

Impacts of Flowering Density on Pollen Dispersal and Gametic Diversity Are Scale Dependent

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ABSTRACT: Pollen dispersal is a key evolutionary and ecological process, but the degree to which variation in the density of concurrently flowering conspecific plants (i.e., coflowering density) shapes pollination patterns remains understudied. We monitored coflowering density and corresponding pollination patterns of the insect-pollinated palm *Oenocarpus bataua* in northwestern Ecuador and found that the influence of coflowering density on these patterns was scale dependent: high neighborhood densities were associated with reductions in pollen dispersal distance and gametic diversity of progeny arrays, whereas we observed the opposite pattern at the landscape scale. In addition, neighborhood coflowering density also impacted forward pollen dispersal kernel parameters, suggesting that low neighborhood densities encourage pollen movement and may promote gene flow and genetic diversity. Our work reveals how coflowering density at different spatial scales influences pollen movement, which in turn informs our broader understanding of the mechanisms underlying patterns of genetic diversity and gene flow within populations of plants.

Keywords: pollen dispersal distance, allelic diversity, pollen dispersal kernel, phenology, flowering density.

Introduction

Mating patterns have important implications for natural plant populations, ranging from shaping individual-level fitness to influencing the distribution of genetic diversity and variation across the landscape (Ennos 1994; Lowe et al. 2005; Petit et al. 2005; Breed et al. 2012). A wealth of research has provided important insights into pollination patterns of natural populations of outcrossing plant species, revealing that pollen dispersal is often extensive and mediates gene flow to increase genetic diversity (Ashley

2010; Ellstrand 2014). However, while many of these studies evaluate mating patterns at specific points in time over a predetermined area, the factors that affect pollen dispersal are likely to change across spatial and temporal scales. For example, the density of concurrently flowering conspecific plants (hereafter, “coflowering density”) often varies substantially over time because of differences in the number of individuals reproducing among flowering seasons (Augsburger 1981; Murawski and Hamrick 1991; Koenig et al. 2012; Masuda et al. 2013) or throughout a single flowering season (Augsburger 1983; Bogdziewicz et al. 2017). Similarly, the number of coflowering plants may vary spatially across a species’ range (Murawski and Hamrick 1992; Park 2014) or at finer spatial scales because of habitat fragmentation (Hadley and Betts 2012) or microhabitat preferences (Condit et al. 2000). For these reasons, employing a longitudinal approach that also evaluates the effect of spatial scale is likely to improve our understanding of the factors, such as coflowering density, that shape pollination patterns and its microevolutionary consequences.

While variation in coflowering density is thought to be vital in influencing patterns of pollen dispersal (reviewed in Ghazoul 2005), its dynamics are relatively poorly studied and likely to be complex. For example, in both intact and fragmented systems, low adult densities are often associated with increased pollen dispersal distance (Stacy et al. 1996; Kramer et al. 2008; C rtes et al. 2013; Lobo et al. 2013). However, in many instances variation in coflowering density has had heterogeneous effects on the diversity of the pollen pool (Murawski and Hamrick 1992; Sork et al. 2002; Masuda et al. 2013). In addition, many studies are limited by low sampling effort over time (Hamrick 2012) or an inability to control for potentially confounding spatial and ecological variables, such as differences in land cover (Lander et al. 2011). Consequently, we lack a detailed

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understanding of how variation in coflowering density impacts pollen dispersal distance and pollen pool diversity.

Spatial changes in coflowering density may also lead to variation in forward pollen dispersal kernels, which estimate the probability of a pollen grain dispersing a certain distance from a paternal tree, potentially leading to a fertilization event and ultimately influencing gene flow and genetic diversity (Nathan et al. 2012; Klein et al. 2013; Duminil et al. 2016). Pollination patterns for animal-pollinated plants are primarily influenced by coflowering density (Murawski and Hamrick 1991, 1992; Stacy et al. 1996; Córtes et al. 2013) and may be further impacted by the density-dependent foraging behaviors of different pollinators (Feldman 2006). If changes in coflowering density substantially modify pollinator behavior, multiple dispersal kernels may be needed to best explain the variation observed in pollination patterns in high- versus low-coflowering contexts (Robledo-Arnuncio and Austerlitz 2006). For example, scenarios of high coflowering density may encourage near-neighbor mating, resulting in a leptokurtic dispersal kernel, while low coflowering density could result in pollinators moving considerably greater distances to access pollen resources, leading to a distinct dispersal kernel with intermediate dispersal distance. Alternatively, the classical kernel model presents the null hypothesis that a single dispersal kernel can account for the variation observed in pollination patterns due to changes in coflowering density per se and not through altered pollinator behavior (Meagher and Vassiliadis 2003; Robledo-Arnuncio and Austerlitz 2006). Distinguishing between these two hypotheses would provide a mechanistic understanding of the factors that determine the movement of pollen across the landscape, further highlighting the need for empirical studies capable of providing this resolution.

Palms (Arecaceae) are fundamental components of tropical floristic communities and are of substantial ecological and economic importance worldwide (Henderson et al. 1995). *Oenocarpus bataua* (Mart.) is a Neotropical palm that, as is the case for many tropical plants, exhibits asynchronous flower production (Rojas-Robles and Stiles 2009; Ramirez-Parada et al. 2020) and a patchy spatial distribution of adults. These attributes allowed us to evaluate mating patterns within a single population across a range of coflowering densities that change across spatial scales and over time. More specifically, we evaluate how variation in coflowering density at neighborhood versus landscape spatial scales may drive average pollen dispersal distance, the shape and scale of the pollen dispersal kernel, and the genetic diversity within the pollen pool. We predict that mating patterns will vary across time and that low neighborhood and landscape densities will result in greater pollen dispersal distance and pollen pool diversity. We also predict that changes in density at both neighborhood and

landscape scales will substantially alter pollinator behavior so that two pollen dispersal kernels, rather than a single dispersal kernel, will be required to generate the relationships observed between density and pollen dispersal distance and between density and pollen pool genetic diversity.

