ORIGINAL ARTICLE

WILEY **bio**TROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Integrating effects of neighbor interactions for pollination and abiotic resources on coffee yield in a multi-strata agroforest

Gordon Fitch[1] | John Gonzalez[2] | Anna M. Oana[1] | Maggie Oliver[1] | John Vandermeer[1,2]

[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

[2]Program in the Environment, University of Michigan, Ann Arbor, Michigan, USA

Correspondence
Gordon Fitch, Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA.
Email: fitch.gordon@gmail.com

Present address
Gordon Fitch, Department of Biology, University of Massachusetts Amherst, Amherst, MA, USA

Abstract

Animal-pollinated plants interact with neighbors for both abiotic resources and pollination, with consequences for reproduction and yield. Yet few studies have compared the relative magnitude of these effects, particularly in agroecosystems. In vertically stratified communities, such as agroforests, neighbor effects may be stratum-dependent. Understanding the net effects of neighbors on crop yield is important for managing multifunctional agroecosystems to simultaneously support production and biodiversity. This study evaluated the effects of neighboring plants on pollen deposition, fertilization, and yield in *Coffea arabica* in a shaded organic coffee farm with high non-crop plant abundance and diversity in Chiapas, Mexico. We assessed the impact of (1) floral resources at three vertical strata (herbs, coffee bushes, and canopy trees) on stigma pollen load (a measure of interaction for pollination), and (2) floral density and canopy cover (proxies for competition for abiotic resources) on yield (final fruit set and per-fruit weight), using structural equation modeling to evaluate the relative effect of each interaction type. Coffee competed for pollination with neighbors (conspecifics and heterospecifics) across strata. Pollen load influenced final fruit set, but the effect of neighbor competition for pollination was weaker than effects mediated by interactions for abiotic resources. Effects of interactions for abiotic resources were heterogeneous across strata, with negligible effects of herb-layer or coffee flower density but net positive effects of canopy trees on final fruit set. Overall effects of neighbors on coffee yield were weak, suggesting that coffee agroecosystems can be managed to maintain high plant density and diversity without sacrificing yield.

Abstract in Spanish is available with online material.

KEYWORDS
agroecosystem multifunctionality, Chiapas, *Coffea arabica*, Mexico, neighborhood effects, pollinator-mediated plant interactions, structural equation modeling

1 | INTRODUCTION

Plants frequently compete with neighbors for abiotic resources including light, water, and soil nutrients, often with profound effects on growth and population dynamics of wild plants (Goldberg & Barton, 1992; Gurevitch et al., 1992) and yields of crop plants (Njoroge, 1994; Oerke, 2006). At the same time, co-flowering plants commonly interact for pollination, with outcomes ranging from mutually detrimental to mutually beneficial (Braun & Lortie, 2019; Mitchell et al., 2009). For a given pair of organisms, the net outcome of interaction will depend on the effect of both types of interactions. Moreover, there may be complex feedbacks between interaction types, since the availability of abiotic resources—influenced by neighbors—can impact floral traits and pollinator attraction (Fitch & Vandermeer, 2020; Prado et al., 2019). Integrating the effects of multiple interaction types in a single study can therefore lead to a better understanding of the net effect of neighbors on plant fitness and crop yield. Yet, while interactions for shared abiotic resources and interactions for shared pollinators have each received significant attention in isolation, studies that consider both types of interactions simultaneously are less common (Underwood et al., 2014).

This is particularly true for agroecosystems. While the agronomy literature includes many studies investigating the effects of competition for abiotic resources on crop yield (reviewed in Radosevich et al., 1997, Zimdahl, 2007), few studies have investigated interactions for shared pollinators in crop systems (but see Badillo-Montaño et al., 2019, Klein et al., 2008), and even fewer have looked at both types of interactions together (but see Klein et al., 2015). The low plant diversity of conventional agroecosystems may ameliorate neighbor effects on pollination (Albor et al., 2019), but rising interest in agricultural practices that increase on-farm plant diversity—including intercropping, hedgerows and wildflower strips—may increase competition for pollination between crop and non-crop species (Lander et al., 2011, Nicholson et al., 2019; but see Lundin et al., 2017) and/or among crop species (Osterman et al., 2021). The higher plant diversity and greater vertical stratification of agroforests may strengthen the effect of neighbor interactions for pollination relative to other agroecosystems, though this remains untested. Most of the existing research on interactions for shared pollinators focuses on forbs in semi-natural meadow-type habitats (reviewed in Braun & Lortie, 2019), where flowers tend to occur in a single stratum of vertical space. In habitats with greater vertical stratification, neighbor effects on pollination may be stratum-specific, given evidence for stratum fidelity in some forest bee communities (Roubik et al., 1995, Ulyshen et al., 2010, but see Roubik, 1993), but this has received scant attention.

Coffee (*Coffea* spp.; Rubiaceae) is an important animal-pollinated crop where we might expect complex effects of neighbor interactions, particularly on farms with abundant non-crop plants. The question of whether plant neighborhood influences yield is particularly salient in coffee, given the potential for coffee farms to support high levels of biodiversity (De Beenhouwer et al., 2013; O'Brien & Kinnaird, 2003; Perfecto et al., 1996). This depends on on-farm plant diversity, including canopy trees and herbaceous vegetation (De Beenhouwer et al., 2013; Hipólito et al., 2018; Iverson et al., 2019).

Canopy trees modulate temperature extremes and evapotranspiration rates in the understory, reducing coffee plant stress and maintaining environmental conditions that maximize photosynthesis (Lin, 2009; Staver et al., 2001). Thus, coffee yields commonly peak under moderate shade levels (Prado et al., 2018; Soto-Pinto et al., 2000; Staver et al., 2001). But high levels of shading (>~50% canopy cover) frequently reduce yield (Soto-Pinto et al., 2000; Staver et al., 2001). High shade may also encourage the growth of coffee fungal diseases (Avelino et al., 2006; López-Bravo, 2012). Interactions for abiotic resources with herbaceous vegetation appear to be more generally competitive, and unmanaged herbaceous vegetation can substantially reduce coffee yield (Eshetu & Kebede, 2015; Moraima García et al., 2000; Njoroge & Kimemia, 1990). This is likely due to competition for soil nutrients and, in drier conditions, water (Njoroge, 1994; Staver et al., 2001). The distinct patterns of effect for interactions with herb-layer and canopy-layer neighbors highlights the value of considering each stratum separately when evaluating neighborhood effects on coffee yield.

The organic management practices (particularly no herbicide or synthetic fertilizer use) and moderate to high shade tree density on the farm where this study occurred are likely to contribute to competitive interactions for abiotic resources between coffee bushes and neighboring plants. Many of the common non-crop plants in coffee agroecosystems (both trees and herbs) produce abundant, animal-pollinated flowers. In our study region, the bloom period of coffee coincides with high floral abundance in both canopy and herb strata (Fisher et al., 2017), setting the stage for interactions for shared pollinators.

Yet several aspects of the reproductive biology of *Coffea arabica* may limit the impact of neighbor interactions for pollination. First, *C. arabica* is self-compatible and often not pollen limited (Prado et al., 2018; though biotic pollination generally improves yield; Moreaux et al., 2022). Thus, even if floral neighborhood influences pollination, its effects on yield may be small. Second, coffee is mass-blooming (Philpott et al., 2006). High conspecific density may increase floral fidelity by pollinators (Duffy & Stout, 2011), reducing the effects of heterospecific neighbors. Indeed, a recent study from coffee agroecosystems in Puerto Rico found no effect of floral neighborhood on the proportion of coffee pollen in the pollen loads of foraging bees (Prado et al., 2021). Together with evidence that resource competition with neighbors reduces coffee yield (Campanha et al., 2004; Eshetu & Kebede, 2015; Ronchi et al., 2007), these factors suggest that interactions for abiotic resources are more important than interactions for shared pollinators in determining net neighbor effects on *C. arabica*. Moreover, coffee is perennial; inter-annual variation in pollinator availability, climatic conditions, plant vigor, and resource availability make it difficult to evaluate the relative importance of different types of interactions in determining coffee yield, as this is likely to vary from year to year.

