Article

THE ECOLOGICAL AND FUNCTIONAL VALUE OF NATIVE BEES IN AVOCADO (*PERSEA AMERICANA*) POLLINATION

Laura C. Pérez-Giraldo[1,*], José M. Cerda-Paredes[1,2], Sharon Rodríguez S.[3]

[1]*Data Observatory Foundation, ANID Technology Center No. DO210001, Santiago 7510277, Chile.*
[2]*Facultad de Ingeniería y Ciencias, Universidad Adolfo Ibáñez, Diagonal Las Torres 2640, Santiago 7941169, Chile.*
[3]*Laboratorio de Ecología de Abejas, Universidad Católica del Maule, Chile.*

Journal of Pollination Ecology, 42(19), 2026, pp 261-275
DOI: 10.26786/1920-7603(2026)869
Received 13 May 2025, accepted 29 September 2026

*Corresponding author: laura.perez@dataobservatory.net

Abstract—Although bees provide essential ecosystem services, the contribution of native bee functional groups to avocado pollination remains poorly quantified. We aimed to (1) evaluate the effect of distance from semi-natural vegetation on native bee visitation rates and (2) compare pollen transfer potential and fruit production among native bee functional groups. We surveyed bee visitation along a 6–72 m gradient from semi-natural vegetation in two commercial Hass avocado (*Persea americana* Mill.) orchards in central Chile (20 trees each; 2018). We conducted pollinator exclusion experiments in one orchard during 2018 and 2019. Visitation frequencies, pollen load, and exclusion data were combined to quantify pollen transfer potential (Ept), fruit production, and Pollination Service Index (PSI). Generalized additive models showed no significant effect of distance on visitation frequency or pollen transfer potential, suggesting the gradient lies within typical foraging distances. However, functional groups differed. Medium- and small-sized bees showed higher pollen transfer potential than large bees, driven mainly by greater per-capita pollen load rather than visitation. Self-pollination and medium-sized bees sustained fruit number closest to open control (highest PSI) but showed no advantage in fruit weight, whereas small bees produced the heaviest fruit despite the largest reduction in fruit number, though this pattern varied between seasons. No single treatment excelled across all metrics, revealing a partial decoupling between pollen transfer potential and fruit development highlighting the multidimensional nature of pollination services. A functionally diverse pollinator assemblage serves best to sustain both fruit quantity and quality. Conserving semi-natural habitats and native pollinator diversity may help sustain pollination services and avocado productivity.

Keywords—Functional groups, fruit set, pollen transfer potential, pollination service, bee size, visitation rate.

INTRODUCTION

Pollination is a critical ecosystem service due to its essential role in sustaining food production. More than three-quarters of global fruit, vegetable, and seed production depend, to some extent, on pollinators, particularly bees (Klein et al. 2007; Bartomeus et al. 2014; Eilers et al. 2011). Bees contribute to increased crop yields by efficiently transferring large quantities of pollen and by being highly abundant in natural and agricultural landscapes (Khalifa et al. 202; Robinson et al. 2023). Their positive effect on fruit and seed sets has been widely recognized across diverse crop systems (Layek et al. 2021; Zhang et al. 2025). In recent decades, growing concern has emerged regarding the global decline of pollinators due to habitat loss and climate change (Dicks et al. 2021; Turley et al. 2022), a trend that may compromise crop productivity, especially in pollination-dependent species. This trend is further exacerbated by the increasing gap between crop pollination demand and the supply of effective pollinators, including managed species (Aizen et al. 2019; Lavín et al. 2023).

However, not all bees contribute equally to pollination services. Species with different functional traits (i.e., traits that directly affect

fitness; Greenop et al.l 2023) vary in their efficiency. According to previous works, body size is a key determinant of pollination performance, making it an appropriate trait for grouping bees by functionality (Hoehn et al 2008; Földesi et al. 2020). Larger bees, for instance, often deposit more pollen on the stigmas of plants with small flowers due to better contact with reproductive structures. They also tend to forage over longer distances, which promotes cross-pollination (Jaboor et al. 2022). Researchers commonly estimate pollination efficiency (i.e., the contribution of a pollinator to successful pollen transfer) using proxies such as fruit set, pollen deposition, or composite indices like the Pollination Service Index (PSI; Ne'eman et al. 2010; Bartomeus et al. 2016). Additionally, recent research has shown that wild pollinators may provide more stable pollination services than managed species, especially in complex landscapes (Garibaldi et al. 2013; Requier et al. 2022).