Material and Methods

Study System and Field Methods

Oenocarpus bataua is a monoecious, solitary canopy palm tree widely distributed throughout South America (Henderson et al. 1995). The species is protandrous, and self-fertilization is rare (Ottewell et al. 2012; Browne et al. 2018). Inflorescences are large (2 m) and present >600,000 flowers, which are active for 28–32 days and are visited by dozens of insect species, with the most effective and abundant pollinators being obligate Curculionidae beetles that feed on pollen throughout their larval and adult life cycles (Núñez-Avellaneda and Rojas-Robles 2008). Thermogenic, nocturnal anthesis and a heavily scented inflorescence serve to attract these pollinators over large areas (Núñez-Avellaneda and Rojas-Robles 2008; Barfod et al. 2011). Pollinated flowers develop into large-seeded drupes consumed and dispersed by many vertebrates (Henderson et al. 1995; Mahoney et al. 2018).

Our study took place at Bilsa Biological Station (BBS; 0°22'N, 79°45'W; 330–730 m elevation), a 3,500-ha reserve of humid Chocó forest in northwestern Ecuador. *Oenocarpus bataua* is common at BBS. From May 2008 to August 2015, we recorded monthly phenological states for all adults ($n = 181$) within a core 130-ha plot (fig. S1) by visiting each tree within the study plot and recording the number of reproductive structures. In 2015 we surveyed a 250-m buffer zone around the 130-ha plot and recorded 60 additional adults, all mapped and genotyped, but for which phenology was not recorded (see above). This yielded 241 geolocated and genotyped candidate fathers, of which 181 also had monthly phenology data for analysis (fig. S1).

To collect progeny for genetic analysis, we collected ripe fruits directly from the infructescence of *O. bataua* individuals; we refer to these as “maternal” trees and refer to pollen sources as “paternal” trees, noting that the same individual could be both. We randomly sampled maternal trees with complete phenology records. We germinated the seeds in a nursery and collected and stored a tissue sample from the first leaf of each seedling. For each maternal tree, we used monthly phenology data to calculate the coflowering density in the time frame that the maternal tree was flowering. We calculated density at two spatial scales: the landscape scale, defined as the entire 130-ha study plot, and the neighborhood scale, defined as the average effective

pollination neighborhood (A_{ep} ; Crawford 1984; Levin 1988) of all progeny arrays included in this study, which was a circular area surrounding maternal trees with a radius of ~ 320 m and an area of 33.40 ha (supplement A; fig. S1). If the boundary of the neighborhood area extended beyond that of the study plot, neighborhood coflowering density was estimated using the subset of individuals within the neighborhood area for which phenology data were available.

Genetic Analyses

We extracted genomic DNA from 962 offspring leaf samples representing 43 progeny arrays collected from 35 maternal trees. All samples were genotyped using 11 microsatellite loci through polymerase chain reaction following established protocols (Ottewell et al. 2012). We calculated a genotyping error rate of 1.5% by resequencing $\sim 5\%$ of samples (Pompanon et al. 2005). We checked for null alleles using Micro-Checker version 2.2.3 (Van Oosterhout et al. 2004) and did not find evidence of null alleles. Loci Ob10 and Ob11 amplified poorly and were excluded, leaving a suite of nine loci for analysis. We excluded 17 samples because of poor amplification, small sample size of progeny array, or multiple peaks, leaving 945 genotyped seedlings. We genotyped the 181 adults (pollen sources and maternal trees) in the study plot and the 60 additional adults in the 250-m buffer zone around the study plot using equivalent methods (Browne and Karubian 2016), totaling 241 genotyped parental trees. We used offspring and adult genotypes in the program CERVUS (ver. 3.0.3; Marshall et al. 1998) to assign paternity with the aim of (1) calculating the average A_{ep} area (supplement A), (2) quantifying the “observed” distance pollen dispersed from paternal to maternal trees, and (3) estimating the paternal contribution to the genetic diversity of each progeny array. We used critical trio (Δ) values with at least 80% confidence, and the following simulation parameters used previously for parentage analysis in our study area (Ottewell et al. 2012; Browne et al. 2018; supplement B).

Pollination Patterns

Once paternity was assigned, we estimated the paternal contribution to the genetic diversity of each progeny array by calculating the haploid male gametic contribution to offspring using the maternal genotypes and seedling genotypes with the TwoGener gametic extraction in GenALEX version 6.502 (Peakall and Smouse 2006, 2012). In cases where the maternal and paternal allelic contributions were ambiguous, meaning both the maternal and offspring genotypes were heterozygous at a locus with the same alleles ($\sim 16\%$ of cases), we assigned a 50% probability of each allele

being contributed maternally or paternally (Browne et al. 2018). We used this genetic information to quantify alpha diversity per progeny array, which represents the paternal contribution to the allelic diversity per progeny array, using the R package dispersalDiversity (Sork et al. 2015). In brief, alpha diversity estimates the effective number of alleles per locus for each progeny array (Sork et al. 2015).

We used the genetic information to estimate the forward pollen dispersal kernel (hereafter, “dispersal kernel”) using the spatially explicit NEIGHBORHOOD model provided in the software $NM\pi$ (Chybicki and Burczyk 2010; Chybicki 2018; supplement C). We estimated dispersal scale (d_p), mean pollen dispersal distance ($1/d_p$; m), kernel shape (b_p), self-fertilization (s), and pollen immigration (m_p) for Weibull, exponential power, and lognormal distributions. We used $NM\pi$ to estimate the dispersal kernels under high and low levels of coflowering densities at two spatial scales including fertilization events during periods of high (>89 coflowering trees) and low (≤ 89 coflowering trees) landscape densities, fertilization events during periods of high (>36 coflowering trees) and low (≤ 36 coflowering trees) neighborhood densities (fig. S2), and all fertilization events. As six maternal trees were sampled more than once, four $NM\pi$ analyses included multiple progeny arrays from the same maternal tree (table S1). To account for uncertainty in the best-fit kernel for each flowering density, we used a model-averaging approach to generate weighted multimodel estimates of the model parameters (Chybicki and Oleksa 2018). We did not produce multimodel estimates for the shape parameter (b_p) because the interpretation of shape parameters varies depending on the dispersal kernel (Chybicki and Oleksa 2018). In addition, we quantified observed pollen dispersal distances by using parentage assignments from CERVUS to calculate average Euclidean distance between the maternal tree and the assigned paternal source.

