Adding landscape genetics and individual traits to the ecosystem function paradigm reveals the importance of species functional breadth

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Animal pollination mediates both reproduction and gene flow for the majority of plant species across the globe. However, past functional studies have focused largely on seed production; although useful, this focus on seed set does not provide information regarding species-specific contributions to pollen-mediated gene flow. Here we quantify pollen dispersal for individual pollinator species across more than 690 ha of tropical forest. Specifically, we examine visitation, seed production, and pollen-dispersal ability for the entire pollinator community of a common tropical tree using a series of individual-based pollinator-exclusion experiments followed by molecular-based fractional paternity analyses. We investigate the effects of pollinator body size, plant size (as a proxy of floral display), local plant density, and local plant kinship on seed production and pollen-dispersal distance. Our results show that while large-bodied pollinators set more seeds per visit, small-bodied bees visited flowers more frequently and were responsible for more than 49% of all long-distance (beyond 1 km) pollen-dispersal events. Thus, despite their size, small-bodied bees play a critical role in facilitating long-distance pollen-mediated gene flow. We also found that both plant size and local plant kinship negatively impact pollen dispersal and seed production. By incorporating genetic and trait-based data into the quantification of pollination services, we highlight the diversity in ecological function mediated by pollinators, the influential role that plant and population attributes play in driving service provision, and the unexpected importance of small-bodied pollinators in the recruitment of plant genetic diversity.

bees | body size | ecological services | pollination | pollen-mediated gene flow

As habitat alteration and climate change transform global ecosystems, there is growing concern about how subsequent changes in biodiversity will impact ecosystem functioning and the provision of ecosystem services (1, 2). In this regard, the biodiversity–ecosystem function hypothesis posits that a reduction in biological diversity will lead to a concomitant reduction in ecosystem-level processes, potentially compromising service provision (3–5). For instance, if multiple species perform distinct roles with respect to a particular ecological function, then overall function may be maximized by increasing biodiversity, as seen in the case of pollinator-mediated seed production (6, 7), pest removal rates (8), or plant contributions to C and N sequestration (9, 10). In contrast, some studies have challenged the relevant role of biodiversity and have alternatively suggested that a few keystone species can be sufficient for ecological function; this has been proposed for a number of indices quantifying mobile agent-based ecosystem functions, such as seed production in pollination (11) and pest removal in pest-control (12, 13).

However, ecological function can be characterized by multiple indices, and effectiveness at one index does not guarantee effectiveness at another (14). In the case of mobile agent-based ecosystem services, ecological function is mediated by foraging organisms engaging in trophic interactions (15–17), and thus the quality of these functions depends on the traits of both the recipient and the mobile provider organism (18, 19); this potentially creates more opportunity for species-level differences across multiple indices of ecological function. For example, in animal pollination, which is critical for 85% of all plant species (20), mobile provider organisms not only mediate seed production but also engage in pollen dispersal between plants, potentially enhancing genetic diversity within and across populations. While both seed production and pollen dispersal are critical measures of pollination success, the latter is rarely measured or incorporated into indices of pollinator function (15, 21). This measure is particularly relevant, given that pollen dispersal can provide insight into the origin of offspring traits, the mechanisms driving variation in offspring fitness, and the future of pollen-mediated gene flow for a plant population. Despite the economic and ecological value of pollination services, little is known about the functional breadth of different pollinator species (22, 23) or how these vary between functional indices, including pollen dispersal, across key pollinator and plant traits.

Pollinator body size has long been assumed to be a critical driver of pollination service, given that body size often correlates with the amount of pollen adhered to pollinator bodies (24), ability to buzz-pollinate flowers (25–27), and capacity to trigger specialized pollination mechanisms (28). Further, it is generally believed that large-bodied animals have longer foraging ranges than small-bodied

Significance

Pollinators mediate reproductive processes between plants; however, little is known about how plant and pollinator traits impact pollen dispersal and resulting genetic connectivity. Our study quantifies pollen-dispersal distances and pollination effectiveness for individual pollinator species. We demonstrate that seed set is positively driven by pollinator body size, but long-distance pollen dispersal is mediated by both large-bodied and small-bodied bees. We also reveal that individual plant and population attributes impact pollen-dispersal distances and seed production, respectively. Thus, we show that plant and pollinator traits mediate pollination function and that the entire pollinator community, large and small, plays an important role in the maintenance of genetic connectivity.