Semi-natural vegetation edges can support native bee functional groups and enhance their contribution to crop pollination (Devkota et al. 2021). Studies show that the spatial structure of the landscape (e.g., connectivity and proximity to natural habitat) influences pollinator diversity and activity (Kennedy et al. 2013; Capera-Aragones et al. 2024). These effects are especially relevant in agroecosystems where fruit crops dominate, where forest remnants serve as pollinator sources (Fahrig et al. 2011; Lázaro & Alomar 2019). Pollination deficits may be enhanced by reduced habitat complexity and limited presence of effective wild pollinators in agroecosystems, where local floral resources and biophysical habitat heterogeneity structure native bee communities (Garibaldi et al. 2013; Rodríguez et al. 2021; Requier et al. 2022). Understanding how bee traits interact with landscape features is essential for designing sustainable strategies to secure pollination services under changing agricultural conditions (Liu et al. 2020) and for promoting efficient native pollinator communities that improve productivity.

In this study, we aimed to (1) evaluate the effect of distance from natural vegetation on the visitation rate of native bees in avocado crops, and (2) compare differences in pollen transfer potential and fruit production associated with different native bee functional groups. To address these objectives, we used avocado (*Persea americana* Mill.) as a model crop to assess the contribution of native bee functional groups to pollen transfer and fruit production. Recent studies have reported active visitation by native bees in avocado orchards, but few have quantified the pollination performance of functional groups (Sagwe et al. 2022; Monzón et al. 2020).

MATERIALS AND METHODS

STUDY SITE AND PERIODS

We conducted experiments in Melipilla, Metropolitan Region, Chile, during the avocado flowering season (October-November) between 2018 and 2019. We divided them into two parts: 1) quantification of pollination efficiency by counting pollen load and recording the rate of visits to avocado flowers, and 2) assessment of pollination services provided by native and managed bees using a pollinator exclusion. We conducted the first experiment in 2018 in two commercial avocado orchards, Mallarauco 2 (71°00'33"W, 33°33'51"S) and Cuncumen (71°20'32"W, 33°43'44"S). We developed the second experiment only in the Cuncumen orchard, during the 2018 and 2019 seasons. We carried out all experiments throughout the avocado flowering period, on sunny days with low wind and temperatures around 18°C, to ensure comparability of data across weather conditions. We chose the study sites because of their different and heterogeneous landscape structures. For a more detailed description of the study sites, please refer to Rodríguez et al. (2021).

QUANTIFICATION OF NATIVE BEE VISITATION FREQUENCY

In each orchard, we selected 20 avocado trees (var. Hass) based on a gradient of distance from semi-natural vegetation to the interior of the orchards. For each tree, we recorded all floral visits by bees for five minutes per exposed face of the tree, during two periods per day (AM and PM). We sampled between 9:00 A.M and 6:00 P.M. We specifically recorded the number and species of floral visitors, the number of flowers visited, and the number of open flowers per avocado tree during the observation periods. We calculated the visit rate by the total number of recorded bees visiting flowers on each tree during the sampling period, divided by the number of open flowers

observed, and multiplied by the total observation time, totalling a sampling effort of 100 minutes per tree.

Sample sizes for these measurements differ among functional groups because small-bodied native bees were captured less frequently than medium- and large-bodied bees during sampling, not because of any difference in sampling effort applied across groups.

Potential pollen transfer capacity quantification by counting the pollen load of native bees

We collected native bees from the flowers of pollinated avocado trees (var. Edranol). We transported bees to the laboratory and extracted the pollen adhering to their bodies following the glycerinated method (Ospina-Torres et al. 2015). We mounted the extracted pollen and counted with a Neubauer chamber and a Nikon microscope at 40X magnification. We used body pollen load as an indicator of the relative potential pollen transfer capacity of different bee species and functional groups, reflecting the amount of pollen available for transfer during floral visits, rather than a direct measure of pollination efficiency or reproductive success.

Pollinator functional group effects on fruit production assessed using netted trees

We conducted a pollinator exclusion experiment using netted avocado trees (Fig. 1) to assess how different bee functional groups contributed to realize reproductive output. The experiment comprised six treatments: three native bee functional groups defined by body size (small, medium, and large), *Apis mellifera*, self-pollination, and an open control. For each netted treatment, we placed a cage around a pair of trees. Cages assigned to a native functional group or to *Apis mellifera* were stocked with 10 individuals, comprising multiple bee species for the native groups. Cages remained closed throughout the flowering period to prevent entry of external insects. Each week, we inspected the cages and introduced new individuals to maintain a constant number of bees per cage. This weekly replacement was necessary because bees survive and forage less effectively in field cages than within an intact colony, given the absence of a queen and normal colony structure (Lattorf 2022). The self-pollination treatment consisted of complete pollinator-exclusion cages without the introduction of bees, in which incidental insect visitors were removed and treated with insecticide during weekly inspections (see Appendix I for full details). The control treatment consisted of a pair of unnetted trees exposed to ambient pollinators. In total, the experiment included 12 trees (six treatments, two trees each; see Appendix I). After one year, we harvested and counted all fruits produced by each tree. We weighed each fruit to quantify realized reproductive output and fruit quality in each treatment. The experiment ran over two consecutive years (treatments applied in 2018 and 2019, with fruit harvested and measured in 2019 and 2020, respectively). Between years, treatments were reassigned across cages (i.e., which functional group or *A. mellifera* was introduced to a given pair of caged trees) to prevent any single tree pair from being permanently confounded with one treatment; self-pollination cages were