In this study, we examined how plant neighborhood influences pollination and yield in *C. arabica*, using path analysis to determine

the relative contribution of interactions for shared pollinators and for abiotic resources to the net effect of neighboring plants on coffee yield. For both types of interactions, we asked whether the impact of neighbors is mediated by the strata in which they occur (herb, coffee, or canopy layer). To assess pollination, we measured stigma pollen load (including coffee pollen and heterospecific pollen) and the number of pollen tubes reaching the base of the style. Stigma pollen load is a measure of pollination quantity, although some portion of the coffee pollen present was likely self pollen, since even coffee stigmas blocked from pollination receive substantial pollen (Klein et al., 2003, G. Fitch *unpublished data*). Since ovules can only be fertilized when pollen tubes reach the ovaries, the number of pollen tubes that grow to the base of the style is a measure of pollination quality. We considered three measures of coffee fruit production, all assessed at the branch level: initial fruit set, final fruit set, and per-fruit weight. Initial fruit set is determined largely by pollination levels and is therefore a measure of successful fertilization, but coffee frequently aborts developing fruits that they cannot adequately provision (Bos et al., 2007). Final fruit set and fruit weight are therefore the product of an interplay between pollination and resource availability (along with fruit predation and climatic factors) (Klein et al., 2015; Tamburini et al., 2019), and are the two measures of yield we assessed. In coffee, micronutrient deficiency is a key driver of fruit abortion (DaMatta et al., 2007), with water stress also contributing (Lin, 2009); competition with neighboring plants for soil nutrients and water are therefore likely to influence levels of fruit abortion.

We present the hypothesized relationships in Figure 1, elaborating on them below (parenthetical letters correspond to specific links illustrated in Figure 1). We expected that neighborhood coffee flower density would be positively related to coffee pollen load, due to the enhanced potential for cross-pollination (a), while canopy- and herb-layer flower density would reduce coffee pollen load, indicating competition for pollination with heterospecifics but not conspecifics (b). We predicted that co-flowering canopy trees (which are generally >3 m above the height of coffee plants) would reduce coffee pollen load but not affect heterospecific pollen, since the vertical separation of coffee bushes and canopy trees would lead to limited pollinator movement between canopy and coffee layers within a foraging bout (Roubik et al., 1995). Co-flowering forbs are less spatially separated from coffee flowers, so we anticipated more pollinator switching, leading to reduced coffee pollen and increased heterospecific pollen (c). We expected coffee pollen load to positively influence pollen tube number, while heterospecific pollen would reduce pollen tube number via stigma clogging (d). We expected pollen tube number to independently influence both initial and final fruit set (Niesenbaum & Casper, 1994), thus linking pollen receipt to coffee yield (e). However, because *C. arabica* is not pollen-limited, we thought interactions for abiotic resources would be more important in determining the net effect of neighbors. We expected competition with canopy trees to reduce both final fruit set and per-fruit weight (f), mediated primarily by access to light since nearly half the surveyed plants had >50% canopy shading (Table S1). While we anticipated competition for soil nutrients with canopy trees, we expected its effect to be weaker than, and covary with, competition for light. We expected competition with herbs and conspecifics for soil nutrients and/or water to negatively influence final fruit set and per-fruit weight (g) (Njoroge, 1994; Njoroge & Kimemia, 1990). Biomass is a commonly used, if imperfect, proxy measure for competition in
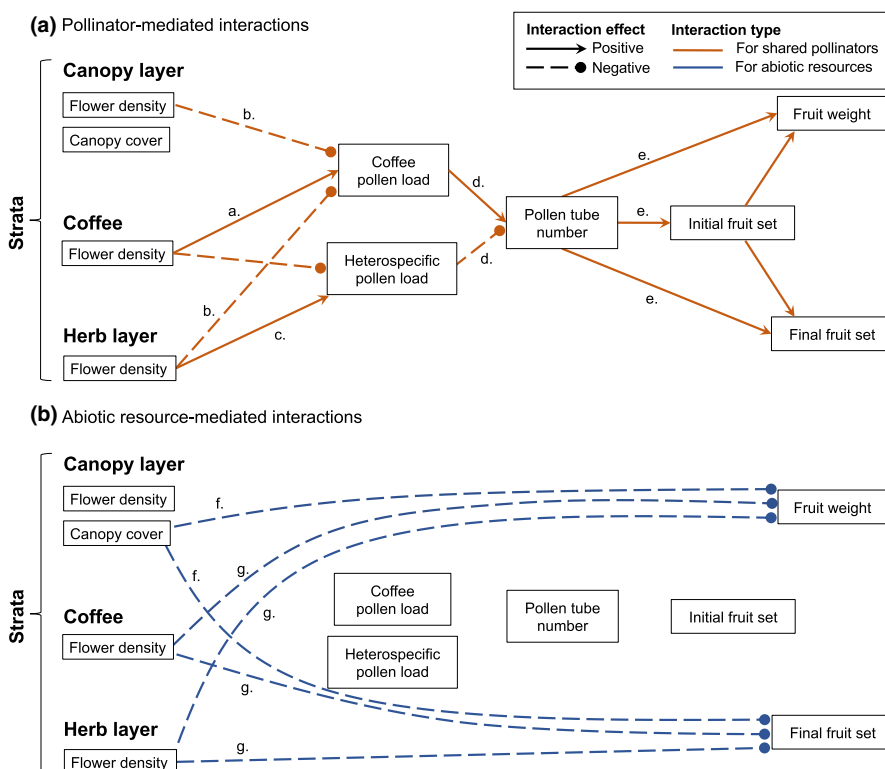

FIGURE 1 Hypothesized effects of neighbor interactions for (a) shared pollinators and (b) abiotic resources on coffee pollination and yield. Letters correspond to specific hypotheses described in the Introduction. In (b), canopy cover is used as a proxy for the strength of competition for abiotic resources (especially light) with canopy trees, while coffee and herb-layer flower density are used as proxies for the strength of competition with neighboring coffee plants and herbs, respectively. See *Data analysis* section for more details

plants (Damgaard & Weiner, 2017; Trinder et al., 2013), but we could not accurately, nondestructively measure herb-layer biomass, so we used floral density, which is often highly correlated with biomass (Younginger et al., 2017) (see Appendix S1: Methods).

2 | METHODS

2.1 | Study system

Research took place in Finca Irlanda (15.17358–92.33827), a ca. 300-ha shaded organic coffee farm in SE Chiapas, Mexico. Multiple varieties of *C. arabica* are cultivated on the farm. This study included individuals from two varieties, Catimor and Java; we did not distinguish between varieties. Coffee mass blooms during the dry season, December–April. This research occurred during consecutive mass blooms, 19–24 February and 6–10 March 2018.

The understory of Finca Irlanda is a spatially heterogeneous assemblage of herbaceous plants, most of which, like coffee, bloom during the dry season. Herbs are controlled by periodic cutting with machete, resulting in a mosaic of plants at varying stages of regrowth, generating high spatial heterogeneity in herb biomass and floral abundance (Figure S1). The canopy layer includes diverse shade trees; spatial variation in species composition and density of shade trees contributes to heterogeneity in the availability of both light and floral resources. Soil nutrient levels strongly influence coffee plant vigor on the farm (Gonthier et al., 2013).

