryover. We demonstrate the degree to which pollination studies may reach inaccurate conclusions regarding pollination service delivery when pollen carryover and pollinator movement patterns are ignored. Our finding of the strong context dependence of pollination efficiency, even within a single plant–pollinator taxon pair, cautions that future studies in both basic and applied pollination biology should explicitly consider the ecological context in which pollination interactions take place.

KEYWORDS

Andrena, *Apis*, *Bombus*, crop pollination, geitonogamy, self-incompatibility, simulation model, visitation frequency

INTRODUCTION

Animal-mediated pollination is essential for the maintenance of terrestrial biodiversity (Ollerton et al., 2011). Thus, evaluating functional differences among pollinator taxa (i.e., in addition to numerical differences) is important in both basic eco-evolutionary research (e.g., Barrios et al., 2016; Medel et al., 2018; Stebbins, 1970) and applied conservation and agriculture (e.g., Jauker et al., 2012; Rader et al., 2009; Vivarelli et al., 2011). In particular, there exist a number of frameworks for quantifying the contributions of pollinator taxa to the delivery of pollination services (reviewed and formalized by Ne'eman et al. [2009]). In empirical studies, researchers often define the contribution of a pollinator taxon as the product of its visitation frequency and its single-visit conspecific pollen deposition (e.g., Medel et al., 2018; Rader et al., 2012; Reynolds et al., 2012). The product of these two measures provides an estimate of the rate of conspecific pollen delivery by a given pollinator, yielding a useful metric for directly comparing the relative contributions of different pollinator species. However, not all conspecific pollen grains deposited are equally beneficial in all cases. For plant species that require or benefit from outcrossing (Igic & Kohn, 2006), pollination service quality further depends upon the ratio of outcross to self-pollen deposited, which is determined by two additional traits of a pollinator: its pollen carryover (Thomson & Plowright, 1980)—that is, the rate at which its deposition of pollen acquired from a previous donor declines as it visits successive flowers—and its tendency to move between plants as opposed to continuing to visit flowers within an individual plant (hereafter “switching rate”; Free, 1960; Klinkhamer & de Jong, 1993). Although these two pollinator traits have each been studied individually, they have hitherto only rarely been explicitly considered in studies that seek to quantify pollination service delivery. Given the key role of these two traits in determining outcross pollen deposition, it is likely that ignoring these measures leads to an incomplete understanding of the relative contributions of different pollinators to a plant species' total outcross pollen receipt.

The phenomenon of pollen carryover, which causes outcross pollen deposition to decline as a pollinator successively visits flowers on the same plant, occurs presumably through grooming, incidental loss, or dilution with freshly acquired self-pollen (Morris et al., 1995). In the latter case, the freshly acquired self-pollen may then be deposited onto stigmas of the same plant individual (i.e., geitonogamy; Arroyo, 1976), such that outcross pollen grains constitute only a subset of the conspecific grains deposited. Pollen carryover has been measured for a number of pollinator and plant taxa (Morris et al., 1994), and numerous mathematical models have been developed to understand the mechanism underlying pollen carryover (Cresswell et al., 1995; Morris et al., 1995; Rademaker et al., 1999). Although few studies have systematically quantified differences between pollinator taxa in their pollen carryover patterns, existing data suggest that pollen carryover likely differs across pollinator taxa as well as across plant species (Castellanos et al., 2003; Santa-Martinez et al., 2021; Waser, 1988; but see Cresswell et al., 1995). Differences in pollen carryover likely contribute to variation among pollinator taxa with respect to their overall ability to deliver outcross pollen, but to what degree remains an open question.

Compared to pollen carryover, pollinator switching rate has received more recognition as a key factor in pollination service delivery, largely in the context of examining the role of geitonogamy (Arroyo, 1976) in plant mating system evolution (e.g., Devaux et al., 2014; Harder & Barrett, 1995; Klinkhamer & de Jong, 1993; Liao & Harder, 2014). Each time a pollinator switches from one compatible plant individual to another, the portion of the pollen carryover process driven by the accumulation of self-pollen on the pollinator's body from previously visited flowers is effectively “reset,” as all pollen grains it carries to a new plant individual are presumably outcross. Thus, pollinator switching rate plays a major role in determining the degree to which pollen carryover erodes the quantity of outcross pollen deposited. A number of studies to date have quantified switching rates of different pollinator taxa (e.g., Brunet & Sweet, 2006; Eeraerts et al., 2020; Mitchell et al., 2004), and one recent study demonstrated that flowers visited by pollinators with low switching rates produced offspring with lower vigor, consistent with lack of outcross pollen (Travis & Kohn, 2023). It thus appears important to incorporate this metric into quantitative estimates of the relative contribution of different pollinator taxa to the total outcross pollen received by a given plant population. Further, switching rate is known to be context-dependent even within the same interacting pair of plant and pollinator species, being influenced by factors such as the size of an individual plant (LoPresti et al., 2018; Mitchell et al., 2004), the size of a floral resource patch (Cresswell, 1997), plant architecture (Liao & Harder, 2014), and interactions among co-foraging flower visitors (Brittain et al., 2013; Greenleaf & Kremen, 2006; Sapir et al., 2017). An additional complication is that the effective switching rate may be lower than the observed movement of pollinators would suggest when switches occur between genetically identical individuals, such as those that grow in clonal stands (Eckert, 2000). This context dependence also needs to be considered when attempting to accurately evaluate the relative contributions of different pollinator species to pollination services.