Figure 1. Photographic overview of the experimental design. (A) Cage-based pollinator exclusion setup. (B) Spatial distribution of experimental treatments within the orchard.

kept fixed across both years by design. Each year, after harvest, we counted and weighed all fruits produced by each tree. Sample sizes for fruit weight therefore differ among treatment-year combinations because some cages did not produce any fruit that year (i.e., zero fruit set) and consequently contributed no fruit-weight data for that cage-year, most notably in 2020 (see Results and Appendix). This approach allowed us to link functional group-specific pollinator assemblages to realized reproductive output at the tree level and complements observational and single-visit approaches commonly used to assess pollination services could be valuable in scaling up the management of pollination services based on other experimental designs (Fründ et al. 2013; Liu et al. 2020).

STATISTICS

To evaluate how pollinator activity and pollen transfer potential varied with distance from semi-natural vegetation, we fitted generalized additive models (GAMs). Native bee visitation frequency and pollen transfer potential (Ept) were used as response variables, while distance to semi-natural vegetation was included as a smooth predictor. Visitation frequency was log-transformed prior to analysis to improve model assumptions. Smooth functions were fitted using thin plate regression splines with a basis dimension of k=4 to allow flexible but parsimonious nonlinear relationships. Pollen transfer potential (Ept) was estimated by quantifying the pollen load carried on the bodies of native bees during floral visits. All analyses were conducted in R v4.5.1 (R Core Team, 2025) using the mgcv package (Wood, 2017).

We conducted a set of complementary statistical analyses to evaluate pollinator contributions at multiple ecological levels, integrating pollen transfer potential, pollinator behaviour, and realized fruit production.

The Pollination Service Index (PSI) calculation following the general framework of pollinator dependence ratios used in exclusion experiments (e.g., Ryan et al. 2023), in which fruit production under a given pollination treatment is expressed relative to fruit production under full, unrestricted (open) pollination Fruit production was assessed as the number of fruits harvested per tree pair, rather than total fruit weight; fruit weight was analysed separately as an independent response variable (see below). We defined PSI as:

$$PSI = \frac{Yc}{Yo}$$

where Yo represents fruit production in open control trees (i.e., without nets) and Yc represents fruit production in netted trees (i.e., enclosed treatments restricting pollinator access to a single functional group). Under this formulation, PSI increases with the effectiveness of a given treatment at sustaining fruit production relative to full, unrestricted pollination: values close to 1 indicate that a treatment alone achieved fruit numbers comparable to the open control, whereas values close to 0 indicate a large reduction in fruit number relative to the open control. PSI is a relative index of pollination service based on fruit production under pollinator exclusion, rather than as a measure of pollination efficiency or fruit quality. To explore variation in Pollination Service Index (PSI) among pollinator functional groups and years, we fitted a linear model including functional group and year as fixed effects. Because PSI values were available for a limited number of observations per treatment-year combination, this analysis was considered exploratory and interpreted cautiously.

To further characterize pollinator contributions at the functional group level, we quantified a functional group–specific pollen transfer potential index by integrating body pollen load, visitation rate, and local abundance, following the general approach proposed by Liu et al. (2020). We calculated pollen transfer potential (Ept) as:

$$\text{Ept} = p*vi*N$$

where p represents the number of compatible pollen grains transported per functional group, vi is the number of flowers visited per unit of time, and N is the number of individuals collected per tree. This index reflects the potential contribution of pollinator functional groups to pollen transfer at the tree level and does not represent pollination efficiency per visit or realized reproductive success.

We also fitted a linear mixed-effects model (LMM) between pollen transfer potential (Ept) and pollinator functional groups. We had to log-transform Ept prior to analysis to improve

normality and homoscedasticity. We incorporated (i) functional group as a fixed effect, and (ii) tree ID as a random intercept to account for hierarchical structure and repeated observations within trees.