2.2 | Data collection

See Figure 2 for a schematic of our sampling design. During the first mass bloom, we established 21 20 m × 2 m transects, following the orientation of coffee rows. Transects were chosen to represent the full range of canopy cover, understory biomass, and floral density present on the farm at the time of the first mass bloom and were >50 m apart (Table S1).

Within each transect, we selected three focal coffee plants. Focal plants had plentiful open flowers, were separated from one another by >1 m, and were distributed across the length of the transect. From each focal plant, we collected the carpel from three haphazardly selected flowers from the outermost node of three branches from the upper third of the bush, cutting the carpel from the flower just above the ovary (Figure S2); carpels were stored in 95% ethanol. For each focal plant, we measured its height and assessed canopy cover above its crown (our primary measure of interaction for abiotic resources with canopy trees) using CanopyApp 1.0.3 (University of New Hampshire, Durham, NH, USA). We selected a fourth branch from each focal plant to assess fruit set, marking it with tape. On this branch, we counted open flowers and nearly-open buds, starting with the outermost node, on four nodes or until we reached >30 open flowers, whichever required more nodes (except in two cases where no available branch had >30 open flowers).

We used neighborhood floral density at each stratum as a measure of interactions for both pollination and abiotic resources (Figure 1, paths a–c, g). To assess neighborhood floral density, we counted and identified all flowers within a 2 m × 2 m plot centered on each focal plant, with separate tallies for each stratum. For highly abundant flowers, we counted the number of flowers in a representative 50 cm × 50 cm area and extrapolated from that count. This plot size encompasses the likely sphere of influence of neighbors interacting for abiotic resources, and is consistent with plot sizes selected for assessing effects of interactions for shared pollinators in other studies (e.g., Bruckman & Campbell, 2014; Duffy & Stout, 2011; Hegland & Boeke, 2006). While plants at greater distances can influence pollination (Albor et al., 2019; Essenberg, 2013), we located transects in areas that were relatively uniform in herb-layer and canopy tree density over the scale of tens of meters, so our 2 m × 2 m neighborhood is representative of the floral community at larger scales.

We hypothesized that proximity to an apiary would increase honeybee (*Apis mellifera*) visitation rates and pollen deposition, so we calculated the distance between the closest apiary and the center of each transect. To confirm that differences in pollination across sites was due to neighbor effects, rather than another environmental factor, we compared pollen deposition on the same plants between two mass bloom events at a subset of 12 transects that varied in neighborhood floral density (see Appendix S1).

In June 2018, when fruits were beginning to swell, we surveyed focal branches for initial fruit set. For each branch, we counted the number of developing fruits on the section of branch where we had tallied flower number. We calculated branch-level initial fruit set by dividing the number of developing fruits by the previously-recorded number of open flowers and large buds.

Once fruits began to ripen in October 2018, we surveyed all plants every 2–3 weeks. At each survey, ripe fruit on focal branches were counted, collected, and weighed. Collection continued until all fruit were collected (December 2018). Branch-level final fruit set was calculated by the number of fruits harvested by the number of open flowers and large buds.

To assess pollen deposition and fertilization, the collected carpels were, upon return to the lab, transferred to NaOH to soften for 24 h. After softening, carpels were rinsed in water, mounted on a microscope slide with decolorized aniline blue stain (Kearns & Inouye, 1993), and squashed. Using a UV fluorescent microscope at 40× magnification, we counted the number of pollen tubes that extended past the base of the style and the number of conspecific and heterospecific pollen grains on one randomly chosen stigma lobe per carpel (Figures 2, S2). Pollen was identified as coffee or non-coffee using a reference collection made on-site.

2.3 | Data analysis

All analyses were conducted using R v.4.0.2 (R Core Team, 2020). To test for spatial autocorrelation across transects in measures of
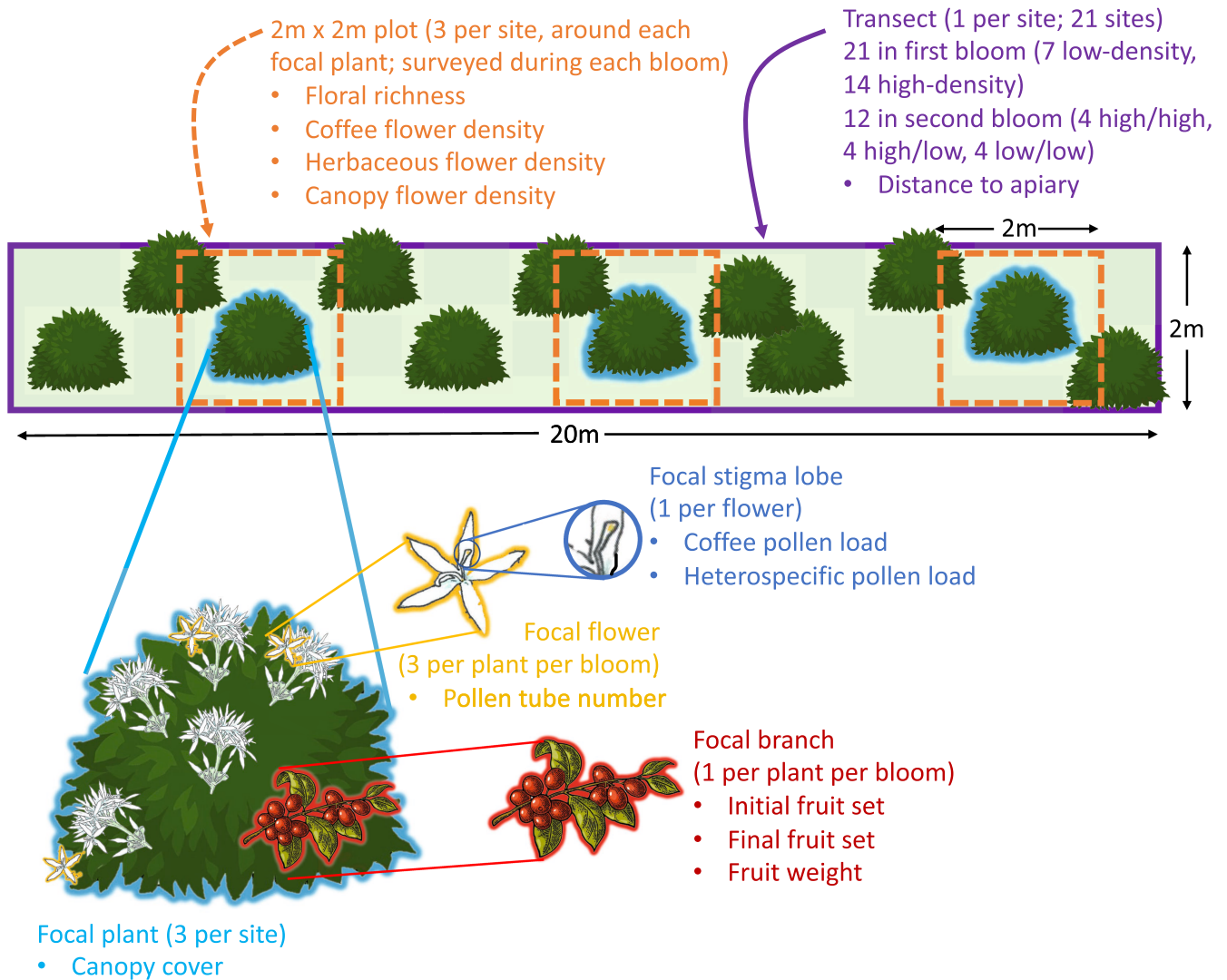
FIGURE 2 Schematic diagram of sampling and survey design. Data collection occurred at 21 sites. Bulleted points indicate variables for which data were collected at that scale. Low/high density refers to the density of co-flowering plants in the neighborhood of target coffee plants. Low density: ≤25 flowers/m², high density: >25 flowers/m² (see *Data collection* section)

pollination, yield, or neighborhood, we calculated Moran's I autocorrelation coefficient for each variable, using transect-level means, and compared this to the null expectation of no autocorrelation using the 'ape' package (Paradis & Schliep, 2019). In all cases, $p > .1$, indicating no spatial autocorrelation (Table S2). We checked for correlation among measures of floral neighborhood using linear mixed-effects models, implemented with the 'lme4' package using the 'lme()' function, with transect as a random effect, using a Bonferroni correction to adjust *P*-values for multiple comparisons.