Here, we address the knowledge gap concerning the importance of pollen carryover and pollinator switching rate in pollination service delivery by examining outcross pollen deposition by three pollinator taxa in apple orchards. As apple is a pollinator-dependent crop, there is a long history of investigation into its pollinators and pollen receipt requirements (Free, 1966a; Park et al., 2016; Sáez et al., 2018; Thomson & Goodell, 2001; Visser et al., 1988), though each previous study generally investigated only one or two aspects of pollination. Apple orchards represent an ideal system for this research because most commercial apple varieties are self-incompatible at the cultivar level (Ramírez & Davenport, 2013), yet growers usually arrange apple trees in single-cultivar rows or blocks for efficient and scalable orchard management. These orchard layout schemes mean that even intertree visits will frequently result in the deposition of incompatible pollen (Free, 1966a; Kron et al., 2001). In such a system, pollinator switching rate, especially between rows of cross-compatible trees, plays an important role in determining the frequency with which cross-compatible pollen is transferred during a floral visit (Campbell et al., 2017; Eeraerts et al., 2020). In the same vein, pollen carryover patterns will determine the number of flowers receiving cross-compatible pollen each time a pollinator switches between two cross-compatible trees. Further, in apple orchards, different layout schemes of cross-compatible cultivars (e.g., in alternating rows vs. in large blocks) will result in different probabilities that a given switching event will occur between two cross-compatible trees (Sáez et al., 2018). Hence, apple orchards allow for a straightforward test of how one aspect of ecological context (namely, the spatial mosaic of clones) influences the effective switching rates of pollinators.

In this apple orchard study system, we empirically measured single-visit pollen deposition, visitation frequency, and switching rate (both within and across rows) of three pollinator taxa. We then simulated patterns of pollen carryover, pollination requirement, and orchard layout schemes to test the general hypothesis that pollinator single-visit pollen deposition, visitation frequency, switching rate, and pollen carryover interact with one another and with spatial context to jointly determine the relative outcross pollen delivery rates of pollinators. Specifically, we quantified the impacts of these variables on two indices: the number of cross-compatible grains deposited (1) per unit time and (2) per flower visited. In this paper, we will refer to the first index as "temporal efficiency" and the second as "resource efficiency," although we recognize that the wider literature has assigned various names to these indices (Ne'eman et al., 2009). We expect that orchard layout, pollination requirement, and pollen carryover would have a sufficiently strong influence on outcross pollen delivery that the temporal or resource efficiency ranks of pollinator taxa might reorder with different combinations of parameters for these variables.

MATERIALS AND METHODS

Study system

Apple (Rosaceae: *Malus pumila* Mill.), grown in temperate climates throughout the world, is among the most economically important fruit crops (Janick & Moore, 1996). Successful pollination in apple generally requires cross-pollination between different cultivars because of its S-RNAse-driven self-incompatibility system (Ramírez & Davenport, 2013). This varietal self-incompatibility means that much of the pollen transfer occurring in single-cultivar rows or blocks may be ineffective; among six North American fruit crops examined in a recent cross-continental study, apple was the most frequently pollination-limited (Reilly et al., 2020). Apple growers frequently promote effective pollen delivery by arranging orchards with blocks of cross-compatible trees adjacent to one another, or inserting "pollinizer" (i.e., cross-fertile pollen donor) trees among trees of a single cultivar (Ramírez & Davenport, 2013).

Although apple orchards worldwide frequently attract diverse and abundant wild pollinator assemblages (Atwood, 1933; Blitzer et al., 2016; Földesi et al., 2016; Garratt et al., 2016; Wu et al., 2021), many apple growers nevertheless rent or maintain colonies of western honey bees (Apidae: *Apis mellifera* L.) to enhance pollination services (Nalepa et al., 2020; Park et al., 2018). For our study, we compared three focal pollinator types that were among the most abundant taxa in our study orchards: honey bees, mining bees (Andrenidae: *Andrena*), and bumble bees (Apidae: *Bombus*). These taxa exhibit differences in morphology and behavior that are likely to translate into differences in temporal and resource efficiency of pollination service delivery. Honey bees collect pollen as nectar-moistened pellets in their corbiculae (i.e., pollen-carrying baskets; Thorp, 2000), effectively rendering collected pollen unavailable for pollination. They are also known to methodically visit large numbers of flowers on a single plant individual (Brittain et al., 2013; Free, 1966b; Greenleaf & Kremen, 2006; Travis & Kohn, 2023). Bumble bees also collect moistened pollen in corbiculae, but at the time of apple blooms in our study region, most bumble bee individuals we encountered did not collect pollen because they were young queens that had presumably not yet established nests. The many species of mining bees that occurred in our system all collect dry pollen on their hind legs and propodeum, where loose pollen grains may remain available for transfer to stigmas (Thorp, 2000).

Empirical single-visit pollen deposition data

We collected single-visit pollen deposition data on two rows of Honeycrisp apple trees at Cornell University's experimental orchard (Ithaca, New York, USA) over the course of 5 days in May 2010. Full details are reported by Park et al. (2016). Briefly, we used a 0.5-m "interview wand" (Thomson & Goodell, 2001) to offer virgin, emasculated Honeycrisp apple flowers to freely foraging bumble, honey, and mining bees. Bees were "interviewed" opportunistically, roughly proportional to their relative abundance at the site. After a single bee had foraged upon and then departed from the offered flower, we mounted the five stigmas of the flower on a microscope slide and then counted adhering apple pollen grains across all five stigmas at 200× magnification.