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animals due to their higher energy demands (29, 30); a number of multispecies comparisons suggest that body size may indeed correlate with pollinator foraging distance (31–33). If true, then increased mobility in large-bodied pollinators may lead to enhanced levels of pollen-mediated gene flow, with larger pollinators contributing more to long-distance pollen dispersal and playing a more critical role in the maintenance of genetic diversity within and across plant populations.

Additionally, while it has been hypothesized that plant population and individual attributes, such as degree of plant isolation, size of floral display, and level of local kinship, may influence seed production and pollen dispersal (34–36), these traits are rarely incorporated into species-specific assessments of pollination service, especially at large spatial scales. This is unfortunate, given that laboratory-based foraging experiments suggest that pollinator species respond differently to spatial distributions of artificial flowers (37, 38) and transplant studies reveal that pollen dispersal can be mediated by the spatial distribution of individual plants (39). Specifically, increased plant spatial isolation may limit pollination success through a reduction in the number of pollen donors (ref. 40 and references therein) and an increase in the transfer of self-pollen through geitonogamy, a process that may also be driven by large floral arrays (40, 41). Similarly, fine-scale spatial genetic structure (i.e., local kinship) is a common feature in plant populations and may impact estimates of pollination service (42–44), possibly due to increased rates of inbreeding in high-kinship neighborhoods, which could result in increased seed abortion rates (36, 45, 46). Thus, a comprehensive concept of pollination service should incorporate not only pollinator traits but also plant population and individual traits, such as individual floral display, density of pollen donors, and local kinship.

In this study, we conduct a uniquely integrative species-specific analysis of pollinator-mediated gene flow by means of fractional paternity assignment, using 532 seeds and 1,023 leaves gathered from individual pollinator visits to a common understory tree, *Miconia affinis*, across more than 690 ha in central Panama. We compare individual pollination events with respect to three indices of pollinator effectiveness: visitation, pollen-dispersal distance, and seed viability. Specifically, we assess how these indices are impacted by plant and pollinator size, plant density, and local plant kinship. We show that while large-bodied pollinators are more effective in setting viable seeds on a per visit basis, small-bodied pollinators visit more frequently and are responsible for nearly half of all long-distance pollen-dispersal events. Further, we show that plant population and individual attributes, specifically local kinship and plant size, can significantly negatively impact pollination function. By quantifying pollen-mediated gene flow across large spatial scales and adding individual plant and pollinator traits into ecosystem service assessments, we highlight the breadth of ecological function mediated by a community of pollinators and reveal the unexpected importance of small-bodied pollinators for long-distance pollen dispersal.

Results

Flowers of *M. affinis* were visited by a total of 20 bee species during the single-visit experiments, and unvisited flowers did not produce fruits. Fourteen bee species behaved as pollinators, with all visits leading to fruit production, and represented 96.5% of the total visited inflorescences. Pollinators varied markedly in body size as measured by intertegular distance (ITD) (*sensu* ref. 47), with ITD ranging from 0.91 to 7.72 mm. Eusocial species were responsible for 94.1% of the fruit production; thus we did not include sociality as an additional explanatory trait in our seed viability and pollen-dispersal models. The visitation frequency of pollinators was negatively related to their ITD ($\beta = -1.086$; 95% CI = -2.164, -0.238), indicating that smaller-bodied pollinators were more frequent floral visitors. While large-bodied bees visited less frequently, they were more effective in setting viable seeds on a per
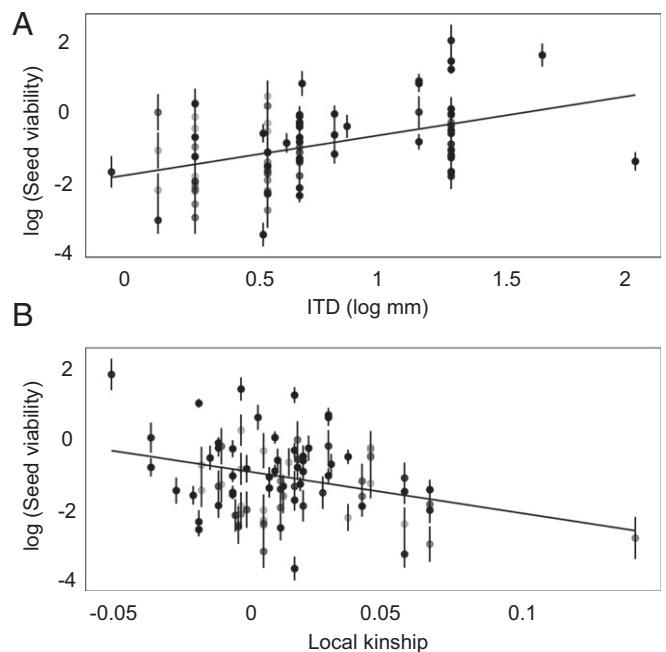