RESULTS

EFFECTS OF DISTANCE TO SEMI-NATURAL VEGETATION ON POLLINATOR ACTIVITY AND POLLEN TRANSFER POTENTIAL

We recorded a total of 2,980 avocado flowers (*Persea americana*) during the observation period, visited exclusively by native bees. We identified five species from three families (Colletidae, Halictidae, and Apidae): *Cadeguala occidentalis*, *Caupolicana gayi*, *Ruizantheda mutabilis*, *Colletes seminitidus*, and *Manuelia gayi*. Our results indicate no detectable relationship between distance from semi-natural vegetation and visitation rate (Fig. 2A). Likewise, pollen transfer potential (Ept) did not significantly associate with distance (Fig. 2B; see Appendix). These findings suggest that, within the sampled spatial range (6–72 m), proximity to semi-natural vegetation did not produce measurable changes in visitation frequency or pollen transfer potential.

POTENTIAL POLLEN TRANSFER CAPACITY QUANTIFICATION BY COUNTING THE POLLEN LOAD OF NATIVE BEES

We found that pollen transfer potential (Ept) varied significantly among pollinator functional groups. Medium- and small-sized bees exhibited significantly higher Ept values than large bees, whereas we detected no significant difference between medium and small groups. Linear mixed-effects models supported this pattern, with Ept increasing significantly in medium ($\beta = 0.89 \pm 0.17$ SE, $t = 5.12$) and small bees ($\beta = 0.88 \pm 0.27$ SE, $t = 3.24$) relative to large bees, while medium and small groups did not differ significantly (Fig. 3; see Appendix). Estimated marginal means confirmed that large bees had the lowest Ept, whereas medium and small bees exhibited similarly elevated values.

To identify the source of this pattern, we examined the individual components of the Ept index (pollen load, visitation frequency, and abundance). Visitation frequency did not differ appreciably between large and medium bees (mean = 0.00085 vs. 0.00090 visits per flower per unit time) and was, in fact, lowest in small bees despite their higher Ept, indicating that visitation rate alone does not explain the observed pattern. Instead, the difference appears to be driven primarily by per-capita pollen load, which increased consistently from large (mean = 3.3 grains) to medium (6.0 grains) to small bees (8.3 grains). The relative abundance of individuals sampled per functional group (9, 27, and 5 for large, medium, and small bees, respectively) likely also contributed to the elevated Ept of medium

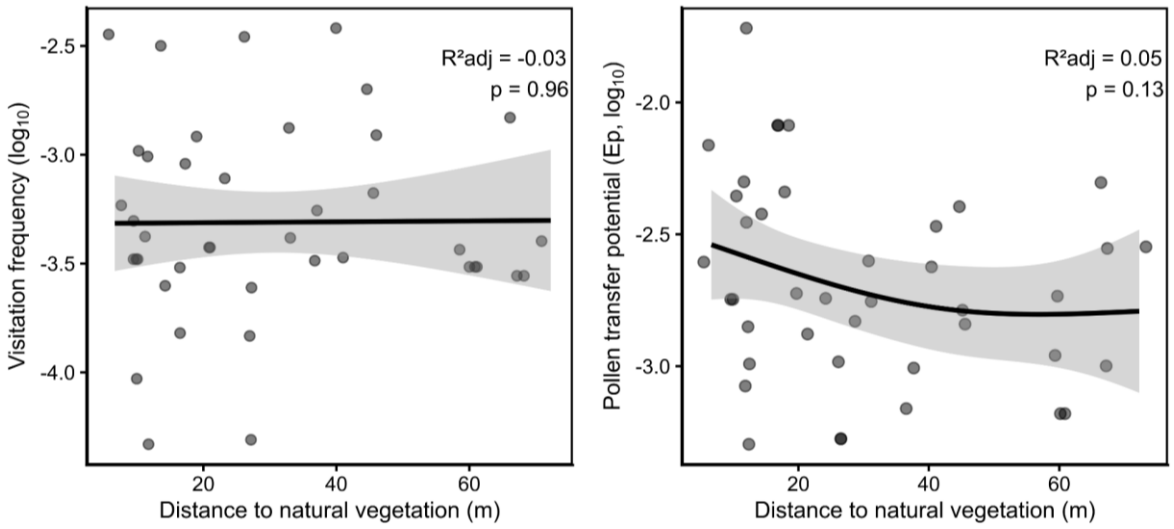


Figure 2. Effects of distance to natural vegetation on pollinator activity and pollen transfer potential in avocado orchards. (A) Native bee visitation frequency measured on individual trees. (B) Pollen transfers potential as a function of distance to natural vegetation. Solid curves represent fitted generalized additive model (GAM) smooths (k = 4), and grey bands indicate 95% confidence intervals.