Empirical pollinator behavior data

We recorded pollinator behavior at two commercial orchards in the Greater Toronto Area (Ontario, Canada) on warm, calm days in May and June 2019 and May 2020. We walked through an orchard and haphazardly chose a focal foraging bee to follow. We followed the focal bee as it foraged for as long as we could, classifying each interfloral move it made as one of four types of transitions: to a flower on (1) the same tree, (2) another tree within the same row, or (3) a tree in a different row; or (4) unknown. Since we invariably lost sight of the bee after it departed the last flower we were able to observe (usually as it departed from the vicinity of the tree it was visiting), the final transition for each observed individual is necessarily inferred based on the bee's flight trajectory at the time we last saw it. In all, we inferred 139 of the 302 within-row transitions and 137 of the 177 across-row transitions. All instances in which we lost sight of the bee without clearly witnessing its direction of departure from the last flower we observed were assigned the "unknown" transition. We also recorded the total amount of time we spent following each bee using a stopwatch.

Simulated temporal and resource efficiency of pollination service delivery

Using our empirical data, we simulated temporal and resource efficiency of the three focal pollinator types in five orchard scenarios with R version 4.0.3 (R Core Team, 2020). One scenario involved a hypothetical apple cultivar that exhibits no self-incompatibility (hereafter referred to as "non-SI," Figure 1a), and four were field-realistic orchard layout schemes of self-incompatible apple cultivars, as follows: diverse cultivars fully interspersed with one another ("interspersed," Figure 1b), single rows of distinct cultivars ("rows," Figure 1c), insertion of a commercially viable pollinizer cultivar within a monoculture of a main cultivar at a ratio of 1:4, after Sáez et al. (2018) ("pollinizers," Figure 1d), and large blocks consisting of six contiguous rows of each cultivar ("blocks," Figure 1e). For each simulated individual of our three focal pollinator types, the general process of the simulations for each of the field-realistic layout schemes is as follows:

1. Randomly generate a sequence, $\mathbf{seq_1}$, here defined as the number of flowers that an observed individual visits on a single tree. Sequences were drawn from a negative-binomial distribution constrained to be >0, parameterized in the R package fitdistrplus (Delignette-Muller & Dutang, 2015) using our empirically observed visitation data for the focal pollinator type. All sequences ending with a transition of "unknown" (i.e., where we were unsure where the

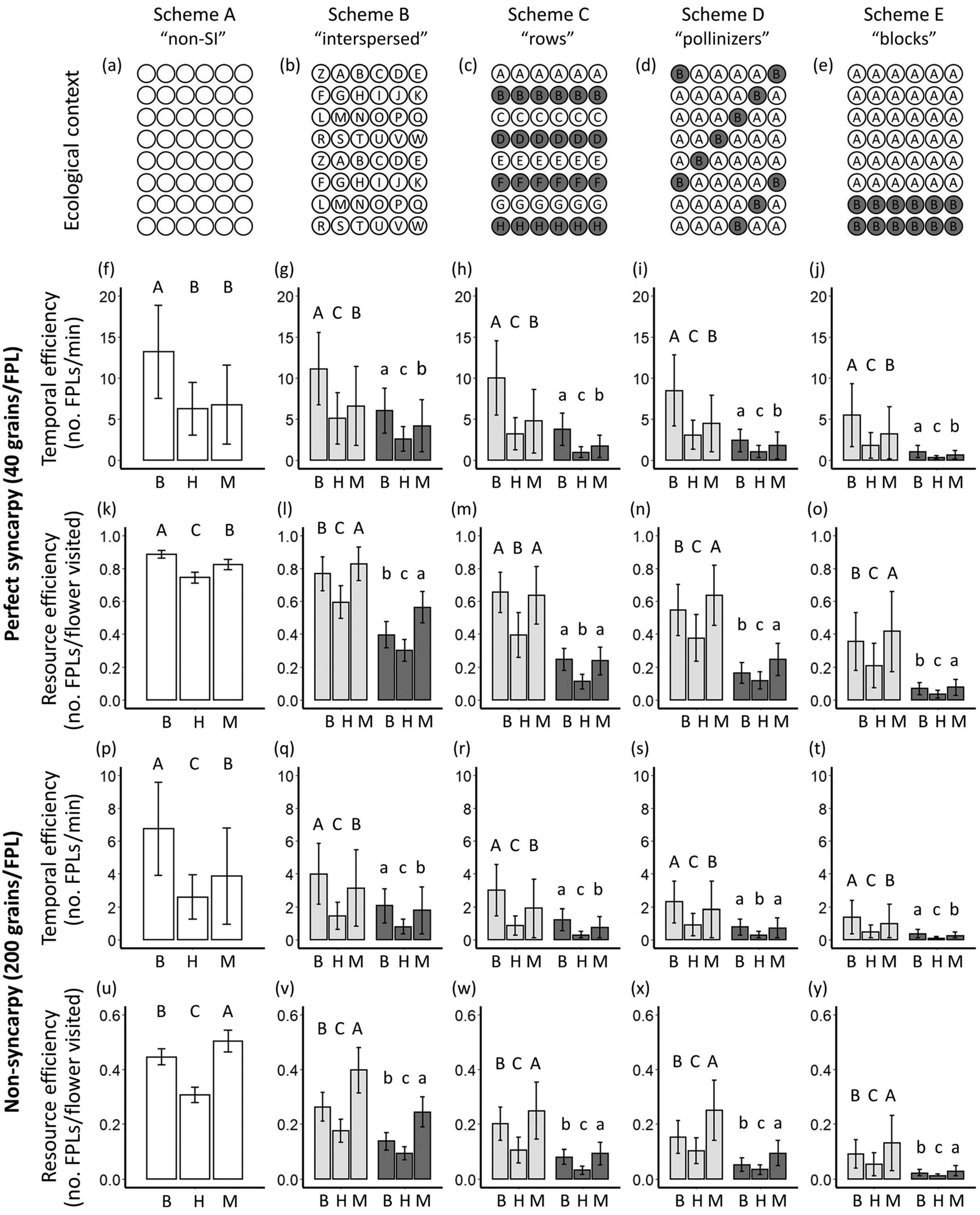

FIGURE 1 Legend on next page.