Fig. 1. Effect of pollinator body size as measured by ITD (*A*) and local kinship (*B*) on seed viability. Seed viability refers to the ratio between viable and aborted seeds. Dots represent the predicted means from the model at the inflorescence level on a logarithmic scale. SEs were calculated using 100 bootstrap replicates.

visit basis than small-bodied bees (Fig. 1*A*). In our fitted model, pollinator body size accounted for most of the variation in mean seed viability among pollinator species. Based on the predicted mean seed viabilities, it is evident that no pollinator species deviated substantially from the positive relationship between ITD and mean seed viability (Fig. S1*A*).

Despite documenting substantial variation in pollinator body size and a total of 532 pollen-dispersal events, we found no significant relationship between the ITD of the pollinator and their mean pollen-dispersal distance (Table 1). Most interestingly, a substantial number of dispersal events reached distances beyond 1 km, even for small-bodied pollinators with <2 mm ITD (Fig. 2). In other words, while pollinators differed in size by more than eight orders of magnitude, they did not exhibit significant differences in their mean pollen-dispersal distance based on body size. Using seed and tree genotypes, we directly modeled pollen flow between trees as a function of physical distance. Across infructescences, we estimated substantial variation in the rates at which paternity probability decays with distance, but we found no evidence that pollinator ITD is the cause of this variation ($P = 0.36$, likelihood ratio test) (Fig. S2). Taken together, these analyses indicate that while the data are sufficient to detect variation in dispersal distances across single visits, there is no evidence that larger bees transport pollen longer distances (Fig. S1*B*).

Our results also revealed a negative relationship between the diameter at breast height for the mother trees (DBH_{mother}) and pollen-dispersal distance (Fig. 3*A* and Table 1), where DBH correlates strongly with floral resource availability ($r_p = 0.85$; $P < 0.0001$) (Fig. 3*B*). In other words, pollinators, independent of their body size, exhibit shorter pollen-dispersal distances when pursuing higher floral-resource sites. In addition, we found a positive relationship between spatial isolation of the mother tree and pollen-dispersal distances to the tree, indicating that more spatially isolated trees tend to receive pollen from more distant trees. For the pollen-dispersal model, repeated analyses removing

Table 1. Results of generalized linear mixed-effects models with binomial (seed viability) and Gaussian (pollen-dispersal distance) error distributions

Fixed effect	Seed viability coefficient (CI percentage)	P value	Pollen-dispersal coefficient (CI percentage)	P value
ITD	0.431 (0.175, 0.686)	<0.001*	0.039 (−0.022, 0.100)	0.400 (0.310)
DBH_{mother}	0.040 (−0.243, 0.323)	0.781	−0.086 (−0.155, −0.018)	0.021* (0.041)
SI	0.069 (−0.244, 0.383)	0.665	0.069 (0.015, 0.124)	0.017* (0.018)
Kinship	−0.274 (−0.519, −0.028)	0.029*	−0.048 (−0.119, 0.023)	0.177 (0.183)

SI, spatial isolation, is defined as the mean distance from the mother tree to its 10 nearest neighbor trees. Kinship refers to the local kinship between the mother tree and all trees in a radius of 400 meters. All explanatory variables were scaled in the analyses. For pollen-dispersal distance, P values in parentheses are approximated by repeatedly permuting covariates at the appropriate level of replication and refitting the model to each permutation.
*Significant relationships ($P \leq 0.05$).

pollinator species with fewer than five dispersal events showed similar results (Table S1).