Statistical Analysis

To evaluate the relationship between coflowering density and fertilization patterns, we fitted two linear mixed models with observed pollen dispersal distance and alpha diversity as response variables and neighborhood density and landscape density as fixed effects (supplement D). In brief, we fitted models for random and fixed effects to test for the influence of temporal correlation and resampling maternal trees as well as an interaction between landscape and neighborhood density (supplement D; table S2). We also fitted models for correlation structures to account for spatial autocorrelation (supplement D; table S2). In addition, we tested the independence of overlapping neighborhood areas (supplement E) and the effect of neighborhood area (tables S3, S4; supplement D). The final model for the response

variable of alpha diversity included the fixed effects of landscape and neighborhood densities and a random effect of maternal tree ID. The final model for mean observed pollen dispersal distance (m) included the fixed effects of landscape and neighborhood densities. Models were fitted using the `lme()` function in the package `nlme` (Pinheiro et al. 2018), and model selection was performed with `model.sel()` from the `MuMIn` package (Bartón 2020). Models met the assumptions of normality in residuals and equal variance, and we did not detect multicollinearity in model terms (variance inflation factor < 2). We used conditional partial residual plots to depict model outputs with the `visreg` package (Breheny and Burchett 2017). All analyses were completed in R version 4.0.2 (R Core Team 2013).

Finally, to test the hypothesis that multiple effective pollen dispersal kernels are required to generate the patterns we observed between pollen dispersal distances, pollen pool alpha diversity, and coflowering at the landscape and neighborhood scales, we developed a spatially explicit, individually based model to simulate mating dynamics at our study site (fig. S3). The main outputs of the model were the mean observed pollen dispersal distance and alpha diversity. The model assumes that pollen dispersal is 100% effective, in that each dispersed pollen grain eventually fertilizes an ovule. We varied whether a single static dispersal kernel was governing pollination patterns or whether distinct dispersal kernels generated during periods of high and low coflowering density at the neighborhood and landscape scales more accurately accounted for pollination patterns while accounting for uncertainty in the best-fit model (supplement F). We note that the simulation analyses presented here compared estimates of forward pollen dispersal kernel parameters with observed dispersal distance and pollen pool diversity of maternal trees, as there are no existing analytical tools that facilitate comparisons in the same direction.

Results

We characterized observed pollen dispersal distance, genetic diversity of the pollen pool, and estimated pollen dispersal kernel parameters using 814 seedlings from 41 separate *Oenocarpus bataua* progeny arrays, corresponding to 34 unique maternal trees, from 2011 to 2015 (i.e., six maternal trees were sampled multiple times; table S3). In doing so, we assigned paternity to 800 *O. bataua* offspring (mean = 20, SD = 3.5 progeny per array, range = 9–25), with 14 unassigned samples. Of the samples with assigned paternal trees, the mean alpha diversity of the pollen pool was 3.38 (SD = 0.60, range = 1.93–5.41), and each progeny array received pollen from an average pollination distance of 391 m (SD = 109 m, range = 91–766 m; table S3).

Temporal Variation

The observed average pollen dispersal distance and alpha diversity of progeny arrays varied substantially depending on flowering date over our 4-year study period (fig. 1A, 1B). Also, neighborhood density around maternal trees ranged from 4 to 69, and landscape density varied from 50 to 104 (fig. 1C, 1D). We did not find evidence of an association between neighborhood and landscape density (Pearson's $r = 0.17$, $t = 1.05$, $df = 39$, $P = .30$), allowing us to separately investigate effects of these two spatial scales on pollination patterns.

Density-Dependent Pollination Patterns

Neighborhood and landscape densities had distinctive impacts on pollination patterns. After accounting for temporal effects, higher neighborhood density was significantly associated with decreased mean observed pollen dispersal distance per progeny array, whereas landscape density had a significant positive association with dispersal distance (table 1; fig. 2A, 2B). Neighborhood and landscape densities also had distinctive impacts on alpha diversity: there was a significant negative relationship with neighborhood density but a significant positive relationship with landscape density (table 1; fig. 2C, 2D).

During periods of high neighborhood densities, observed dispersal events occurred at relatively short distances (observed mean distance = 270 m, SE = 234 m), while observed dispersal occurred at intermediate to long distances from maternal trees during scenarios of low neighborhood coflowering density (observed mean distance = 519 m, SE = 286 m; fig. 3B, 3C). Similarly, the weighted scale parameter of the multimodel pollen dispersal kernels was smaller during periods of high neighborhood density compared with low ($1/d_p = 604.45$ m vs. $1/d_p = 909.13$ m; table 2). Moreover, the best-fit model for the pollen dispersal kernel during scenarios of high neighborhood density was a thin-tailed Weibull distribution, compared with the fat-tailed lognormal distribution for the best-fit low-density model (table S5). In contrast, observed pollen dispersal distance was similar during periods of high versus low landscape densities (observed mean distance = 381 m, SE = 284 m vs. observed mean distance = 393 m, SE = 293 m), and dispersal kernel scale estimates largely overlapped ($d_p = 0.00091$, SE = 0.00061 vs. $d_p = 0.00114$, SE = 0.00054; tables 2, S5; fig. S4). Finally, simulation analyses revealed that two dispersal kernels better explained observed associations between neighborhood coflowering density and alpha diversity and between neighborhood coflowering density and dispersal distance than did a single kernel (fig. 4; table S6). On the other hand, a single kernel better explained the associations between coflowering landscape density and alpha diversity and between