bee flew to or whether it had indeed departed from the tree) were excluded when parameterizing the distribution. In cases where an individual bee was followed across multiple trees, we treated each visited tree as an independent sequence.

2. Randomly generate a transition vector, $\mathbf{vec_1}$, describing whether the bee flew to a tree in the same row or a different row, based on the empirically observed ratio of the two kinds of transitions.
3. Determine whether $\mathbf{vec_1}$ causes the simulated individual to fly to a compatible (i.e., different cultivar) or incompatible (i.e., same cultivar) tree based on the layout of the orchard being considered. Specifically, in "interspersed," all transition vectors lead to a compatible tree. In "rows," transition vectors across rows lead to a compatible tree. In "pollinizers," all transition vectors lead to a compatible tree at a rate of 20% when departing from a main cultivar tree and a rate of 80% when departing from a pollinizer tree. In "blocks," transition vectors across rows lead to a compatible tree at a rate of 16.7%.
4. Randomly generate the next sequence, $\mathbf{seq_2}$, as in Step 1 above. When $\mathbf{seq_2}$ takes place in a compatible tree (as determined in Step 3 above), it is treated as a new, distinct sequence. Alternatively, if $\mathbf{seq_2}$ takes place in an incompatible tree, it is not treated as a new sequence; rather, the number of flowers visited in $\mathbf{seq_1}$ and $\mathbf{seq_2}$ are summed into a single sequence.
5. Repeat Steps 2–4 until the desired number of trees visited during the foraging bout, $\boldsymbol{i}$, from $\mathbf{seq_1}$ to $\mathbf{seq}_{\boldsymbol{i}}$ and $\mathbf{vec_1}$ to $\mathbf{vec}_{\boldsymbol{i-1}}$ have been sampled.
6. For each distinct sequence of floral visit (i.e., after combining consecutive sequences during which the simulated individual did not land in a new compatible tree), randomly generate the number pollen grains deposited on the first flower visited in the sequence. Pollen deposition values were drawn from a negative-binomial distribution constrained to be >0, parameterized in in the fitdistrplus R package using our empirically observed single-visit pollen deposition data for the focal pollinator type. Since our empirical pollen deposition measurements were performed on emasculated flowers (Park et al., 2016), we treat the entirety of this pollen load as outcross pollen.
7. Simulate quantities of outcross pollen deposited on subsequent flowers in each sequence using the following pollen carryover equation from Morris et al. (1994):

$$P_n = P_o \lambda n^b \prod_{k=1}^{n-1} \left(1 - \lambda k^b\right), \tag{1}$$

where P_n is the number of pollen grains deposited on the nth flower visited on an individual plant, P_o represents the total amount of pollen deposited on the individual plant, λ the steepness of the curve, and b the degree to which the curve exhibits a tail longer than given by purely exponential decay (a common feature of empirical carryover curves; Morris et al., 1994). In our simulation, we modify the equation above by setting P_0 equal to 1 and scaling all pollen deposition values to P_1, to obtain the following equation:

$$P_n = \frac{P_1 n^b \prod_{k=1}^{n-1} \left(1 - \lambda k^b\right)}{(1 - \lambda)}. \tag{2}$$

To evaluate the effect of pollen carryover patterns on outcross pollen delivery, we constructed models using two distinct sets of pollen carryover parameters that represent extreme values of empirically measured λ reported by Morris et al. (1994), that is, $\lambda = 0.036$ and $\lambda = 0.335$, respectively. For both sets of simulations, we chose the median b value reported by Morris et al. (1994), that is, $b = -0.289$, which produces a moderately long-tailed carryover curve compared to a purely exponential equation.

8. Re-express counts of outcross pollen grains deposited on each visited flower in terms of full pollen loads (FPLs)

FIGURE 1 Schematics and results of simulations in five apple orchard layout schemes: (a) hypothetical scenario in which apple trees exhibit no self-incompatibility; (b) diverse cultivars fully interspersed with one another; (c) alternating rows of distinct cultivars; (d) insertion of a pollinizer cultivar within a main cultivar at a ratio of 1:4; (e) large blocks consisting of six contiguous rows of each cultivar. Bar plots (f–j) depict simulated temporal efficiency (i.e., number of full pollen loads [FPLs] delivered per minute) by three pollinator types (B: bumble bees, H: honey bees, M: mining bees) in their corresponding orchard layout schemes under the assumption of perfect syncarpy (in which a FPL is defined as 40 outcross grains); bar plots (k–o) similarly depict simulated resource efficiency (i.e., number of FPLs delivered per visited flower) under assumption of perfect syncarpy. Bar plots (p–t) and (u–y) also depict temporal and resource efficiency, respectively, but under the assumption of nonsyncarpy (in which a FPL is defined as 200 outcross grains). Bars show means ±1 SD (which is independent of sample size); bar colors correspond to pollen carryover levels used in simulations (white: no pollen carryover; light gray: high carryover; dark gray: low carryover). Shared letters above bars indicate pollinator types not statistically distinct from one another (i.e., $p > 0.05$) in pairwise tests after Tukey adjustment, with capital and lowercase letters indicating separate analyses.