Interestingly, we found a negative effect of local kinship on the proportion of viable seeds per fruit (Table 1): Fruits from mother trees in high-kinship neighborhoods had fewer viable seeds than those from low-kinship neighborhoods (Fig. 1*B*). This demonstrates that mother trees living near close relatives exhibit increased abortion rates, likely due to elevated levels of biparental inbreeding. Additionally, the interaction between ITD and local kinship was not significant in our seed viability model (likelihood ratio test: $\chi^2 = 0.06$, $P = 0.80$), indicating that increased seed abortion occurs across all pollinator sizes and is not predominantly mediated by small-bodied pollinators. Finally, neither DBH_{mother} nor spatial isolation had significant effects on the proportion of viable seeds per fruit (Table 1).

Discussion

Pollen dispersal is arguably one of the most important components of pollination service, and here we measure landscape-level pollen dispersal across an entire pollinator community. We reveal that visitation, seed production, and pollen-dispersal indices are not mediated by the same individual and plant population traits. Specifically, our results reveal an unexpected and substantial contribution of small-bodied pollinators to long-distance pollen dispersal, highlighting the importance of functional breadth when considering the relationship between biodiversity and ecosystem function. While we find that seed production is positively driven by pollinator body size, we reveal that the entire pollinator community can disperse pollen long distances (>1 km); this is in stark contrast to the classic assumption that large-bodied pollinators are the only vectors of long-distance pollen-mediated gene flow. Further, small-bodied pollinators may play an important role in the maintenance of genetic connectivity in plant populations, given that they are more frequent visitors and engage in a substantial proportion of long-distance dispersal events, either directly or indirectly through secondary pollen transference. Thus, by incorporating gene-flow measures into our quantification of pollination service, we highlight the critical functional breadth exhibited by multiple pollinator species within a community.

While long-distance pollen-dispersal events have frequently been documented for tropical trees (48, 49), they have primarily been ascribed to large-bodied animal species (but see refs. 50 and 51). Specifically, past research has asserted that, because large-bodied pollinators exhibit the greatest foraging distances (32), they are also the most likely to mediate long-distance pollen dispersal (52). In contrast, the contribution of small-bodied pollinators to pollen-mediated gene flow has long been assumed to be minimal, with an expected range of around 100–300 m (reviewed in ref. 53). We found that pollinator body size was positively related to seed production, likely because increased pollinator body size often translates into an improved ability to manipulate complex floral structures, as seen in other buzz-pollinated plant species (25, 26). However,