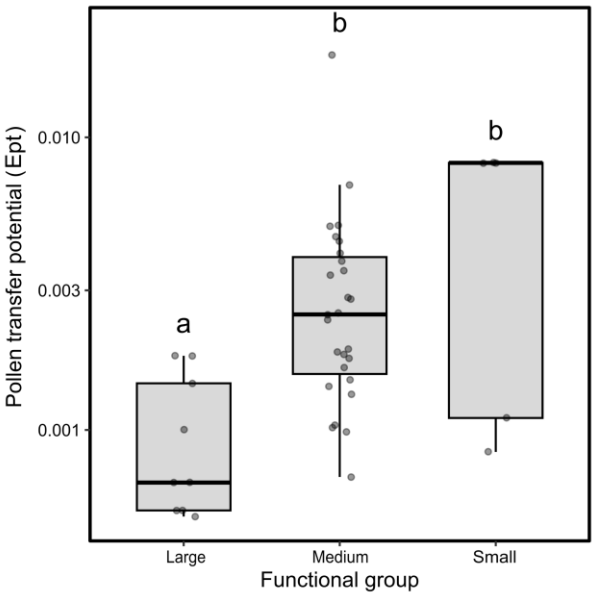


Figure 3. Pollen transfer potential (Ept) across pollinator functional groups in avocado orchards. Each point represents an individual bee for which pollen load was measured; note that multiple individuals were sometimes sampled from the same tree, so points do not correspond one-to-one with trees. Sample sizes differ among functional groups (large: *N* = 9 individuals from 6 trees; medium: *N* = 27 individuals from 19 trees; small: *N* = 5 individuals from 3 trees) because small-bodied native bees, represented here by a single species (*Manuelia gayi*), were captured considerably less often than medium-sized species (*Colletes* sp. and *Ruizantheda* sp.) during field sampling. Boxplots represent medians and interquartile ranges. Different letters indicate significant differences among functional groups estimated using linear mixed models (LMMs) on log-transformed Ept.

bees despite their intermediate pollen load per individual. These results suggest that the lower pollen transfer potential of large bees reflects reduced pollen carriage per individual rather than lower visitation activity.

Together, these results indicate that pollen transfer potential varied significantly with pollinator functional group identity, with smaller-bodied bees contributing disproportionately to pollen transfer at the tree level.

POLLINATOR FUNCTIONAL GROUP EFFECTS ON FRUIT PRODUCTION USING NETTED TREES

The Pollination Service Index (PSI) and fruit weight were obtained from the pollinator exclusion experiment, in which a fixed number of individuals (10 bees per cage, replenished weekly) was introduced for each treatment, independent of natural abundance in the orchard.

The Pollination Service Index (PSI, Fig. 4A), based on the number of fruits harvested, did not differ significantly among functional groups ($F_{4,1}$ = 1.72. P = 0.20) or between yers ($F_{4,14}$ = 2.37, P = 0.15) in the exploratory model, and values varied considerably within groups across years. Descriptively, self-pollination and medium-sized bees showed the highest average PSI (mean = 0.56 and 0.52, respectively), followed by large bees (mean = 0.44), indicating that fruit set under these treatments was, on average, closest to that of the open control. In contrast, *A. mellifera* (mean = 0.14) and small bees (mean = 0.10) showed the lowest average PSI, indicating a comparatively large reduction in fruit number relative to the open control when these groups pollinated alone.

Fruit weight (Fig 4.B), measured for each individual harvested fruit rather than as a total per tree, varied according to a significant treatment × year interaction ($F_{4,13.66}$ = 5.89, P = 0.006); we therefore report treatment effects by year rather than as an average, which would obscure the pattern in either season. In 2019, small-bee treatments produced significantly heavier fruits than medium-bee treatments (213 g vs. 134 g; Tukey-adjusted $P < 0.05$), with *A. mellifera*, large-bee, and self-pollination treatments intermediate and not significantly different from either extreme. In 2020, fruit set was lower overall and more variable across cages (171 fruits from seven cage-years, some represented by a single cage), resulting in wider confidence intervals around the treatment estimates and no significant differences among treatments that year. Fruit weight was also higher overall in 2020 than in 2019 across all treatments ($F_{1,892.84}$ = 60.34, $p < 0.001$), underscoring how markedly the two seasons differed. Given its more balanced replication and narrower confidence intervals, 2019 provides the clearer basis for interpreting how pollinator functional group affects fruit weight