(i.e., number of grains necessary for optimal seed set and production of high-quality fruit). Visser et al. (1988) estimated that optimal pollen tube growth for fruit set in apples necessitates 40 germinated (presumably outcross) pollen grains per stigma, of which there are typically five in an apple flower. Using this information, we constructed models using two different levels of pollination requirement: (1) assuming perfect syncarpy, which has been reported in some apple varieties (Sheffield, 2005), a single fully pollinated stigma will yield fruit, hence a FPL constitutes 40 outcross grains; and (2) assuming nonsyncarpy, a FPL necessitates 200 outcross grains summed across the five stigmas. Quantities of deposited pollen grains less than a FPL are divided by the FPL to yield fractional pollen loads; quantities greater than a FPL are treated as a single FPL.

9. Sum fractions of FPLs across all flowers visited in all sequences from $\mathbf{seq_1}$ to $\mathbf{seq}_i$ as the total amount of pollination service delivered by the focal individual.
10. For each focal bee individual, randomly generate a visitation frequency (i.e., number of flowers visited per second), parameterized in the fitdistrplus R package using our empirically observed visitation data for the focal pollinator type. Visitation frequency values were drawn from a Weibull distribution after log(x) transformation for bumble bees, a gamma distribution after cube-root transformation for honey bees, and a gamma distribution for mining bees. Multiply the inverse of visitation frequency by the number of flowers visited from $\mathbf{seq_1}$ to $\mathbf{seq}_i$ as the total amount of time spent foraging.
11. For each focal individual, divide the total number of FPLs delivered by (1) the total amount of time spent foraging to yield temporal efficiency and (2) the number of flowers visited to yield resource efficiency.

For each field-realistic scheme, we repeated each simulation for 500 individuals of each pollinator type over the course of foraging on 25 trees each. For the “non-SI” scheme, in which tree genotype and pollen carryover have no significance, we simulated 500 individuals of each pollinator type visiting 100 flowers each. Here, we assigned each flower a single-visit pollen deposition value randomly generated as in Step 6 above and assigned each pollinator individual a visitation frequency randomly generated as in Step 10 above. Simulation code and raw data are available from Open Science Framework in Hung et al. (2023) at https://doi.org/10.17605/OSF.IO/VF3X5.

Statistical analyses

All statistical analyses were performed in R. We used the lme4 package (Bates et al., 2015) to construct generalized linear mixed models (GLMMs) to compare the three focal pollinator types with respect to their empirically measured pollination metrics—namely, single-visit pollen deposition, visitation frequency, and switching rate—and used the emmeans package (Lenth, 2020) to perform pairwise tests of statistical significance between pollinator types, with a Tukey adjustment for multiple pairwise comparisons. We compared single-visit pollen deposition using a Poisson GLMM with a log link, with sampling date as a random term. We compared visitation frequency using a Poisson GLMM by including the number of flowers visited by an individual bee as the dependent variable and its length of documented foraging time as the offset variable, with sampling date and year as random terms. We compared total switching rate (i.e., the likelihood of transitioning to another tree in either the same or a different row) using a binomial GLMM with a complementary log–log link, as in Eeraerts et al. (2020). In this binomial GLMM, each pollinator individual is a data point, the dependent variable is the ratio of the number of across-tree transitions to within-tree transitions, and sampling date and orchard identity are random terms. In cases where a bee was assigned a final transition of “unknown,” we truncated its series of observed flower visits at the last transition event in which we observed it leave one tree and arrive at another. Finally, we used an identically constructed model to compare across-row switching rates, where the dependent variable is the ratio of the number of across-row transitions to the sum of within-tree and within-row transitions. We selected random terms for each of the aforementioned models by constructing candidate models that included all possible combinations of variables pertaining to sampling events (sampling date for single-visit pollen deposition and sampling year, sampling date, orchard identity, and observer identity for visitation frequency and switching rate), fitted as random-intercept terms, and choosing the model whose combination of random terms resulted in the lowest Akaike information criterion (AIC) value (Akaike, 1974).

The use of frequentist statistics to compare outputs of simulation models has been discouraged by some for two reasons: first, significant p-values could often be obtained with a sufficiently large number of simulation iterations; and second, statistical rejection of the null hypothesis that samples are drawn from the same distribution is meaningless when the distributions are ultimately predetermined by model parameters (White et al., 2014). Hence, we examined differences across models constructed using different simulation parameters via qualitative comparisons of effect sizes (White et al., 2014). Nonetheless, we chose to perform statistical comparisons of pollinator types to one another within each model, since the relative ranking of pollinator types was not deterministically governed by simulation parameters but, rather, depended upon how the populations of random values generated from empirically informed distributions interacted with one another and with simulation parameters. Even in this case, we report only the qualitative results of these comparisons (i.e., $p > 0.05$ or < 0.05 in pairwise post-hoc comparisons between pollinator types) for the purpose of formally ranking pollinator types relative to one another.