pollinator body size was not correlated with pollen-dispersal distance; for example, some of the smallest-bodied species, *Tetragonisca angustula* (ITD = 1.28 mm) and *Trigona buyssoni* (ITD = 1.07 mm), regularly mediated pollen-dispersal distances beyond 2 km. While surprising, these long-distance dispersal events are indeed possible and have occasionally been documented for small-bodied tropical bees in the past (53, 54). Past research has also interpreted declines in pollinator visitation, diversity, and seed set with increasing distance from natural habitat as evidence that tropical pollinator communities exhibit limited foraging, especially relative to temperate pollinator communities (55). Our mapping of pollen dispersal reveals substantially longer pollen movement distances than expected from these tropical pollinator models. Although long-distance pollen-dispersal events could be explained by secondary pollen transfer (56), this process is expected to be equally if not more likely for large-bodied pollinators due to their greater body surface area (57). Furthermore, the short flowering period of *M. affinis* (24–36 h) acts as a strong temporal limitation for secondary pollen transfer. Future studies should explore the role of secondary pollen transfer
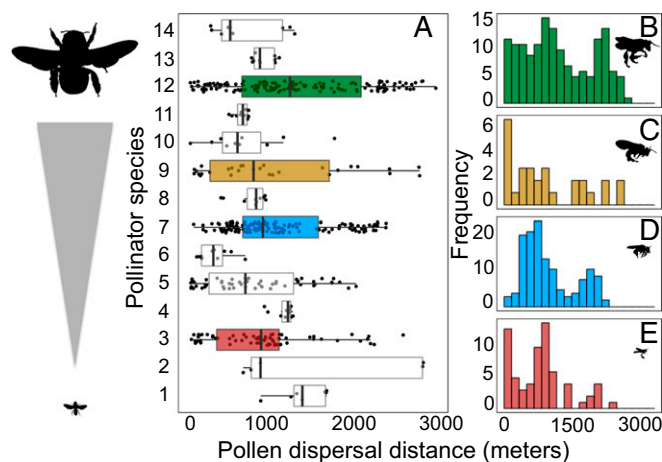
Fig. 2. Pollen-dispersal distances recorded for each *M. affinis* pollinator. (*A*) Boxplots indicate the median, upper, and lower quartile for each *M. affinis* pollinator. Increasing numbers in the *y* axis correspond with the following pollinator species sorted in ascending order regarding their body size (ITD): 1: *Halictidae sp 2*; 2: *Trigonisca buyssoni*; 3: *Tetragonisca angustula*; 4: *Halictidae sp 1*; 5: *Trigona muzoensis*; 6: *Paratetrapedia lineata*; 7: *Trigona fuscipennis*; 8: *Trigona amalthea*; 9: *Trigona fulviventris*; 10: *Pseudaugochloropsis sp 1*; 11: *Melipona fuliginosa*; 12: *Melipona panamica*; 13: *Centris dichrootricha*; 14: *Xylocopa fimbriata*. (*B–E*) Frequency distribution of the pollen-dispersal distances for a subsample of *M. affinis* pollinators representative of the body-size gradient: (*B*) *Melipona panamica*; (*C*) *Trigona fulviventris*; (*D*) *Trigona fuscipennis*; and (*E*) *Tetragonisca angustula*.
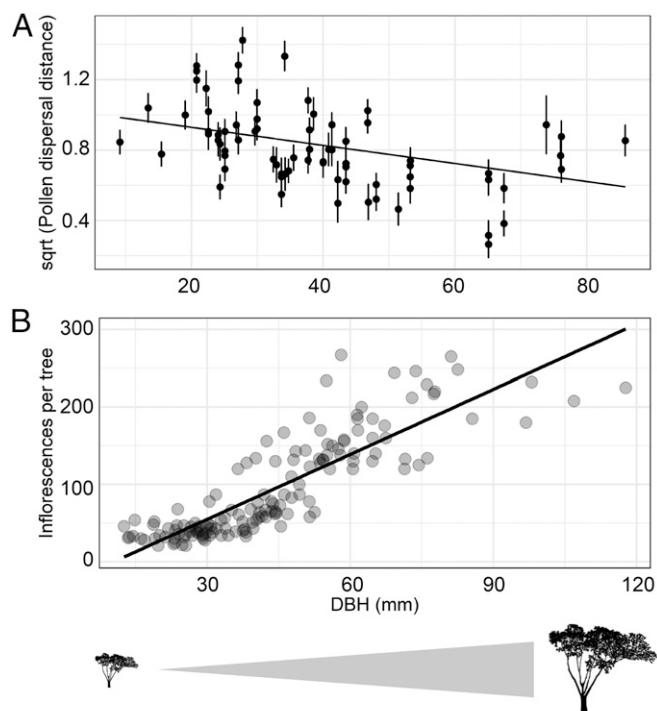
Fig. 3. Effect of DBH_{mother} on pollen-dispersal distance. (*A*) Pollen-dispersal distance was square root (sqrt) transformed, and DBH_{mother} is plotted at its original scale. Dots represent the predicted means from the model at the infructescence level. SEs were calculated using 1,000 bootstrap replicates. (*B*) Relationship between DBH_{mother} and total number of inflorescences per tree. Transparency was used to show the level of overlapping among dots.

in pollen-mediated gene flow and should examine the generality of our findings for plant species with different functional traits and under different ecological contexts.