We used piecewise structural equation modeling (SEM) to examine the effect of neighborhood on conspecific and heterospecific stigma pollen load, pollen tube number, initial fruit set, final fruit set, and fruit weight. The neighborhood metrics we included in the maximal model were: coffee flower density, herb-layer flower density, canopy flower density, total flower richness, and canopy cover. Canopy cover was included as a measure of interaction for abiotic resources with canopy trees; flower density in all three strata were

included as measures of interaction for shared pollinators. We used total floral richness in all strata, rather than considering each stratum separately, because most flowering species were in the herb layer. Coffee flower density, canopy-layer flower density, and herb-layer flower density were additionally included in submodels of final fruit set as measures of competition for abiotic resources with conspecifics, flowering canopy trees, and herbaceous weeds, respectively. Coffee flower density, rather than coffee plant density, was used because coffee plants differed substantially in vigor and size both within and across transects (G. Fitch *personal observation*), and therefore likely differed in resource use. Moreover, analysis of data from a pilot project indicated that neighborhood coffee flower density was a better predictor of final fruit set than coffee plant density (G. Fitch *unpublished data*). We considered herb flower density the best available measure to assess competitive effects of herbs for two reasons. First, the herbs considered most noxious by farmers produce profuse floral displays. Second, stem density decreases during regrowth

post-cutting, so stem density does not reflect biomass. We included coffee plant height (a proxy for age), distance from transect centroid to nearest apiary, and mass bloom event as covariates.

Using function 'lme()' from package 'nlme' (Pinheiro et al., 2020), we constructed linear mixed-effects models describing the hypothesized relationships between these variables. We tested for collinearity of predictors in all submodels by calculating the variance inflation factor (VIF) using function 'vif()' from package 'car'(Fox & Weisberg, 2019). In all cases, VIF <2, indicating negligible collinearity. We combined these submodels in a SEM using the 'psem()' function from 'piecewiseSEM' (Lefcheck, 2016). Submodels of pollen load and pollen tubes included plant nested within transect as random effects; submodels of fruit set and weight included transect only. Coffee pollen load was $\log_{10}$-transformed to achieve normality.

To evaluate SEM fit, we used Fisher's C and a chi-squared test comparing the hypothesized model to a null model. We examined tests of directed separation to determine if our initial model had omitted significant, biologically plausible relationships, and updated the model to include these where necessary (the only such relationship linked coffee pollen load to final fruit set). While we retained all measures of neighborhood plant density in the final model, regardless of significance, we dropped covariates from the model in cases where $p > .05$ and omission increased AIC value by <2. We also omitted neighborhood plant richness from the final model, since (1) it was strongly correlated with all measures of floral density (see *Results*), (2) it did not have a significant effect on any response variable, and (3) its omission substantially improved model fit (ΔAIC = 14). To calculate the net effect of each stratum on final fruit set, we multiplied standardized coefficients along each causal chain, adding resulting values together where the same stratum had multiple distinct effects.

3 | RESULTS

We found high levels of coffee pollen and low levels of heterospecific pollen on coffee stigmas (Table S1); 35% of stigmas had no heterospecific pollen. Coffee pollen load and pollen tube number differed substantially among flowers within a plant and among plants within a transect (Figure S3). Neighborhood coffee flower density was negatively correlated with both herb-layer flower density ($t = -5.11$, df = 194, $p < .001$) and canopy-layer flower density ($t = -2.84$, df = 194, $p = .01$); herb-layer flower density was not correlated with canopy-layer flower density ($t = 0.85$, df = 194, $p = .4$). Floral richness was strongly correlated with floral density at all strata ($p < .001$ in all cases).

Results from SEM, discussed below, are summarized in Figures 3, S4 and Table 1. The global model provided good fit to the data (Fisher's C = 47.12, df = 50, $p = .6$; $p > .05$ indicates reasonable fit). Neighborhood floral density reduced coffee pollen load, indicating competition for pollination. Contrary to our expectation (Figure 1, hypotheses a & b), the magnitude of this effect was consistent across strata. Neighborhood floral richness did not significantly influence coffee pollen load ($t = -0.39$, df = 154, $p = .7$), and was not included in the final SEM. Heterospecific pollen load was not significantly influenced by any component of floral neighborhood. Distance to
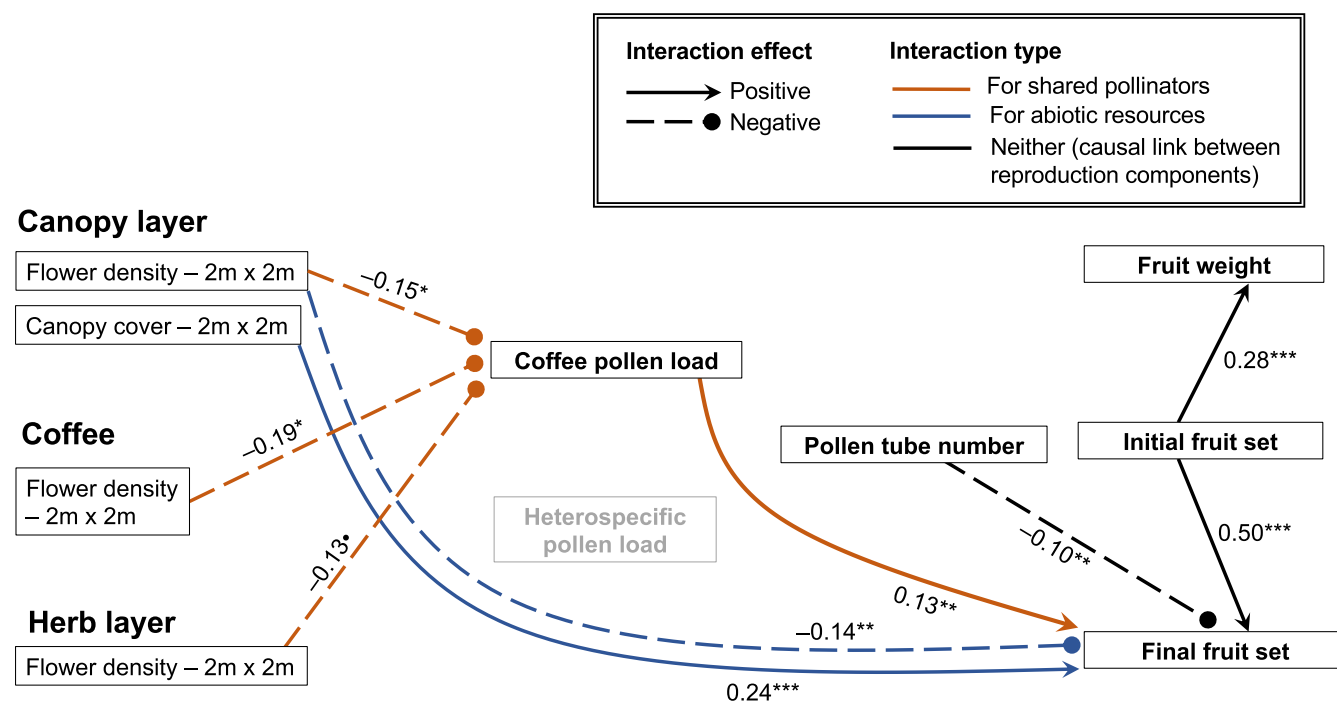