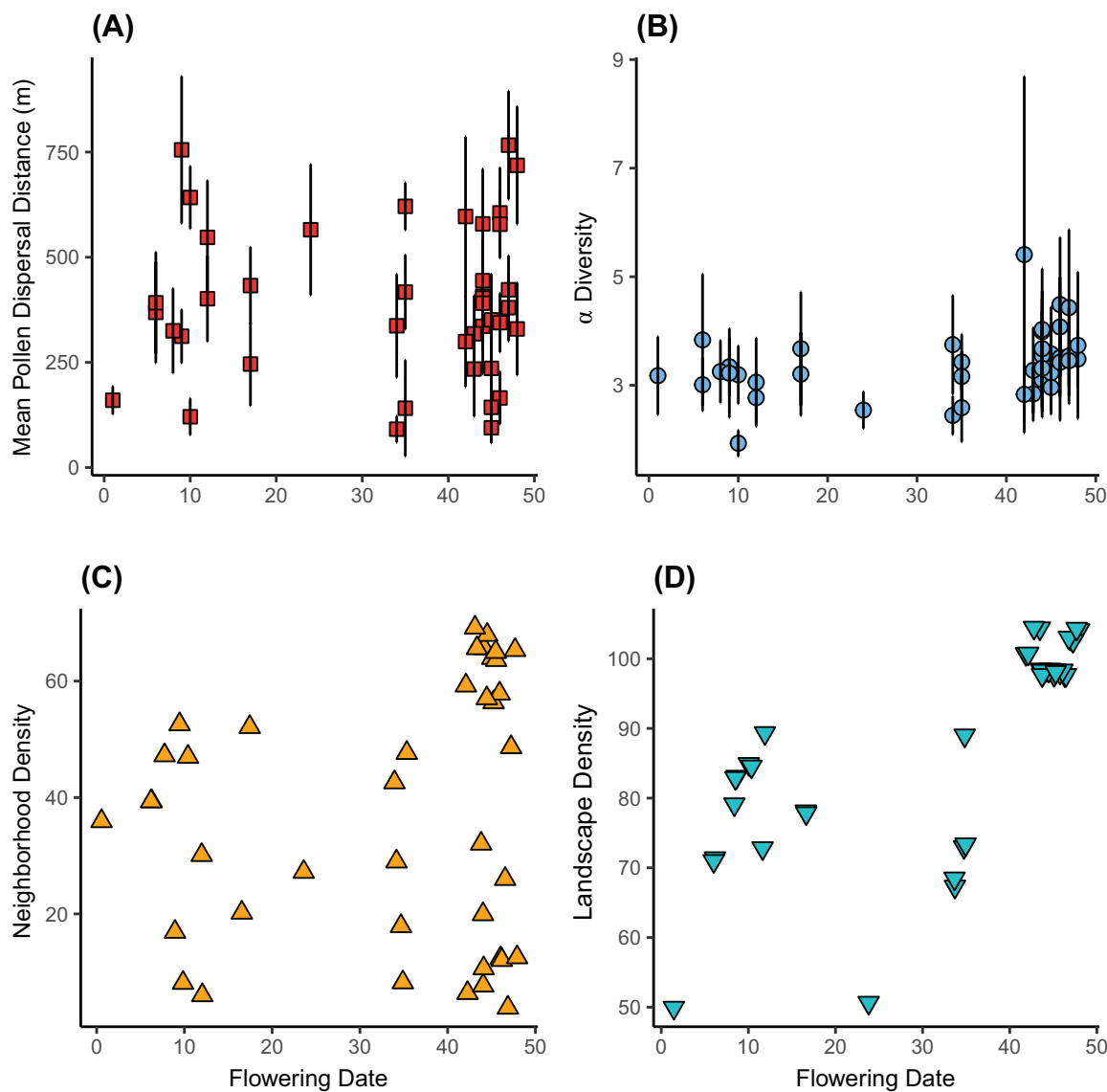


Figure 1: Temporal variation in the number of conspecific trees concurrently producing pollen and the mating pattern metrics of *Oenocarpus bataua* over a 4-year period at Bilsa Biological Station, northwest Ecuador. For each of the 41 progeny arrays studied, *A* illustrates the observed mean pollen dispersal distance (m), *B* shows the diversity of paternally inherited alleles (alpha diversity), *C* depicts the density of concurrently flowering trees at the neighborhood scale (33 ha), and *D* shows the density of conspecific trees concurrently bearing pollen at the landscape scale (130 ha). Flowering date ranges from September 2011 (corresponding to 0 on the *x*-axis) to August 2015 (corresponding to 48). Error bars show 95% confidence intervals.

coflowering landscape density and pollen dispersal distance (fig. 4; table S6).

Discussion

This research advances our understanding of how the flowering density of conspecific plants shapes variation in patterns of pollen movement and genetic diversity, with implications for gene flow and the maintenance of genetic

diversity. In addition, this work contributes to our understanding of how conspecific flowering density may impact observed differences in pollination patterns between temperate versus tropical systems. Contrary to our expectations, the relationship between coflowering density and pollination patterns in our study system appears to vary with spatial scale: increasing neighborhood density significantly decreased dispersal distance and alpha diversity of the pollen pool. In contrast, increasing landscape density

Table 1: Summaries of linear and linear mixed model terms evaluating the impacts of neighborhood density and landscape coflowering density on mean observed pollen dispersal distance and paternal gametic diversity (alpha diversity) for 41 progeny arrays of *Oenocarpus bataua* seedlings collected in northwest Ecuador

| Response variable, model predictor variable | Estimate | SE | <i>t</i> | <i>P</i> |
|--|----------|--------|----------|-----------|
| Mean observed pollen dispersal distance (m): | | | | |
| Neighborhood density | -6.79 | .78 | -8.78 | <.0001*** |
| Landscape density | 3.45 | 1.15 | 3.01 | .0046** |
| Alpha diversity (log transformed): | | | | |
| Neighborhood density | -.0015 | .00052 | -2.91 | .033* |
| Landscape density | .0028 | .00057 | 4.96 | .0042** |

* $P \leq .05$.** $P < .01$.*** $P < .001$.

was significantly associated with increased pollen pool diversity and pollen dispersal distance. These findings suggest that changes in coflowering density alter pollen flow and, by extension, the maintenance of genetic diversity in out-crossing plant populations.