Whatever the explanatory mechanism, our findings are particularly important, given that small bees are often the most frequent floral visitors across plant taxa and study systems (58, 59) and thus are potentially mediating substantial portions of the long-distance pollen-dispersal events in other systems, although they may not be conferring the highest seed production. Overall in our study, small-bodied pollinators (ITD <2 mm) were the most common visitors and were also responsible for 49% of all pollen-dispersal events involving distances above 1 km. Thus we show that, both as frequent visitors and as capable long-distance pollen dispersers, small-bodied pollinators play a previously unacknowledged but critical role in maintaining pollen-mediated gene flow. Given that large-bodied bees are often less common visitors and tend to be more vulnerable to extinction caused by human activities (60), small-bodied bees could be particularly important for maintaining effective plant population sizes and genetic diversity in the face of global land use change. Thus, our results reveal that pollination-service quantification that does not incorporate pollen dispersal may overlook important attributes of ecological function that are critical for the conservation of genetic diversity and the long-term viability of plant populations.

The results of this study also indicate that pollen-dispersal distance is a function of plant size, where plant size is a proxy of floral resource offering. We document a significant decrease in pollen-dispersal distance for large mother trees, likely driven by changes in pollinator behavior in response to large floral displays. Specifically, our results suggest that when pollinators visit large flowering trees, they tend to arrive from nearby localities and continue their foraging more locally (exhibiting shorter pollen-dispersal distances). Past studies provide complementary evidence that plants with large floral displays offer a high rate of reward relative to travel, and thus

pollinators use spatial memory to preferentially return and revisit these high-resource plants (41, 61–63). Similarly, our results suggest that *M. affinis* pollinators within high-resource patches behave as "area-restricted" searchers (sensu ref. 37), moving stochastically but over short distances and engaging in long-distance foraging only after encountering low-reward patches (i.e., trees with reduced floral displays).

Finally, our results show that plant population and individual attributes mediate pollinator performance through significant impacts on seed production. Specifically, our analyses reveal a negative effect of local kinship on the proportion of viable seeds per fruit, likely driven by greater biparental inbreeding and thus higher abortion rates for plants living in higher-kinship neighborhoods. While fine-scale spatial genetic structure is a common feature in plant populations (64, 65), few studies have addressed its impact on the reproductive success of individual plants (but see refs. 43–45). Our findings have important implications for the provision of pollination service in rare and threatened wild plant populations, given that they typically exhibit neighborhoods with high levels of kinship among plants (66, 67). Under this scenario, highly mobile pollinators may be critical for preventing the mating of closely related individuals and consequent reductions in seed production.

In this study, we quantify pollen movement and fine-scale spatial genetic structure across extensive spatial scales to reveal an unexpected level of breadth in pollination function. Our results do not support the long-standing assumption that pollinator body size drives pollen dispersal and instead provide unique support for the role of plant size and local kinship in mediating the provision of pollination services. Further, we show that pollinator traits can influence some indices of pollination service, but not others; thus, utilizing only a single index of pollinator effectiveness can critically underestimate the role of functional diversity in overall service provision. Our findings are especially salient given current concerns about the loss of functional diversity driven by ongoing declines in global biodiversity (68, 69) and a need to safeguard these multifaceted ecological functions. Overall, results from this study highlight the value of incorporating vector-mediated gene flow, as well as individual and population traits, to effectively describe ecosystem service dynamics across large spatial scales.

Materials and Methods

Study Species and Regions. *M. affinis* D.C. (Melastomataceae) is a self-incompatible understory tree (3–6 m high) that is broadly distributed in the Neotropics, ranging from Mexico to Brazil (70, 71). Inflorescences have 50–300 white flowers, and the species exhibits a "big bang" flowering pattern with all individuals in a population producing a large number of flowers over a short time frame [i.e., ~1–2 d (70, 72)]. The flowers have deep poricidal anthers which must be vibrated by a pollinator in order for pollen to be released (i.e., "buzz-pollination") and are visited by a diversity of bees (70). Fruit ripening takes 3–4 mo (May–July), and the black globose berries (3 mm long; 6 mm wide) are dispersed by a variety of birds and bats (73, 74). Each fruit contains numerous minute seeds (30–50 seeds per fruit); fertilized seeds are yellow, pyramidal, and three to four times larger than the dark, crescent-shaped unfertilized ovules.