FIGURE 3 Results from SEM analysis of neighborhood coffee on pollination and yield. Only relationships with $p < .1$ are included. Coefficients represent standardized effect sizes; significance codes: •$p < .1$; *$p < .05$; **$p < .01$; ***$p < .001$. For visual clarity, covariates (mass bloom event and coffee bush height) have been omitted from the diagram (see Table 1 for full model output)

TABLE 1 Model output from structural equation models relating plant neighborhood to stigma pollen load, pollen tube number, fruit set, and fruit weight in coffee

Response *marginal R²*	Predictor	SE	Estimate ± SE	df	Critical value	P
log (Coffee pollen load) *0.11*	**Coffee flower density**	**−0.19**	**−0.03 ± 0.01**	**155**	**−2.10**	**.048**
	Herb-layer flower density	−0.13	−0.02 ± 0.01	155	−1.78	.08
	Canopy-layer flower density	**−0.15**	**−0.006 ± 0.003**	**155**	**−2.29**	**.03**
	Mass bloom event	**–**	**–**	**1**	**9.26**	**.002**
Heterospecific pollen load *0.07*	Coffee flower density	−0.06	−0.17 ± 0.23	155	−0.73	.5
	Herb-layer flower density	0.08	0.22 ± 0.21	155	1.00	.3
	Canopy-layer flower density	0.11	0.08 ± 0.05	155	1.43	.2
	Mass bloom event	**–**	**–**	**1**	**4.39**	**.04**
Pollen tube number *0.00*	log(Coffee pollen load)	0.02	0.14 ± 0.63	157	0.21	.8
	Heterospecific pollen load	−0.05	−0.02 ± 0.03	157	−0.77	.4
Initial fruit set *0.00*	Pollen tube number	0.04	0.002 ± 0.002	194	0.76	.4
Final fruit set *0.34*	**log (Coffee pollen load)**	**0.13**	**0.03 ± 0.01**	**187**	**2.91**	**.004**
	Pollen tube number	**−0.10**	**−0.003 ± 0.001**	**187**	**−2.61**	**.01**
	Initial fruit set	**0.50**	**0.47 ± 0.04**	**187**	**10.91**	**<.001**
	Canopy cover	**0.24**	**0.002 ± 5e⁻⁴**	**187**	**3.65**	**<.001**
	Coffee flower density	0.01	2e⁻⁴ ± 0.002	187	0.11	.9
	Herb-layer flower density	−0.07	−0.003 ± 0.002	187	−1.58	.1
	Canopy-layer flower density	**−0.14**	**−0.002 ± 5e⁻⁴**	**187**	**−2.95**	**.004**
	Mass bloom event	**–**	**–**	**1**	**5.13**	**.02**
Fruit weight *0.28*	Pollen tube number	0.02	0.001 ± 0.003	188	0.34	.7
	Initial fruit set	**0.28**	**0.44 ± 0.09**	**188**	**4.81**	**<.001**
	Canopy cover	0.06	7e⁻⁴ ± 0.001	188	0.65	.5
	Coffee flower density	−0.04	−0.002 ± 0.004	188	−0.62	.5
	Herb-layer flower density	−0.05	−0.004 ± 0.004	188	−0.90	.4
	Canopy-layer flower density	0.06	7e⁻⁴ ± 0.001	188	0.68	.5
	Coffee bush height	**−0.45**	**−0.002 ± 3e⁻⁴**	**188**	**−6.70**	**<.001**

Note: Boldface indicates a significant effect at $p < .05$.

the nearest apiary did not influence pollen load. Neither conspecific nor heterospecific pollen load predicted pollen tube number, and pollen tube number was not correlated with initial fruit set, indicating that pollen receipt did not limit fertilization. As expected, given that initial fruit set tends to reflect fertilization rather than resource availability, we found no effect of neighbors on initial fruit set. Focal plant height did not influence initial or final fruit set and was omitted from the final model.

Initial fruit set strongly predicted final fruit set. Neither coffee flower density nor herb density influenced final fruit set, indicating minimal effects of resource competition with neighbors in these strata. Canopy trees did influence final fruit set, but in complicated ways that suggest a role for both facilitation and competition. Floral richness did not influence final fruit set ($t = 1.14$, df = 186, $p = .3$) and was omitted from the final model. We observed a strong positive effect of canopy cover on final fruit set, with a weaker negative effect of canopy-layer flower density. There was no relationship between

focal plant flower number and canopy cover ($R^2 = 0.0$, $F_{1,99} = 0.34$, $p = .6$)

We found a positive effect of coffee pollen load on final fruit set and a negative effect of pollen tube number on final fruit set. Per-fruit weight was strongly positively correlated with initial fruit set and negatively correlated with plant height but was not affected by pollen tube number or any measure of floral neighborhood or pollination.

Via the influence of pollen load on final fruit set, competition for pollination ultimately affected yield, despite the lack of connection between pollen load and pollen tube number. The net standardized effect size of interactions for pollination on final fruit set was −0.06, compared with the net effect of +0.1 for interactions for shared abiotic resources (as assessed by the effects of canopy cover and canopy-layer flower density on final fruit set). There was a small net competitive effect of both coffee flower density ($ß = −0.022$) and flowering forb density ($ß = −0.016$) (which we used as a proxy for the

strength of competition for abiotic resources) on final fruit set, but a net facilitative effect of canopy trees, via the positive influence of canopy cover ($\beta = 0.072$).

4 | DISCUSSION

This study provides one of the first estimates of the relative strength of interactions between coffee and neighboring plants for (a) shared pollinators and (b) abiotic resources in a coffee agroforest. Uniquely, we assessed these effects independently for three strata of plant neighborhood (herb layer, coffee layer, canopy layer), providing a nuanced picture of the net effect of neighbors on coffee. Our results demonstrate that interactions for both pollination and abiotic resources influence coffee fruit set and fruit weight, albeit weakly, with interaction for abiotic resources appearing to have a greater effect. Below, we discuss each interaction type separately, then integrate them to discuss the implications for agroecosystem management.

4.1 | Neighbor interactions for pollination

The magnitude of competition for pollination was similar across strata (i.e., herb, coffee, and canopy layers). This is surprising, given that insect pollinator assemblages often differ across strata in forests (Ulyshen et al., 2010; Urban-Mead et al., 2021). But stratification complexity is lower in this agroforest relative to adjacent semi-natural forest, potentially reducing the extent to which individual bees forage exclusively in one stratum. At the same time, we found strikingly little heterospecific pollen on coffee stigmas, consistent with the findings of Prado et al. (2021), and suggesting high pollinator fidelity. This in turn suggests that competition largely arises from individual bees specializing on non-coffee flowers, rather than bees switching between coffee and non-coffee flowers. Intriguingly, we found that the taxonomic richness of the co-flowering community had no effect on coffee pollination.

Floral neighborhood, however, explained a small amount of the overall variance in coffee pollen load, and even less in heterospecific pollen. Moreover, there was high variability in pollen load among flowers from the same plant. *Coffea arabica* is capable of self-pollination; it may be that flowers vary in the amount of pollen they produce [documented in other species (e.g. Lau et al., 1995, McKone, 1989)], which in turn could affect the number of self-pollen grains deposited on the stigma.