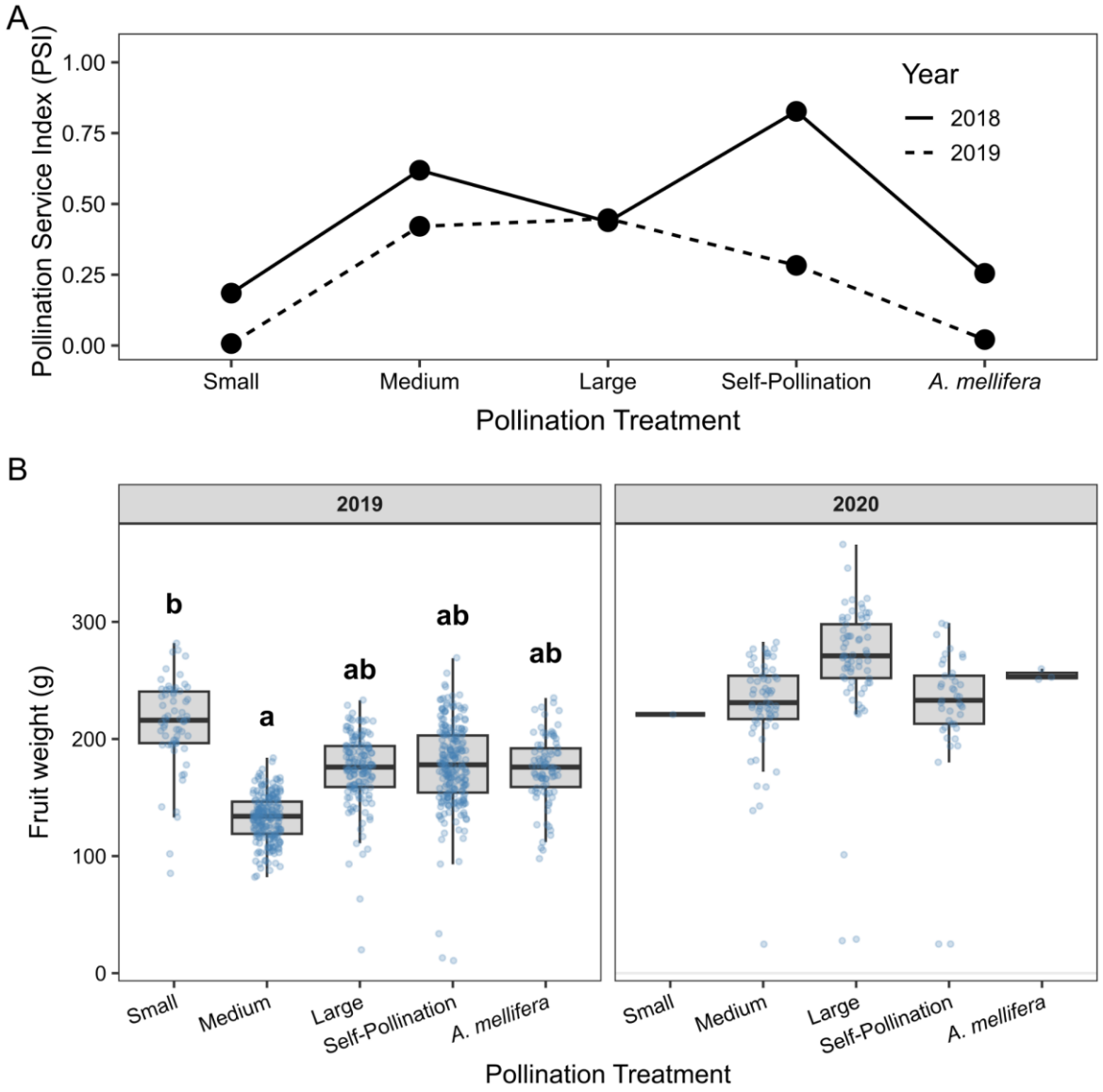


Figure 4. Pollination quantity across treatments in avocado orchards. Treatments in avocado orchards. Treatments are ordered consistently across panels (small, medium, and large native bee functional groups, self-pollination, and *A. mellifera*). (A) Pollination Service Index (PSI) across treatments by year (solid line: 2018; dashed line:2019); PSI increases with the effectiveness of a treatment at sustaining fruit number relative to the open control (PSI = Yc/Yo). Year was not a significant factor for PSI (see Results), and both years are shown for descriptive completeness. (B) Fruit weight (g) across treatments, shown separately by year given a significant treatment x year interaction (see Results). Boxplots show medians and interquartile range; points represent individual fruits. Different letters denote significant differences among treatments in 2019, based on linear mixed models with tree identity as a random effect and Tukey-adjusted pairwise comparisons (Kenward-Roger degrees of freedom).