As low neighborhood density encourages long-distance pollen movement and increases pollen pool diversity of maternal progeny arrays, lower coflowering densities at this scale may promote gene flow and genetic diversity, with implications for drift-migration trade-offs. For example, decreasing neighborhood density may increase immigration (C ortes et al. 2013), reducing genetic differentiation between neighborhoods or populations (Mu oz-Pajares et al. 2020). For species with significant spatial genetic structure at short distances, low neighborhood densities among flowering adults may therefore increase gene movement and homogenize fine-scale genetic structure (Aguilar et al. 2008; Sork et al. 2015). However, there likely exists some threshold beyond which excessively low neighborhood density could lead to isolation and higher relatedness of progeny (Fuchs et al. 2003), correlated paternity (Feres et al. 2012), or increased spatial genetic structure (Sebbenn et al. 2010). At the landscape scale, higher flowering densities may encourage dispersal between unrelated adults and introduce relatively distinct genotypes to progeny arrays, increasing the diversity of the pollen pool, decreasing genetic structure (Austerlitz et al. 2004; Sork and Smouse 2006), and boosting the effective breeding size of the population (Lowe et al. 2005).

While scale-dependent, interactive effects can influence ecological processes such as plant community heterogeneity and predation (Collins and Smith 2006; Frey et al. 2018), less is known about how these effects impact processes that generate patterns of genetic diversity. Because neighborhood and landscape coflowering densities can vary independently from one another, variation in coflowering density across scales may produce additive effects on dispersal distance and pollen pool di-

versity. For example, pollen dispersal distance and diversity may be maximized when neighborhood coflowering density is low and landscape coflowering distance is high. Alternatively, pollen dispersal distance and diversity may be minimized when neighborhood coflowering density is high and landscape coflowering density is low. Although we did not observe any evidence of significant interactive effects between neighborhood and landscape coflowering densities, it remains important to consider patterns of coflowering across spatial scales to understand how these density-dependent processes may contribute to the maintenance of genetic diversity in other systems.

Our results are largely consistent with the hypothesis that coflowering density at the neighborhood scale substantially impacts pollen movement. In addition to the significant association between coflowering neighborhood density and pollen dispersal distance, we found that both observed pollen dispersal distances and the estimated scale of pollen dispersal tended to be greater during periods of low versus high neighborhood density. Unlike the scale parameter that describes the mean dispersal distance, the shape parameter lends insight into the peak and fatness of tail of the dispersal kernel, which is of relevance for long-distance dispersal events that are disproportionately important for gene flow and colonization events (Klein et al. 2006; Nathan et al. 2012). Recognizing that there was some model uncertainty and that in some cases the same maternal tree was sampled for more than one progeny array, the best-fit models in our study were a relatively fat-tailed lognormal distribution that characterized dispersal during periods of low neighborhood coflowering density and a thin-tailed Weibull distribution during periods of high neighborhood density. Biologically speaking, these differences suggest relatively dampened potential for long-distance dispersal during periods of high neighborhood density, as has been shown for various wind-pollinated temperate species of trees (Austerlitz et al. 2004; Pluess et al. 2009; Saro et al. 2014). In contrast, thicker tails, like that