We were surprised by the lack of relationship between pollen load and proximity to managed colonies of honeybees, a major pollinator of coffee. But apiary density is high across the farm; all transects were <600 m from an apiary, and over half were <250 m away [well within the typical foraging range of honeybees (Bänsch et al., 2020, Danner et al., 2016, Visscher & Seeley, 1982)], so honeybee forager densities may not be strongly related to apiary locations. Moreover, coffee was also commonly visited by other pollinators, particularly stingless bees (G. Fitch *personal observation*).

Despite reducing stigma pollen load, co-flowering neighbors had no effect on fertilization, since (1) stigma pollen load did not influence pollen tube number, and (2) pollen tube number did not influence initial fruit set. The lack of relationship between pollen load and pollen tubes is likely due to the very high levels of coffee pollen found on all stigmas surveyed; in all but three carpels, coffee pollen load exceeded pollen tube number by >10×, while coffee flowers generally contain only two ovules. Furthermore, it is likely that self pollen comprised a large portion of the overall pollen load; in another study, we found that stigmas on *C. arabica* flowers where pollinators were excluded had 559 ± 96 (mean ± SE) pollen grains, only 30% less, on average, than on flowers open to pollination (G. Fitch *unpublished data*). While *C. arabica* is capable of self-pollination, fruit set increases with cross pollen (Klein et al., 2003); perhaps because pollen tubes from self pollen do not reach the ovule (Cruzan & Barrett, 1993, 1996). Our study did not distinguish between self and cross pollen, but given the likelihood that most pollen grains were self, it is unsurprising that pollen load did not correlate with pollen tube number.

While we found no link between pollen load and either pollen tube number or initial fruit set, the direct, positive effect of coffee pollen load on final fruit causally links neighbor effects on pollination to coffee yield. This suggests that coffee plants respond to information about pollen load in determining how to allocate limited resources for fruit maturation—a common phenomenon (Stephenson, 1981; Winsor et al., 1987), presumably because stigma pollen load reliably predicts offspring vigor (Mitchell, 1997). One mechanism linking pollen load to offspring vigor is increased pollen tube competition (Mulcahy, 1971; Niesenbaum & Casper, 1994). It is surprising, then, that we find a negative effect of pollen tube number on final fruit set. It may be that large numbers of pollen tubes clog the style, reducing fertilization and increasing the likelihood of fruit abortion (Young & Young, 1992; but see Niesenbaum & Casper, 1994), while large pollen loads increase the likelihood of receiving vigorous pollen grains that rapidly fertilize ovaries (Mulcahy, 1971). However, our measures of fruit set did not include the flowers from which we collected data on pollen load and pollen tube number. With substantial variation in pollen load and pollen tube number among flowers within a plant, we cannot assume that the flowers assessed for fruit set experienced equivalent pollination to the harvested flowers. The positive correlation between coffee pollen load and final fruit set may alternatively reflect differences in plant vigor, with plants that are able to put more resources towards developing fruit—leading to high fruit set—also producing more pollen per flower, which translates to high stigma pollen load via self-pollination.

4.2 | Neighbor interactions for abiotic resources

We found no evidence for competition for abiotic resource with neighboring conspecifics or flowering herbs. The lack of influence of conspecifics may reflect the low planting density on this farm, which at ~2400 coffee plants/ha² (Schmitt & Perfecto, 2020) is about half

that recommended for optimal yield (DaMatta et al., 2007). We did not assess competition with herbaceous plants directly, but rather used forb flower density as a proxy for measure for the strength of competition, so we may have missed the signal of competitive interactions with herbs—though we note that the herbs considered to be significant weeds by farmers were in bloom at the time of our surveys, and flower density was grossly correlated with biomass, a common measure of competitive effect (Trinder et al., 2013).

The observed positive effect of canopy cover on final fruit set is consistent with several other studies finding higher coffee fruit set in shaded vs. unshaded farms (Lin, 2009; Prado et al., 2018), despite opposing evidence that shading may reduce yields (Campanha et al., 2004). This may stem from beneficial effects of shade trees on soil moisture, soil nutrients, or both. Lin (2009) found that fruit abortion in coffee was negatively correlated with soil moisture, which was positively correlated with canopy shading. At the same time, litter from canopy trees is an important nutrient source in low-intensity coffee cultivation (Beer et al., 1997), and trees reduce nitrogen leaching (Tully et al., 2012). Further research is needed to determine the relative importance of canopy trees' influence on soil moisture and soil nutrients for supporting high coffee yields.

The negative effect of canopy flower density on final fruit set may represent competition for soil nutrients with two tree species [*Roseodendron donnell-smithii* (Bignoniaceae), 58% of canopy-layer flowers, and *Schizolobium parahyba* (Fabaceae), 35%]. Like coffee, these species are mass-blooming, and produce large-seeded fruit which take several months to mature. Thus, resource needs—and consequently soil nutrient uptake—of these species are synchronous with those of coffee, leading to competition despite the facilitative effect of canopy cover overall. Future research should more directly assess competition for soil nutrients between coffee and canopy trees (see next section), to determine whether the observed pattern is indeed driven by synchronicity in resource demands between coffee and large-fruited canopy trees.

4.3 | Management implications

We demonstrate that heterospecific floral neighborhood can influence pollination even of hyper-abundant mass-blooming crops. While research has examined the converse effect of mass-blooming crops on pollination of neighboring non-crops (e.g. Holzschuh et al., 2011), evidence of neighbor effects on mass-flowering crops is scarce. In this case, these effects did not substantially impact yield because the focal crop was not pollen-limited. We expect the effect of co-flowering neighbors on pollination to be more significant in crops, such as *C. canephora*, that require animal pollination.

Our results indicate that tradeoffs between coffee yield (final fruit set and per-fruit weight) and non-crop flowering plant density are weak. This is heartening both from a conservation perspective and for the prospects of diversifying on-farm production streams. Supporting high densities of managed honeybees, alongside wild pollinator populations, requires the maintenance of temporally

consistent high floral densities. Therefore, management that maintains high densities of flowering forbs in the landscape is essential to maintaining farm multifunctionality (Machado et al., 2021).

This study was conducted on a single farm, allowing us to evaluate the effects of plant neighborhood while holding constant other management practices that influence pollination and yield. But it would be instructive to examine neighbor effects across a wider range of farms, to determine whether our findings are robust to different management practices, and across varying climatic and edaphic conditions. Additionally, *C. arabica* is known for biennial bearing (DaMatta, 2004; DaMatta et al., 2007), which may have introduced noise into our data on fruit set and weight, obscuring the effects of neighbors; conducting research on the same plants over consecutive years would avoid this issue, and might also reveal interesting patterns relating the strength of bienniality to neighborhood composition. Future studies would also do well to measure competition for abiotic resources more directly, including with conspecifics, herbaceous vegetation, and canopy trees (see Trinder et al., 2013 for a review of promising approaches). Furthermore, there are other interactions that we did not investigate that influence coffee yield and are likely affected by neighborhood conditions, in particular interactions with herbivores (Escobar-Ramírez et al., 2019; Soto-Pinto et al., 2002) and pathogens (López-Bravo, 2012; Soto-Pinto et al., 2002). On the farm studied, at least, our results indicate that maintaining high non-crop plant abundance and diversity in coffee agroecosystems does not lead to significant yield losses—a promising finding for efforts to promote win-win scenarios in managing lands simultaneously for agricultural production and biodiversity conservation.

AUTHOR CONTRIBUTIONS

GF and JV conceived the ideas and designed methodology; GF collected field data and samples; GF, JG, AO, and MO processed samples; GF, JG, AO, and MO analyzed the data; GF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

ORCID

Gordon Fitch https://orcid.org/0000-0002-2471-1160
Maggie Oliver https://orcid.org/0000-0003-3763-2741

REFERENCES

Albor, C., García-Franco, J. G., Parra-Tabla, V., Díaz-Castelazo, C., & Arceo-Gómez, G. (2019). Taxonomic and functional diversity of the co-flowering community differentially affect Cakile edentula pollination at different spatial scales. *Journal of Ecology*, 107, 2167–2181.