To compare the three focal pollinator types with respect to their simulated temporal and resource efficiency, and especially to investigate whether different scenarios of orchard layout and pollen carryover led to rank reorders among pollinator types, we constructed gamma generalized linear models (GLMs) with an inverse link. We constructed a separate model for each combination of orchard layout, pollen carryover level, and pollination requirement (i.e., nine models each for temporal and resource efficiency for each level of pollination requirement, for a total of 36 models). Here, the dependent variable is either the number of full loads of compatible pollen deposited per minute (i.e., temporal efficiency) or per visited flower (i.e., resource efficiency). We again used the emmeans package in R to perform pairwise tests of statistical significance between pollinator types, with a Tukey adjustment for multiple pairwise comparisons. Finally, to examine whether scenarios of orchard layout and pollen carryover influenced the magnitude of differences among pollinator types, we examined the effect sizes of the statistical interactions among pollinator category, orchard layout, and pollen carryover level, within each level of pollination requirement. To do so, we constructed a gamma GLM that included the aforementioned variable as main effects and three additional gamma GLMs that included, respectively, the interaction between pollinator category and the other two variables and the three-way interaction among all three variables. We obtained Cox and Snell's pseudo-R^2 (Cox & Snell, 1989) values from each of the GLMs using R package DescTools (Signorell, 2020) and used them to calculate Cohen's f^2 (Cohen, 1988) effect size for each interaction term, where $f^2 \geq 0.02$ corresponds to a small effect size and $f^2 \geq 0.15$ and $f^2 \geq 0.35$ correspond to medium and large effect sizes, respectively. We calculated effect sizes for both temporal and resource efficiency; the "non-SI" scheme (Figure 1a), which did not model pollen carryover, was excluded from this analysis.

RESULTS

Empirical pollination metrics

With respect to single-visit pollen deposition on emasculated flowers, mining bees ($n = 49$) deposited the largest number of pollen grains, followed by bumble bees ($n = 8$) and then honey bees ($n = 51$; Figure 2a). All three types generally deposited fewer than the 200 pollen grains (i.e., 40 grains per stigma) thought to be necessary for optimal pollen tube growth (Visser et al., 1988) when nonsyncarpy is assumed. While foraging, bumble bees ($n = 95$) visited the most flowers per minute, followed by honey bees ($n = 194$) and then mining bees ($n = 117$; Figure 2b). Total switching rates were highest for mining bees ($n = 89$) and lowest for honey bees ($n = 155$), with bumble bees ($n = 91$) not differing from either mining or honey bees (Figure 2c). Mining bees and bumble bees both had higher across-row switching rates than did honey bees, with the former two types not differing from each other (Figure 2d). Statistical outputs of the pairwise comparisons are reported in Appendix S1: Table S1.

Simulated temporal efficiency

In both perfect syncarpy and nonsyncarpy scenarios, bumble bees had the highest temporal efficiency out of the three pollinator types (Figure 1f–j and p–t), except in the case of the "pollinizer" scheme under the nonsyncarpy scenario (Figure 1s), in which their temporal efficiency was not distinguishable from that of mining bees when we simulated low pollen carryover. Mining bees, in turn, consistently outperformed honey bees, except in the case of the "non-SI" scheme under the perfect syncarpy scenario (Figure 1f), in which their temporal efficiency was not distinguishable from that of honey bees. In both pollination requirement scenarios, the magnitude of differences among pollinator types varied to a small degree due to orchard layout (Cohen's $f^2 = 0.059$ with syncarpy; $f^2 = 0.051$ without syncarpy) and pollen carryover curve shape ($f^2 = 0.041$ with syncarpy; $f^2 = 0.042$ without syncarpy) individually and to a large degree due to the interaction between the two ($f^2 = 0.41$ with syncarpy; $f^2 = 0.32$ without syncarpy). As expected, overall temporal efficiency decreased as the likelihood of switching to a cross-compatible tree (i.e., effective switching rate) decreased in both pollination requirement scenarios, being highest in the "non-SI" scheme, followed by "interspersed," then "rows" and "pollinizers" with similar overall levels (except in the case of bumble bees, whose temporal efficiency was distinctly higher in "rows"), and then, finally, "blocks." Temporal efficiency also scaled positively with pollen carryover level, with the impact of varying carryover increasing as effective switching rate decreased (Figure 1f–j and p–t).