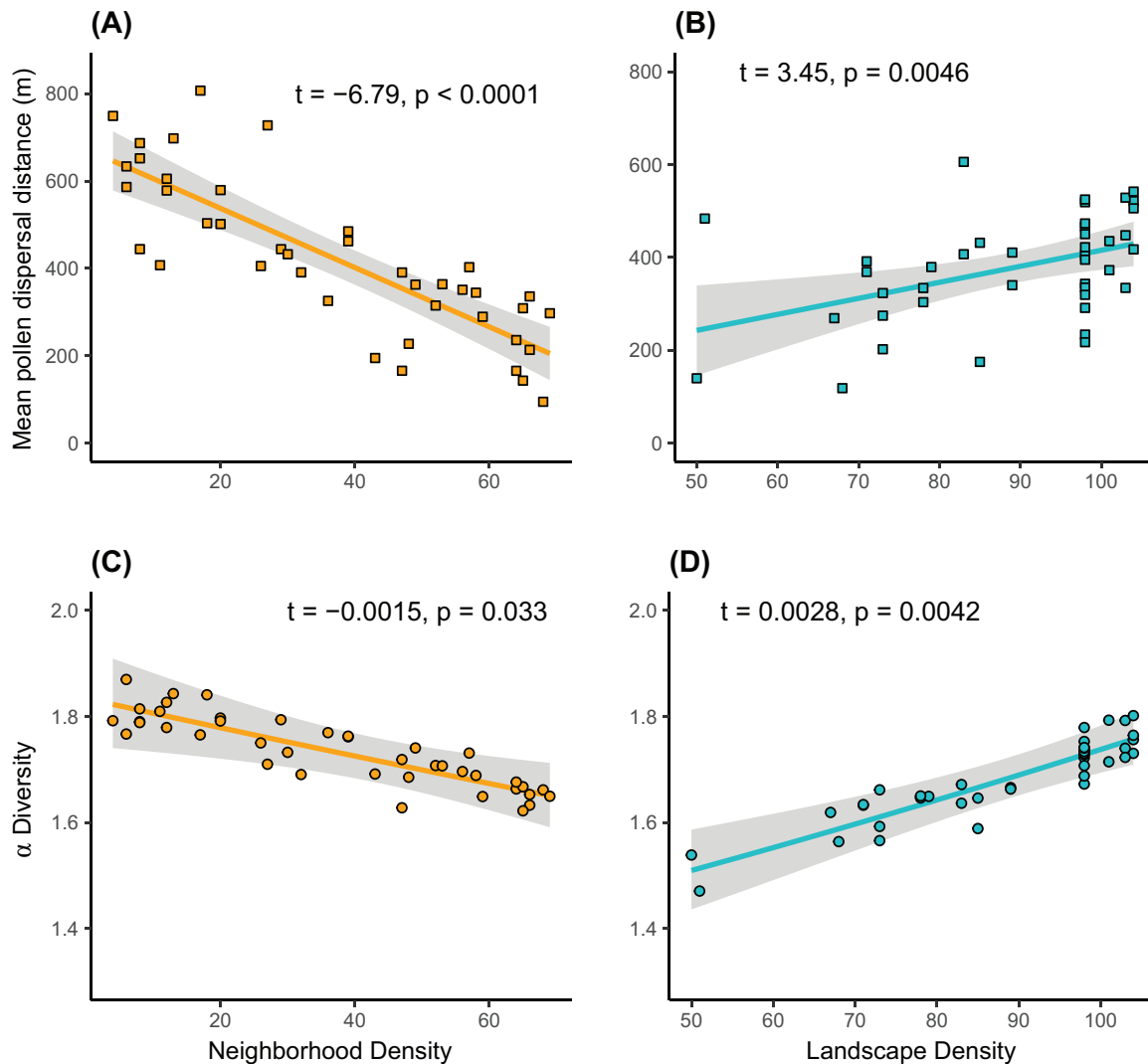


Figure 2: Partial residual plots illustrating the relationships between neighborhood and landscape densities of concurrently flowering trees and observed pollen dispersal distance (m) as well as associations between neighborhood and landscape coflowering densities and allelic diversity of the pollen pool (alpha diversity) of *Oenocarpus bataua* in northwest Ecuador. Shown are the significant negative relationship between average pollen dispersal distance (m) and neighborhood density (A), significant positive relationship between average pollen dispersal distance (m) and landscape density (B), significant negative association between alpha diversity and neighborhood density (C), and significant positive relationship between alpha diversity and landscape density (D). Data represent 800 pollination events from 41 progeny arrays occurring from 2011 to 2015. Shaded areas indicate 95% confidence intervals.

exhibited by the lognormal distribution during low-density scenarios, have been shown to characterize extensive pollen dispersal in dioecious species (Chybicki and Oleksa 2018). These findings suggest that low-density neighborhoods may generate fat-tailed kernels that in turn promote gene flow and genetic mixing across the landscape and increase genetic diversity in populations (Klein et al. 2006). However, because it is notoriously difficult to capture long-distance dispersal events and accurately describe the tail of pollen dispersal kernels because of the inherent variation in this complex process (Bullock and Clarke 2000), we recommend

additional data collection at larger spatial scales in the future. While the appropriate scale of analysis will depend on the plant species and the associated pollinator community, we suggest that studies examine pollination patterns in a landscape area that exceeds the neighborhood area by at least four times, which is the difference in area between our observed scales.

Our simulations also revealed that at the neighborhood scale, separate pollen dispersal kernels for high and low coflowering densities better explain our empirical data than a single kernel, suggesting that pollen dispersal is shaped

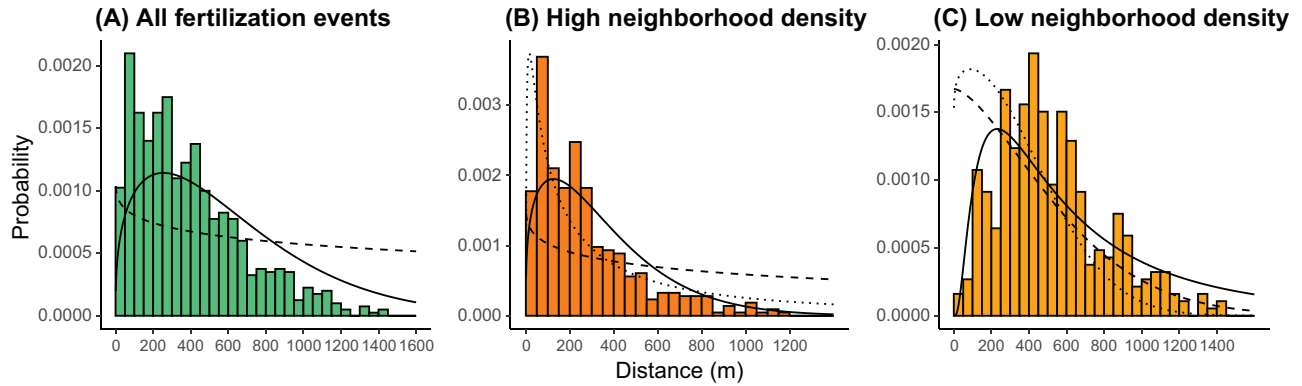


Figure 3: Estimated forward pollen dispersal kernels (black lines) and a frequency distribution of observed pollen dispersal distances (m; histogram) for *Oenocarpus bataua*. Shown are the dispersal kernel estimates for all fertilization events (A) and periods of high (B) and low (C) neighborhood densities of concurrently flowering trees. Best-fit models are shown with solid lines, second-best-fit models are shown with dashed lines, and third-best-fit models are shown with dotted lines. Distribution models were normalized using the sum of probabilities. Only two models for all fertilization events (A) had Akaike information criterion weights >0.00 . Data represent 814 pollination events from 41 progeny arrays occurring from 2011 to 2015 in northwest Ecuador.