Discussion

Our study demonstrates that native bee functional groups, rather than proximity to semi-natural vegetation, structures multiple components of pollination services in Mediterranean avocado (*Persea americana*) orchards. While visitation rate and pollen transfer potential (Ept) did not vary significantly with distance to semi-natural vegetation, our findings reveal that pollinator functional groups mediated Ept and realized fruit production. Medium- and small-sized bees exhibited higher pollen transfer potential than large bees, whereas individual fruit weight varied according to a treatment x year interaction, with small-bee treatments producing

significantly heavier fruits than medium-bee treatments in the better-replicated season. Although this partially contrasts with the expectation that greater pollen transfer directly translates into higher reproductive output (Delaplane et al. 2013; Ne'eman et al. 2010), our results highlight: i) the multidimensional nature of pollination effectiveness, in which intermediate and final reproductive metrics may not respond congruently (King et al. 2013: Page et al. 2021), and ii) the importance of functional trait difference among pollinators in shaping distinct stages of pollination process (Greenleaf et al. 2007: Földesi et al. 2020). Taken together, our findings show that visitation rates or landscape proximity alone do not determine pollination services in agroecosystems but are structured by trait-mediated functional differences among pollinator groups.

The absence of detectable effects of distance on visitation frequency and pollen transfer potential suggests that, within the sampled spatial range (6–72 m), short-range gradients in semi-natural vegetation did not constrain native pollinator activity. This contrasts with studies reporting strong distance-decay effects on pollination services in fragmented landscapes (Ricketts et al. 2008; Garibaldi et al. 2011), but aligns with evidence that pollinator mobility, local nesting availability, and mass-flowering crop dynamics can buffer fine-scale spatial heterogeneity in agroecosystems (Kennedy et al. 2013; Kleijn et al. 2015; Dainese et al. 2019). According to Greenleaf et al. (2007) body size influences foraging range and dispersal capacity, yet our results indicate that functional differences among size classes did not translate into spatially structured variation in visitation or pollen transfer across the orchard. One possible explanation is that abundant and spatially continuous floral resources within the orchard may reduce the influence of short-distance landscape gradients by promoting extensive pollinator movement across the crop. Alternatively, the spatial scale of pollinator movement may exceed the spatial extent of our sampling design. Together, these mechanisms suggest that local floral resource distribution and orchard configuration may override short-distance landscape effects, reinforcing the idea that landscape–pollination relationships are strongly scale-dependent and highly context dependent (Tscharntke et al. 2012; Grab et al. 2017).

In contrast to the spatial neutrality observed along the distance gradient, pollen transfer potential varied significantly among functional groups. Medium- and small-sized bees exhibited higher Ept values than large bees, reflecting a greater overall contribution to pollen transfer at the tree level, since Ept is a composite index that incorporates visitation frequency and pollen load (see Methods). . As shown in our component-level analysis, this pattern was driven primarily by per-capita pollen load, which was highest in small bees and lowest in large bees, rather than by differences in visitation frequency, which did not follow the same gradient across groups. These differences are consistent with trait-based mechanisms linking body size to stigma contact probability, grooming behaviour, and pollen placement precision (Harder and Barrett 1996; King et al. 2013; Junker et al. 2013). Although stigma contact, grooming behaviour, and pollen placement precision were not directly measured in this study, these mechanisms are proposed as plausible explanations for our findings drawn from the broader literature. In avocado specifically, smaller-bodied bees may handle the small, morphologically constrained flowers more efficiently than larger bees; for instance, *A. mellifera* foragers have been observed to take longer to land and position themselves on avocado flowers, likely because their larger body size makes it more difficult to grasp the flower, compared with smaller native bee species (Can-Alonzo et al. 2005). Such findings support the growing recognition that pollinator effectiveness depends not only on pollen quantity but also on deposition quality and compatibility dynamics (Ne'eman et al. 2010; Page et al. 2021). Our results therefore reinforce the need to distinguish overall pollen transfer potential and single-visit pollination effectiveness when assessing pollinator performance. More broadly, these findings highlight the importance of functional diversity within pollinator communities, as different functional groups may contribute unequally to pollination effectiveness while collectively maintaining pollination services. This pattern suggests that functional complementarity among pollinators may help sustain pollination processes even when

individual groups differ in their efficiency or behavioural traits.

However, realized fruit production followed a pattern that diverged from PSI and varied between years. In 2019, small-bee treatments produced significantly heavier fruits than medium-bee treatments; in 2020, fruit set was lower and more variable across cages, and no significant differences among treatments were detected that year (see Results). This divergence indicates that PSI, based on the number of fruits harvested, and fruit weight, measured per individual fruit rather than as total harvest mass, capture different aspects of pollination performance (Ne'eman et al. 2010; King et al. 2013). Because 2019 had more balanced replication than 2020, we consider that season's results the clearer basis for characterizing how pollinator functional groups affect fruit weight.