The research was conducted in three study regions along Soberania National Park in Central Panama: Gamboa (GB), Camino de Plantaciones (CP), and Alfagia (AG) (Table S2; see ref. 75 for a more detailed description of the study regions). Our sampling covered a total area of 698 ha, ~10 times the size of most molecular marker-based dispersal studies (often 50 ha; reviewed in ref. 53). Geographic distances between the study regions ranged from 5.0 to 19.2 km (mean, 12.9 ± 4.2 km). In each study region, we surveyed all reproductive *M. affinis* trees and recorded their geographic coordinates using a portable GPS GARMIN eTrex Vista (GARMIN). Additionally, we surveyed 50-m transects that were randomly distributed across the study system, in which we simultaneously evaluated the reproductive status (reproductive if inflorescence present) and DBH of all trees within 2.5 m on either side (*n* = 36, 46, and 60 transects in GB, CP, and AG, respectively). In two study regions (GB and CP), we also counted the total number of inflorescences for each reproductive tree within each transect. For these two study regions, we analyzed the relationship between DBH and the total number of inflorescences per tree using Pearson correlation.

Single Pollinator Visit Experiment. During the dry season in 2013, we randomly chose 25 *M. affinis* reproductive trees (herein, "mother trees") in each study

region with which to conduct a 30-min single-pollinator-visit experiment ($n = 75$ mother trees). For each mother tree, we recorded its DBH and calculated the mean distance to the 10 nearest conspecific neighbors as an estimate of the tree's spatial isolation. We bagged five closed inflorescences per mother tree in March and April, at the beginning of the dry season ($n = 375$ inflorescences). On the day of flowering, inflorescences were unbagged for up to 30 min, allowing a single insect visit. After flower visitation, visitors were captured using entomological nets, and the total number of flowers open per inflorescence was counted. Inflorescences were then rebagged to allow the development of fruits. We also rebagged the nonvisited inflorescences to confirm the absence of fruit formation without pollinator visitation. Floral visitors were identified to species by A.S. at the Museo de Invertebrados G. B. Fairchild, Panama, and ITD was measured as the linear distance between a specimen's tegula (the cap at base of wing) as a proxy for pollinator size (32). During July–August, we collected the ripe fruits from each visit and quantified the number of viable and aborted seeds per fruit using a stereo microscope. We also estimated the percentage of forest cover in a radius of 100 m around each mother tree using the software QGIS and a 2008 land-cover map (strimaps.si.edu/portal/home/).

Fine-Scale Genetic Structure and Paternity Analyses. We collected leaf material from all reproductive trees in each study region. Total genomic DNA was extracted from adult leaf tissue using the cetyltrimethylammoniumbromide (CTAB) protocol (76). For the paternity analyses, we used up to 10 fruits for each infructescence resulting from a single pollinator visit. For infructescences with more than 10 fruits, we randomly chose 10 fruits. We collected one viable seed per fruit, and its total genomic DNA was extracted using the DNSA isolation (DNazol) protocol (76). All trees and seeds were screened at eight polymorphic microsatellite loci following the protocols described in refs. 77 and 78 and were genotyped on an ABI 3730 Sequencer. Alleles were scored manually using GeneMarker (SoftGenetics).

Using the genotypes of the reproductive trees, we performed an analysis of their fine-scale spatial genetic structure, also known as "local kinship" (43). We calculated the metric F_{ij} using the software SPAGeDi (spatial pattern analysis of genetic diversity) (79, 80) as a measure of kinship between paired trees (i.e., higher pairwise F_{ij} represents greater kinship between two individuals). For each focal mother tree, we estimated local kinship as the mean F_{ij} for all pairwise comparisons with other reproductive trees within 400 m. We used fractional paternity assignment to calculate the probability of paternity across trees for each seed, under the model of genotyping error given in ref. 81, which accounts for allelic dropouts and stochastic genotyping error (described in detail in *SI Appendix*).