not only by coflowering density per se but also by changes in pollinator movement. Animal pollinators navigate an intricate landscape, and a variety of interacting factors shape their movement patterns (Kremen et al. 2007). The density of flowering sources can influence pollinator population size, feeding behavior, energy expenditure, and movement (Ghazoul 2005; Bernhardt et al. 2008; Essenberg 2013), which in turn would be expected to impact the dispersal services they provide. Moreover, the spatial scales of pollinator mobility and coflowering density are likely to interact with the area over which the spatial aggregation of pollen sources occurs (i.e., area of clumpedness). The interactions between these factors are likely to be complex (Robledo-Arnuncio and Austerlitz 2006), but their impact on pollination patterns has received scant empirical attention. In our study system, insect pollinators with large dispersal capabilities (Núñez-Avellaneda and Rojas-Robles 2008; Hoddle

et al. 2015) interact with a plant species characterized by a naturally patchy distribution and asynchronous flowering phenological cycle, which creates clumps of pollen sources across the landscape (Ramirez-Parada et al. 2020). As we observe an excess of near-neighbor mating during periods of high neighborhood density, the scale of the pollen dispersal kernel likely exceeds that of the clumps (Robledo-Arnuncio and Austerlitz 2006). In addition, when the area over which clumps occur is small, the effective pollen pool size and the variance in pollen dispersal distance are expected to decrease with more leptokurtic dispersal kernels, as they favor near-neighbor mating and infrequent long-distance dispersal at the expense of intermediate dispersal (Robledo-Arnuncio and Austerlitz 2006). Such a change is mirrored in our work, with pollen pool alpha diversity and dispersal distance decreasing under high coflowering neighborhood densities when the best-fitting model has a

Table 2: Multimodel pollen dispersal kernel estimates from $NM\pi$ output for progeny arrays sired during periods with varying coflowering densities of conspecific adults (high/low neighborhood density, high/low landscape density)

| Coflowering density | s | m_p | d_p (SE) | $1/d_p$ |
|---------------------------|-------|-------|-----------------|----------|
| High neighborhood density | .0031 | .42 | .00165 (.00117) | 604.45 |
| Low neighborhood density | .0000 | .65 | .0011 (.00058) | 909.13 |
| High landscape density | .0048 | .50 | .00091 (.00061) | 1,098.90 |
| Low landscape density | .0000 | .50 | .00114 (.00054) | 874.99 |
| All fertilization events | .0021 | .54 | .00132 (.00051) | 757.93 |

Note: s = frequency of self-fertilization; m_p = frequency of immigration; d_p = scale; $1/d_p$ = mean distance of pollen dispersal (m).