Avelino, J., Zelaya, H., Merlo, A., Pineda, A., Ordoñez, M., & Savary, S. (2006). The intensity of a coffee rust epidemic is dependent on production situations. *Ecological Modelling*, 197, 431–447.

Badillo-Montaño, R., Aguirre, A., & Munguía-Rosas, M. A. (2019). Pollinator-mediated interactions between cultivated papaya and co-flowering plant species. *Ecology and Evolution*, 9, 587–597.

Bänsch, S., Tscharntke, T., Ratnieks, F. L. W., Härtel, S., & Westphal, C. (2020). Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. *Agriculture, Ecosystems & Environment*, 291, 106792.

Beer, J., Muschler, R., Kass, D., & Somarriba, E. (1997). Shade management in coffee and cacao plantations. *Agroforestry Systems*, 38, 139–164.

Bos, M. M., Veddeler, D., Bogdanski, A. K., Klein, A.-M., Tscharntke, T., Steffan-Dewenter, I., & Tylianakis, J. M. (2007). Caveats to quantifying ecosystem services: Fruit abortion blurs benefits from crop pollination. *Ecological Applications*, 17, 1841–1849.

Braun, J., & Lortie, C. J. (2019). Finding the bees knees: A conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, 36, 33–40.

Bruckman, D., & Campbell, D. R. (2014). Floral neighborhood influences pollinator assemblages and effective pollination in a native plant. *Oecologia*, 176, 465–476.

Campanha, M. M., Santos, R. H. S., de Freitas, G. B., Martinez, H. E. P., Garcia, S. L. R., & Finger, F. L. (2004). Growth and yield of coffee plants in agroforestry and monoculture systems in Minas Gerais, Brazil. *Agroforestry Systems*, 63, 75–82.

Cruzan, M. B., & Barrett, S. C. H. (1993). Contribution of cryptic incompatibility to the mating system of *Eichhornia paniculata* (Pontederiaceae). *Evolution*, 47, 925–934.

Cruzan, M. B., & Barrett, S. C. H. (1996). Postpollination mechanisms influencing mating patterns and fecundity: An example from *Eichhornia paniculata*. *The American Naturalist*, 147, 576–598.

DaMatta, F. M. (2004). Ecophysiological constraints on the production of shaded and unshaded coffee: A review. *Field Crops Research*, 86, 99–114.

DaMatta, F. M., Ronchi, C. P., Maestri, M., & Barros, R. S. (2007). Ecophysiology of coffee growth and production. *Brazilian Journal of Plant Physiology*, 19, 485–510.

Damgaard, C., & Weiner, J. (2017). It's about time: A critique of macroecological inferences concerning plant competition. *Trends in Ecology & Evolution*, 32, 86–87.

Danner, N., Molitor, A. M., Schiele, S., Härtel, S., & Steffan-Dewenter, I. (2016). Season and landscape composition affect pollen foraging distances and habitat use of honey bees. *Ecological Applications*, 26, 1920–1929.

De Beenhouwer, M., Aerts, R., & Honnay, O. (2013). A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. *Agriculture, Ecosystems & Environment*, 175, 1–7.

Duffy, K. J., & Stout, J. C. (2011). Effects of conspecific and heterospecific floral density on the pollination of two related rewarding orchids. *Plant Ecology*, 212, 1397–1406.

Escobar-Ramírez, S., Grass, I., Armbrecht, I., & Tscharntke, T. (2019). Biological control of the coffee berry borer: Main natural enemies, control success, and landscape influence. *Biological Control*, 136, 103992.

Eshetu, T., & Kebede, T. (2015). Effect of weed management methods on yield and physical quality of coffee at Gera, Jimma zone, south West Ethiopia. *Journal of Resources Development and Management*, 11, 82–89.

Essenberg, C. J. (2013). Scale-dependent shifts in the species composition of flower visitors with changing floral density. *Oecologia*, 171, 187–196.

Fisher, K., Gonthier, D. J., Ennis, K. K., & Perfecto, I. (2017). Floral resource availability from groundcover promotes bee abundance in coffee agroecosystems. *Ecological Applications*, 27, 1815–1826.

Fitch, G., Gonzalez, J., Oana, A. M., Oliver, M., & Vandermeer, J. (2022). Data from: Integrating effects of neighbor interactions for pollination and abiotic resources on coffee yield in a multi-strata agroforest. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.v6wwpzgzw

Fitch, G., & Vandermeer, J. H. (2020). Light availability influences the intensity of nectar robbery and its effects on reproduction in a tropical shrub via multiple pathways. *American Journal of Botany*, 107, 1–10.

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression* (3rd ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Goldberg, D. E., & Barton, A. M. (1992). Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *American Naturalist*, 139, 771–801.

Gonthier, D. J., Dominguez, G. M., Witter, J. D., Spongberg, A. L., & Philpott, S. M. (2013). Bottom-up effects of soil quality on a coffee arthropod interaction web. *Ecosphere*, 4, art107.

Gurevitch, J., Morrow, L. L., Wallace, A., & Walsh, J. S. (1992). A meta-analysis of competition in field experiments. *American Naturalist*, 140, 539–572.

Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, 31, 532–538.

Hipólito, J., Boscolo, D., & Viana, B. F. (2018). Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. *Agriculture, Ecosystems & Environment*, 256, 218–225.

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B*, 278, 3444–3451.

Iverson, A. L., Gonthier, D. J., Pak, D., Ennis, K. K., Burnham, R. J., Perfecto, I., Ramos Rodriguez, M., & Vandermeer, J. H. (2019). A multifunctional approach for achieving simultaneous biodiversity conservation and farmer livelihood in coffee agroecosystems. *Biological Conservation*, 238, 108179.

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for pollination biologists*. University Press of Colorado.

Klein, A.-M., Cunningham, S. A., Bos, M., & Steffan-Dewenter, I. (2008). Advances in pollination ecology from tropical plantation crops. *Ecology*, 89, 935–943.

Klein, A.-M., Hendrix, S. D., Clough, Y., Scofield, A., & Kremen, C. (2015). Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biology*, 17, 201–208.

Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003). Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). *American Journal of Botany*, 90, 153–157.

Lander, T. A., Bebber, D. P., Choy, C. T. L., Harris, S. A., & Boshier, D. H. (2011). The Circe principle explains how resource-rich land can waylay pollinators in fragmented landscapes. *Current Biology*, *21*, 1302–1307.

Lau, T.-C., Lu, X., Koide, R. T., & Stephenson, A. G. (1995). Effects of soil fertility and mycorrhizal infection on pollen production and pollen grain size of *Cucurbita pepo* (Cucurbitaceae). *Plant, Cell & Environment*, *18*, 169–177.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Lin, B. B. (2009). Coffee (*Café arabica* var. Bourbon) fruit growth and development under varying shade levels in the Soconusco region of Chiapas, Mexico. *Journal of Sustainable Agriculture*, *33*, 51–65.

López-Bravo, D. F., E., de Virginio-Filho, M., & Avelino, J. (2012). Shade is conducive to coffee rust as compared to full sun exposure under standardized fruit load conditions. *Crop Protection*, *38*, 21–29.

Lundin, O., Ward, K. L., Artz, D. R., Boyle, N. K., Pitts-Singer, T. L., & Williams, N. M. (2017). Wildflower plantings do not compete with neighboring almond orchards for pollinator visits. *Environmental Entomology*, *46*, 559–564.