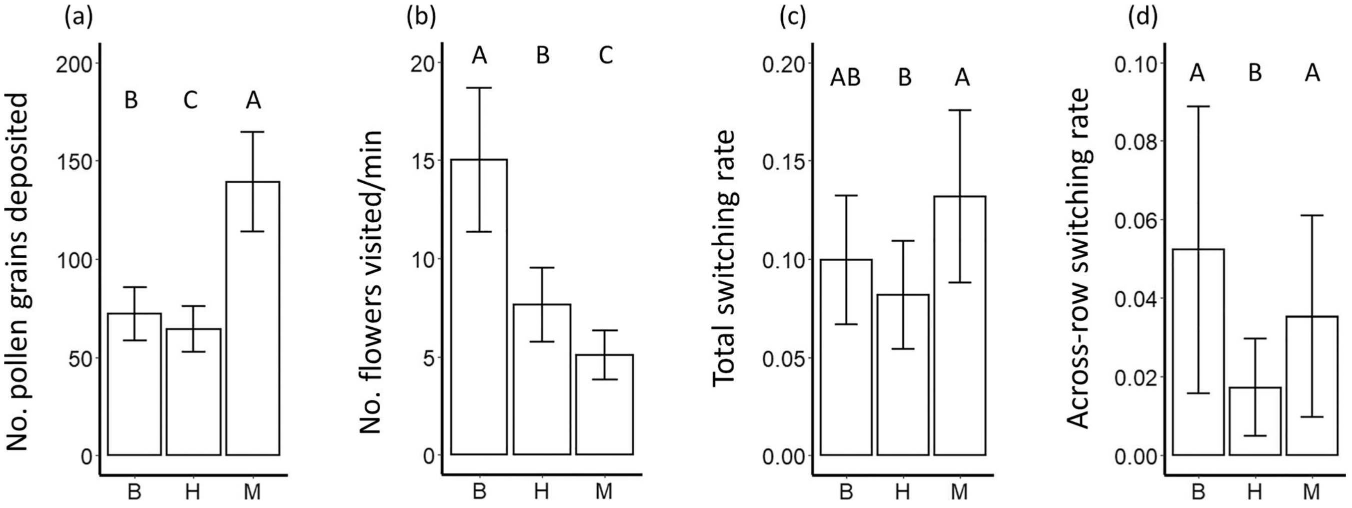

FIGURE 2 Empirically measured metrics of pollination capacity for three pollinator types (B: bumble bees, H: honey bees, M: mining bees) in apple orchards. Bar plots show (a) number of pollen grains deposited during a single visit to a virgin, emasculated flower; (b) number of flowers visited per minute; (c) total switching rate, that is, likelihood of flying to a different tree in any row upon exiting a flower; and (d) across-row switching rate, that is, the likelihood of flying to a tree in a different row upon exiting a flower. Bars show estimated marginal means and SE; letters above bars are as in Figure 1.

Simulated resource efficiency

Resource efficiency ranks reordered between bumble and mining bees in the perfect syncarpy scenario, with bumble bees ranking first in the "non-SI" scheme (Figure 1k) and ranking co-first alongside mining bees in the "rows" scheme under both pollen carryover scenarios (Figure 1m). In the remainder of the schemes, mining bees ranked first (Figure 1l,n,o); and in all schemes, honey bees ranked last. In contrast, in the nonsyncarpy scenario, pollinator types had consistent ranks, with mining bees ranking first, bumble bees ranking second, and honey bees ranking third in all scenarios (Figure 1u–y). As was the case for temporal efficiency, the magnitude of differences among pollinator types varied to a small degree due to orchard layout (Cohen's $f^2 = 0.049$ with syncarpy; $f^2 = 0.065$ without syncarpy) and pollen carryover curve shape ($f^2 = 0.053$ with syncarpy; $f^2 = 0.066$ without syncarpy) individually and to a large degree due to the interaction between the two ($f^2 = 0.88$ with syncarpy; $f^2 = 0.63$ without syncarpy). The qualitative effects of orchard layout and pollen carryover on overall levels of resource efficiency mirrored those in models of temporal efficiency (Figure 1l–o and u–y).

DISCUSSION

Although pollinator movement and pollen carryover patterns have been extensively considered in studies of floral evolution (Devaux et al., 2014; Harder & Barrett, 1995; Morris et al., 1995; Thomson & Plowright, 1980), these phenomena are severely underrepresented in efforts to evaluate functional differences among pollinator species. Given that nearly half of all plant species are thought to be self-incompatible (Igic & Kohn, 2006) and many more benefit from outcrossing, it would appear that counting all deposited conspecific pollen grains without discriminating between outcross and self-pollen may lead to erroneous conclusions, especially for those species without mechanisms to minimize geitonogamy (e.g., temporal or spatial herkogamy). Our study demonstrates that in field-realistic scenarios, in which self-incompatible plants may present numerous flowers and grow in close proximity to incompatible close relatives or clones, failure to account for pollinator switching behavior, pollen carryover, and ecological context will consistently result in overestimating pollinator efficiency (in our case, by up to a factor of 30 when comparing honey bee resource efficiency in the "non-SI" scheme vs. the "blocks" scheme with low carryover in the nonsyncarpy scenario). Additionally, the rank reorders we observed between pollinator types when we varied our simulation parameters imply that variation in pollinator switching behavior, ecological context, and pollen carryover can equal or exceed the importance of variation in metrics that are far more commonly measured, such as single-visit pollen deposition and visitation frequency. Furthermore, the rank reorders that resulted from varying orchard layout schemes and pollination requirements of the recipient plant (i.e., number of grains required for FPL) underscore the fact that the effectiveness of a pollinator for a given plant species is not an intrinsic attribute of the pollinator but, rather, an emergent property that depends upon the context of the interaction between plant and pollinator.

Currently, no empirical data are available on the pollen carryover differences among pollinator taxa for apple (or any tree fruit crop, for that matter). However, differences among pollinators in their floral-approach behavior (Park et al., 2016), pollen-packing behavior (Parker et al., 2015), resource-seeking behavior (Thomson & Goodell, 2001), and morphology could likely lead to different pollen carryover patterns. Pollinators may also exhibit constancy to preferred or familiar cultivars (Free, 1966b), such that movement rates between adjacent rows of different cultivars may not equal those between adjacent rows of the same cultivar. If indeed pollinator types differ with respect to their pollen carryover patterns and their degree of varietal constancy, then simulation models parameterized with such pollinator-specific attributes could yield even greater divergence from classical models where only visitation frequency and single-visit deposition are considered. These "known unknowns" underscore the pressing need to collect empirical data on the difficult-to-measure aspects of plant–pollinator interactions in order to further our understanding of pollination service delivery in both agricultural (e.g., Jauker et al., 2012; Rader et al., 2009; Vivarelli et al., 2011) and evolutionary (e.g., Barrios et al., 2016; Medel et al., 2018; Stebbins, 1970) contexts.