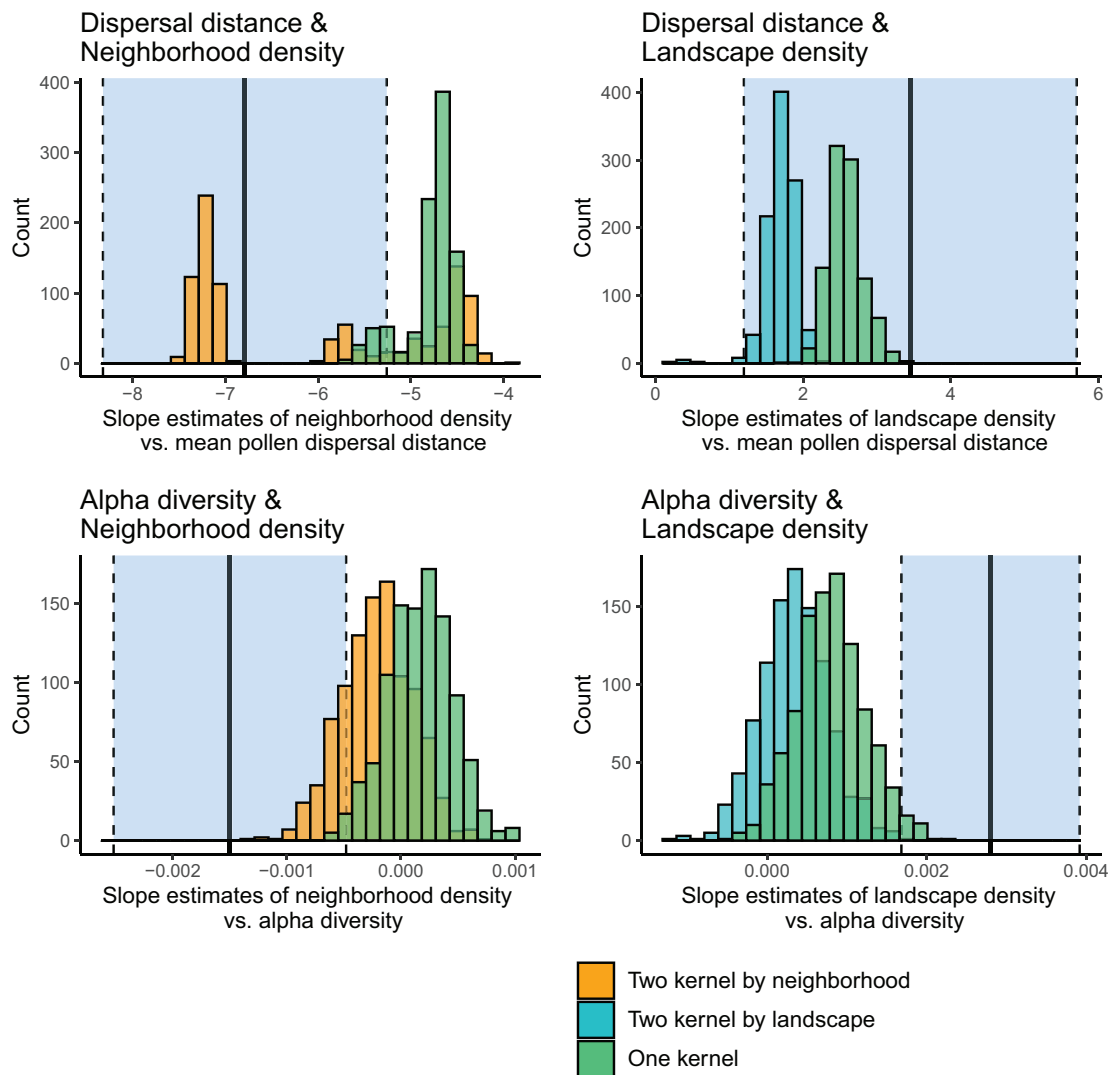


Figure 4: Slope estimates from simulations from three scenarios where pollen dispersal kernels varied by the coflowering density of individuals at the landscape (blue) and neighborhood (yellow) scales and as a single static pollen dispersal kernel (green). The top-left panel shows histograms of the slope estimates of neighborhood density and mean pollen dispersal distance across 999 simulation iterations, along with the bold line showing the observed slope estimate in the empirical data set, with the dashed lines and shaded area showing the range of the 95% confidence interval. Similarly, the top-right panel shows the slope estimates for mean pollen dispersal distance and landscape density, the bottom-left panel shows the slope estimates for alpha genetic diversity and neighborhood density, and the bottom-right panel shows the slope estimates for alpha genetic diversity and landscape density.

smaller scale and thinner tail compared with the low-density counterpart. Our data suggest that during periods of low neighborhood coflowering densities, pollinators move beyond the area over which clumps of pollen sources occur, resulting in a pollen dispersal kernel with greater scale parameters and relatively thicker tails compared with periods of high neighborhood density. While higher resolution data would better characterize the foraging ecology of pollinator communities, this work highlights the importance of integrating pollinator behavior, phenology, and spatial scale into understanding dispersal outcomes.

While our sampling was not dense enough to accurately characterize detailed temporal trends in pollination patterns, it does allow some insights into the degree to which coflowering density may influence mating patterns in a single population of outcrossing plants over time. For example, we observed substantial variation in the average pollen dispersal distance and alpha diversity of the pollen pool based on flowering date over the 4-year study period. Although not statistically tested, this suggests that single year “snapshot” approaches may capture only one point along a broad spectrum of possible mating patterns for a single population

(Hamrick 2012). In addition, we observed substantial sampling variance, and given that the 95% confidence intervals for alpha diversity overlap regardless of flowering date, it is likely that pollen pool diversity is more stable across time compared with pollen dispersal distance. In sum, this work suggests that our field requires more pollination biology studies that employ a longitudinal sampling approach to accurately capture temporal variation in coflowering density and characterize pollination patterns. An alternative approach that incorporates a longitudinal perspective is to sample established seedlings that are likely to represent a variety of ages and therefore fertilization events across time (e.g., Browne et al. 2018).

Our results suggest that coflowering density may be an important factor in shaping differences in gene flow between tropical and temperate plant species, which is a topic in need of more rigorous investigation. A recent study on seed plants found that genetic differentiation (i.e., F_{ST}) is higher in tropical regions compared with temperate regions, even while controlling for potential confounding factors such as differences in pollination mode (Gamba and Muchhala 2020). One potential explanation for this pattern would be that pollen dispersal is generally less extensive in the tropics, though several studies have found that pollen kernels in tropical plants often have relatively fat tails and thus higher potential for long-distance dispersal (Dick et al. 2003; Côrtes et al. 2013; Wang et al. 2014; dos Santos et al. 2018). In this study, we demonstrate a scale-dependent influence of coflowering density on pollen dispersal kernel parameters. An important unresolved question is how the interaction between spatial extent and coflowering density may translate into regional patterns of genetic diversity and structure. On one hand, reduced pollen dispersal distance and diversity at low landscape coflowering densities would likely lead to increased genetic differentiation among populations. Most tropical species occur at relatively low density at broad scales (Clark et al. 1999; Dick et al. 2008), which may explain why these species exhibit greater population genetic structure (i.e., F_{ST} ; Gamba and Muchhala 2020). At the same time, we found that low coflowering density at the neighborhood scale was associated with increased pollen dispersal and diversity, which may lead to reduced genetic differentiation across a landscape if pollination neighborhoods overlap. Resolving the relative influence of this interaction between spatial scale, coflowering density, and pollen dispersal may help uncover the role of pollen-mediated gene flow in producing differences in genetic differentiation between temperate and tropical plant populations. More broadly, our findings suggest that the density of pollen sources may serve as a key driver of pollination patterns, both within and among systems, and that explicitly incorporating the scale-dependent effects of coflowering will significantly improve our under-

standing of mating patterns in outcrossing populations of wild plants.

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Statement of Authorship

Z.D.-M. and J.K. conceptualized the study and acquired funding. J.K. developed the study methods and experimental design and supervised the project. D.C. collected long-term phenology data. J.O. collected progeny array data, grew seedlings, and collected samples. Z.D.-M. conducted laboratory work and analyzed, validated, and visualized data. Z.D.-M. conducted model analysis with support from L.B. L.B. conducted $NM\pi$ analysis and coding simulation. Z.D.-M. wrote the original draft and reviewed and edited the manuscript. J.K. and L.B. reviewed and edited the manuscript.

Data and Code Availability

Genotype and other related data, including simulation code, have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.gf1vhhmng>; Diaz-Martin et al. 2022) and are freely available.

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“The flowers are of a bright scarlet, and form racemes at the ends of the branches. . . . The plant is certainly one of the most striking of all found on the deserts of Arizona.” Figured: “Flowers of *Fouquieria (spinosa) spendens* Engelm.” From “Botanical Notes from Tucson” by Jos. F. James (*The American Naturalist*, 1881, 15:978–987).