Data Analysis. All analyses were performed in R 3.3.2 (82). Data are available from the Dryad digital repository (https://doi.org/10.5061/dryad.1cm80). To determine if bees with different body sizes differ in their visitation rates, we modeled visitation frequency (across pollinator species) as a function of ITD, using a multinomial model with pollinator species as a random effect (*SI Appendix*). All parameters were given vague priors, and posterior sampling was conducted by Markov Chain Monte Carlo using the software JAGS (83).

We fitted generalized linear mixed models to evaluate the effects of DBH_{mother}, spatial isolation, local kinship, and ITD on seed viability. We also included the interaction ITD × local kinship in our seed viability model to investigate the existence of seed abortion through biparental inbreeding driven by pollinator body size. We compared the models with and without the ITD × local kinship interaction using the likelihood ratio test (LRT) implemented in the lme4 package (84). The interaction was excluded if the reduced model was not significantly different (using LRT, $\alpha = 0.05$). We did not include forest cover around the mother tree as an additional explanatory variable in either our seed viability or pollen-dispersal model due to its strong collinearity with spatial isolation ($r_p = -0.40$, $P = 0.007$). Further, we know from past work in the study region that spatial isolation can critically influence both seed viability and pollen dispersal, even when forest cover is relatively homogeneous (43). For each fruit, we defined seed viability as the fraction of viable seeds out of the total number of seeds (viable + aborted). We used a binomial error distribution in our models that accounts for differences in sample size [i.e., lme4 package in R, glmer function with cbind (s, n − s) ~ covariates, where $n =$ number of trials, s = number of successes]. The number of trials is the total number of seeds per fruit, and the number of successes is the number of viable seeds per fruit. We included ITD, DBH_{mother}, spatial isolation, and local kinship as the fixed effects in our full model. All the explanatory variables were scaled to a mean of zero and variance of 1. We included random intercepts per population, mother tree, and infructescence, with infructescence nested within mother tree and mother tree nested within population. To account for overdispersion, we included an observational-level effect in which each data point receives a unique level of a random effect that models the extra variation present in the data (84, 85).

We fitted a linear mixed-model to evaluate the effects of ITD, DBH_{mother}, spatial isolation, and local kinship on pollen-dispersal distance. For each seed, we defined pollen-dispersal distance as the linear geographic distance between the mother and the father trees. In the dispersal distance analyses, we used a Gaussian error distribution in our models. We included ITD, DBH_{mother}, spatial isolation, and local kinship as the fixed effects in our full model. All the explanatory variables were centered to mean 0 and scaled to variance 1. We included random intercepts per population, mother tree, and infructescence with infructescence nested within mother tree and mother tree nested within population. There are a finite number of possible observable dispersal distances for each mother, which depend on their locations relative to other trees in the population. For the linear model of pollen-dispersal distance, two possible consequences of spatial context are (i) nonindependence of observations across mothers and (ii) biased regression coefficients, making it challenging to determine the parameter values that would be expected under an appropriate null model. Thus, for a more robust analysis, we approximated the null distribution of regression coefficients in our fitted model by permuting data at the relevant level of replication. For example, by shuffling pollinator identity (and associated ITD) across infructescences, we approximated the sampling distribution of the regression coefficient for ITD under a model in which pollinators were equivalent. Data were permuted only within populations. We note that if the number of dispersal events is much lower for the smallest pollinators and is restricted to highly isolated mother trees, this could inflate mean pollen-dispersal distance at the lower edge of the pollinator size distribution, overriding a potential positive relationship between ITD and pollen-dispersal distance. However, we posit that this situation is unlikely in our analyses for two reasons. First, we had a reasonable number of dispersal events at both edges of the size distribution (174 and 79 dispersal events for the three largest and smallest pollinator species, respectively) (Fig. S3). Second, we did not find that long-distance dispersal events mediated by small pollinators occurred exclusively at spatially isolated mother trees (Fig. S4). Finally, we analyzed our pollen-dispersal data using a multinomial model that directly models pollen flow as a function of distance and incorporates the spatial distribution of individual plants within study regions (described in detail in *SI Appendix*), which yielded results similar to our linear mixed-model.

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