Although our models omitted potentially important sources of variation, such as those discussed above, our results have direct applicability to the management of apple orchards to enhance pollination service delivery and reduce the widespread pollen limitation reported by Reilly et al. (2020). First, our results argue for stronger focus on harnessing populations of nonmanaged native bees already commonly found in apple orchards. For example, in the most extreme examples from our simulation models, bumble and mining bees are 4.5 and 2.7 times as temporally efficient compared to honey bees, respectively (Figure 1r). For bumble bees, whose single-visit pollen deposition rates were only slightly greater than those of honey bees (Figure 2a), their superior temporal efficiency may be attributable to their much higher visitation frequencies (Figure 2b) and across-tree switching rates (Figure 2d). In the case of mining bees, their higher single-visit pollen deposition rates (Figure 2a) were insufficient to compensate for their inferior visitation frequencies compared to honey bees when switching rates and self-incompatibility were not explicitly modeled, at least in the scenario with perfect syncarpy (Figure 1f). Differences among pollinator taxa with respect to their switching behavior may explain the seemingly contradictory findings that diverse pollinator assemblages lead to enhanced apple pollination and fruit set (Blitzer et al., 2016; Campbell et al., 2017; Mallinger & Gratton, 2015), even though managed honey bees tend to occur at high densities and appear to be relatively competent pollinators on a per-visit basis (Garratt et al., 2016; Park et al., 2016).

Second, our results reveal the profound impact that orchard layout may have on the delivery of outcross pollen. In our simulation models, decreasing the size of monocultivar blocks from six contiguous rows to a single row increased overall temporal and resource efficiency of the pollinator assemblage by a factor of 3.4 (averaged across the three pollinator types, two measures of efficiency, and two levels of pollination requirement) in the low-carryover scenario and a factor of 1.8 in the high-carryover scenario. These results confirm previous findings that a trade-off exists between efficient orchard management (in this case, size of monocultivar blocks) and the realized pollination efficiency of an orchard's pollinators (Sáez et al., 2018). Depending on the degree of pollen limitation experienced by a given orchard and the costs of purchasing or renting managed pollinators, the enhanced pollination (and, therefore, fruit set) resulting from altering orchard layout and promoting native pollinator populations—for example, by reducing orchard honey bee dominance (Weekers et al., 2022), maintaining seminatural habitat (Campbell et al., 2017), and planting temporally complementary floral resources (von Königslöw et al., 2022)—could compensate for the increased costs associated with implementing such changes in orchard management. Additionally, as the assemblage composition of apple pollinators vary across apple orchards worldwide (Atwood, 1933; Blitzer et al., 2016; Földesi et al., 2016; Garratt et al., 2016; Wu et al., 2021), farmers may also design their orchard layout to maximize the efficiency of the pollinator taxa that are most numerically abundant in their localities.

In addition to applications for apple orchard management, our results also have direct implications for basic and applied studies in evolution and ecology. For example, in studies of floral evolution, where correctly identifying the pollinator taxa contributing the largest share of pollination service delivery is crucial for proper evaluation of the selective forces acting upon floral traits (Alexandersson & Johnson, 2002; Medel et al., 2018), our findings demonstrate that switching behavior, pollen carryover, and even the landscape context of the plant population in question must all be considered in order to correctly identify the highest-contributing pollinator taxa. Similarly, effective conservation of a threatened plant species often involves identifying its best pollinator (Tepedino et al., 1999; Yoshida et al., 2021; Zych et al., 2013).

Evaluating pollination service delivery more holistically may be important even for the ca. 50% of plant species that are self-compatible to some degree (Igic & Kohn, 2006), as pollinator switching behavior and pollen carryover will still impact the genetic diversity of offspring produced—a factor that may be highly consequential in the context of endangered species conservation (Dostálek et al., 2010; Szczecińska et al., 2016). Lastly, our findings corroborate findings of previous studies that demonstrated that the spatial distribution of compatible plant individuals might determine the relative efficiency of pollinator taxa that differ in their tendencies to transport pollen over long distances (e.g., Castilla et al., 2019), highlighting the importance of explicitly considering the spatial context in which pollination takes place (Wagenius & Lyon, 2010).

Pollination mutualisms are complex and influenced by myriad factors. Our study demonstrates that factors that drive patterns of outcross pollen deposition on sequentially visited flowers warrant serious consideration. Although our simulation models serve as a very basic schematic for incorporating pollinator switching behavior, spatial juxtaposition of compatible plant genotypes, and pollen carryover patterns, it would be straightforward to enhance the models with additional parameters that are known to influence pollinator behavior. For example, tree size (Harder & Barrett, 1995), floral architecture and reward quantities of cultivars under consideration (Thomson & Goodell, 2001), and timing within the blooming day and season (Free, 1960) are all factors that can be incorporated to improve the accuracy and precision of assessments regarding the relative contributions of different pollinators to the delivery of outcross pollen and, ultimately, fruit set. When so parameterized, such models may be useful in the majority of pollination systems in both agricultural and natural settings, as all plant species that simultaneously display multiple flowers are subject to the consequences of pollen carryover.

AUTHOR CONTRIBUTIONS

Keng-Lou James Hung and James D. Thomson conceived the study and designed the methodology. Keng-Lou James Hung, Sophia L. Fan, Caroline G. Strang, and Mia G. Park collected the data. Keng-Lou James Hung analyzed the data. Keng-Lou James Hung and James D. Thomson led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Simulation code and raw data (Hung et al., 2023) are available in the Open Science Framework at https://doi.org/10.17605/OSF.IO/VF3X5.

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SUPPORTING INFORMATION

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

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