Machado, A. C. P., Barônio, G. J., de Oliveira, F. F., Garcia, C. T., & Rech, A. R. (2021). Does a coffee plantation host potential pollinators when it is not flowering? Bee distribution in an agricultural landscape with high biological diversity in the Brazilian campo Rupestre. *Journal of the Science of Food and Agriculture*, *101*, 2345–2354.

McKone, M. J. (1989). Intraspecific variation in pollen yield in bromegrass (Poaceae: *Bromus*). *American Journal of Botany*, *76*, 231–237.

Mitchell, R. J. (1997). Effects of pollen quantity on progeny vigor: Evidence from the desert mustard *Lesquerella fendleri*. *Evolution*, *51*, 1679–1684.

Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M., & Karron, J. D. (2009). New frontiers in competition for pollination. *Annals of Botany*, *103*, 1403–1413.

Moraima García, S., Cañizares, A., Salcedo, F., & Guillén, L. (2000). A contribution to determine critical levels of weed interference in coffee crops of Moagas state, Venezuela. *Bioagro*, *12*, 63–70.

Moreaux, C., Meireles, D. A. L., Sonne, J., Badano, E. I., Classen, A., González-Chaves, A., Hipólito, J., Klein, A. M., Maruyama, P. K., Metzger, J. P., Philpott, S. M., Rahbek, C., Saturni, F. T., Sritongchuay, T., Tscharntke, T., Uno, S., Vergara, C. H., Viana, B. F., Strange, N., & Dalsgaard, B. (2022). The value of biotic pollination and dense forest for fruit set of arabica coffee: A global assessment. *Agriculture, Ecosystems & Environment*, *323*, 107680.

Mulcahy, D. L. (1971). A correlation between gametophytic and sporophytic characteristics in *Zea mays* L. *Science*, *171*, 1155–1156.

Nicholson, C. C., Ricketts, T. H., Koh, I., Smith, H. G., Lonsdorf, E. V., & Olsson, O. (2019). Flowering resources distract pollinators from crops: Model predictions from landscape simulations. *Journal of Applied Ecology*, *56*, 618–628.

Niesenbaum, R. A., & Casper, B. B. (1994). Pollen tube numbers and selective fruit maturation in *Lindera benzoin*. *The American Naturalist*, *144*, 184–191.

Njoroge, J. M. (1994). Weeds and weed control in coffee. *Ex Agric*, *30*, 421–429.

Njoroge, J. M., & Kimemia, J. K. (1990). A comparison of different weed control methods in Kenya. *Kenya Coffee*, *55*, 863–870.

O'Brien, T. G., & Kinnaird, M. F. (2003). Caffeine and conservation. *Science*, *300*, 587.

Oerke, E.-C. (2006). Crop losses to pests. *The Journal of Agricultural Science*, *144*, 31–43.

Osterman, J., Theodorou, P., Radzevičiūtė, R., Schnitker, P., & Paxton, R. J. (2021). Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. *Agriculture, Ecosystems & Environment*, *315*, 107383.

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.

Perfecto, I., Rice, R., & Greenberg, R. (1996). Shade coffee: A disappearing refuge for biodiversity. *Bioscience*, *46*, 598–608.

Philpott, S. M., Uno, S., & Maldonado, J. (2006). The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodiversity and Conservation*, *15*, 487–501.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). Nlme: Linear and nonlinear mixed effects models. https://CRAN.R-project.org/package=nlme.

Prado, S. G., Collazo, J. A., & Irwin, R. E. (2018). Resurgence of specialized shade coffee cultivation: Effects on pollination services and quality of coffee production. *Agriculture, Ecosystems & Environment*, *265*, 567–575.

Prado, S. G., Collazo, J. A., Marand, M. H., & Irwin, R. E. (2021). The influence of floral resources and microclimate on pollinator visitation in an agro-ecosystem. *Agriculture, Ecosystems & Environment*, *307*, 107196.

Prado, S. G., Collazo, J. A., Stevenson, P. C., & Irwin, R. E. (2019). A comparison of coffee floral traits under two different agricultural practices. *Scientific Reports*, *9*, 7331.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Radosevich, S. R., Holt, J. S., & Ghersa, C. (1997). *Weed ecology: Implications for management*. Wiley.

Ronchi, C. P., Terra, A. A., & Silva, A. A. (2007). Growth and nutrient concentration in coffee root system under weed species competition. *Planta Daninha*, *25*, 679–687.

Roubik, D. W. (1993). Tropical pollinators in the canopy and understory: Field data and theory for stratum "preferences". *Journal of Insect Behavior*, *6*, 659–673.

Roubik, D. W., Inoue, T., & Hamid, A. A. (1995). Canopy foraging by two tropical honeybees: Bee height fidelity and tree genetic neighborhoods. *Tropics*, *5*, 81–93.

Schmitt, L., & Perfecto, I. (2020). Who gives a flux? Synchronous flowering of *Coffea arabica* accelerates leaf litter decomposition. *Ecosphere*, *11*(7), e03186. https://doi.org/10.1002/ecs2.3186

Soto-Pinto, L., Perfecto, I., & Caballero-Nieto, J. (2002). Shade over coffee: Its effects on berry borer, leaf rust and spontaneous herbs in Chiapas, Mexico. *Agroforestry Systems*, *55*, 37–45.

Soto-Pinto, L., Perfecto, I., Castillo-Hernandez, J., & Caballero-Nieto, J. (2000). Shade effect on coffee production at the northern Tzeltal zone of the state of Chiapas, Mexico. *Agriculture, Ecosystems & Environment*, *80*, 61–69.

Staver, C., Guharay, F., Monterroso, D., & Muschler, R. G. (2001). Designing pest-suppressive multistrata perennial crop systems: Shade-grown coffee in Central America. *Agroforestry Systems*, *53*, 151–170.

Stephenson, A. G. (1981). Flower and fruit abortion: Proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, *12*, 253–279.

Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W. H., & Marini, L. (2019). Pollination contribution to crop yield is often context-dependent: A review of experimental evidence. *Agriculture, Ecosystems & Environment*, *280*, 16–23.

Trinder, C. J., Brooker, R. W., & Robinson, D. (2013). Plant ecology's guilty little secret: Understanding the dynamics of plant competition. *Functional Ecology*, *27*, 918–929.

Tully, K. L., Lawrence, D., & Scanlon, T. M. (2012). More trees less loss: Nitrogen leaching losses decrease with increasing biomass in coffee agroforests. *Agriculture, Ecosystems and Environment*, *161*, 137–144.

Ulyshen, M. D., Soon, V., & Hanula, J. L. (2010). On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity*, *3*, 222–228.

Underwood, N., Inouye, B. D., & Hambäck, P. A. (2014). A conceptual framework for associational effects: When do neighbors matter and how would we know? *The Quarterly Review of Biology*, *89*, 1–19.

Urban-Mead, K. R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., McArt, S. H., & Danforth, B. N. (2021). Bees in the trees: Diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, *482*, 118903.

Visscher, P. K., & Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology*, *63*, 1790–1801.

Winsor, J. A., Davis, L. E., & Stephenson, A. G. (1987). The relationship between pollen load and fruit maturation and the effect of pollen load on offspring vigor in *Cucurbita pepo*. *The American Naturalist*, *129*, 643–656.

Young, H. J., & Young, T. P. (1992). Alternative outcomes of natural and experimental high pollen loads. *Ecology*, *73*, 639–647.

Younginger, B. S., Sirová, D., Cruzan, M. B., & Ballhorn, D. J. (2017). Is biomass a reliable estimate of plant fitness? *Applications in Plant Sciences*, *5*, 1600094.

Zimdahl, R. L. (2007). *Weed-crop competition: A review*. Wiley.

SUPPORTING INFORMATION

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