Directly testing for a trade-off between fruit number (as captured by PSI) and fruit size, using data from 2019 only (the more reliably replicated year for both metrics), revealed a negative but non-significant association across the five functional groups (Pearson r = -0.594, $P = 0.291$, $N = 5$ groups): treatments achieving a higher PSI tended to produce individually lighter fruit that year consistent with the hypothesis that treatments sustaining fewer fruits relative to the open control allows more resources per fruit. This pattern was clearest for the small-bee and medium-bee treatments, which occupied opposite ends of both the PSI and fruit-weight distributions; the self pollination treatment did not follow it, combining a comparatively high PSI with intermediate rather than light fruit weight. This partial and statistically limited association suggests that successful fertilization and subsequent fruit development may depend on additional processes beyond initial pollen deposition, such as pollen tube growth, resource allocation, or post-pollination physiological constraints (Stephenson 1981; Ashman et al. 2004), though the small number of functional groups (N = 5) limits the power to confirm this relationship directly. Similar discrepancies between intermediate pollination metrics and final reproductive output have been reported in other crop systems (Klatt et al. 2014; Garibaldi et al. 2013), suggesting that pollination effectiveness is best understood as a multi-stage process shaped by both pollinator traits and plant reproductive biology. The relatively high PSI observed for the self-pollination treatment is best understood in light of the multidimensional pattern that emerges across our results, rather than in isolation. Self-pollination and medium-sized bees achieved the highest PSI, indicating that fruit set under these treatments was closest to that of the open control; however, neither treatment produced correspondingly heavy fruit, and small bees, which showed the largest reduction in fruit number relative to the open control, produced the heaviest individual fruit. No single treatment, including self-pollination, performed well across both dimensions of yield that we measured. We interpret this as evidence that a functionally diverse pollinator assemblage is more likely to reliably sustain both fruit quantity and fruit quality than any single pollination strategy on its own, including autogamous self-pollination consistent with broader evidence that functional complementarity among pollinators underpins reliable crop pollination (Blüthgen & Klein 2011; Garibaldi et al. 2013; Dainese et al. 2019; Requier et al. 2022).

This interpretation is consistent with a growing body of evidence that avocado fruit set and quality depend on both self- and cross pollination in ways that that vary across cultivars, sites, and seasons (Alcaraz & Hormaza 2011; Trueman et al. 2024; Reese et al. 2025). Self- pollination can account for the majority of fruit set in some cultivars and orchard conditions (Alcaraz & Hormaza 2011), yet cross-fertilized Hass fruit have been shown to be selectively retained during fruit drop and to mature 6% heavier and 2% larger in diameter than self-fertilized fruit (Hapuarachchi et al. 2024), and yield can become pollen-limited where cross-pollen availability is low, even when self-pollination continues to occur (Reese et al. 2025). Cross-pollination has also been associated with benefits beyond the fruit-count and fruit-weight metrics we measured here, including reduced dependence on a single pollen source for inconsistent yield across years (Alcaraz & Hormaza 2011).

It is also worth noting that, because Hass displays heterodichogamy, with a wide temporal separation between the female and male phases of its flowers, true within-flower autogamy is

thought to be uncommon in this cultivar (Trueman et al. 2024); the fruit set we observed under self-pollination more likely reflects close pollination among different flowers of the same tree or variety, for which wind has been directly implicated as the primary vector in caged-branch experiments that excluded insects with mesh bags and insecticide, methodologically similar to our own exclusion cages (Davenport 1992). This is consistent with reports that, in the absence of a different pollinizer cultivar nearby, the proportion of self-pollinated fruit increases with distance from across-pollen source or a complementary pollinizer cultivar (Trueman et al. 2024; Kämper et al. 2021), and that self-pollination becomes the dominant route to fruit set when a complementary cultivar is not closely interplanted (Davenport 2019). Our self-pollination cages, which enclosed two Hass trees of the same variety with no external pollinizer available, reproduce precisely this condition; it is therefore expected (rather than an artifact of caging) that this design favoured a higher probability of self-pollination between trees of the same variety. This supports the conclusion that the treatment reliably isolated and quantified genuine self-pollination, and that the resulting PSI can be interpreted as a reliable estimate of Hass's capacity for autogamous fruit set, rather than as an experimental artifact. That said, our self-pollination treatment used two trees of the same variety (Hass), whereas most other treatments paired a Hass tree with a pollenizer variety (Edranol); we discuss the potential consequences of this varietal asymmetry below.

An additional consideration concerns the varietal composition of the reference treatment used to calculate PSI. In every treatment, only fruit from the Hass tree was counted and weighed; where a cage paired a Hass tree with an Edranol pollenizer tree (the native functional group and *A. mellifera* treatments), Edranol served exclusively as a pollen source, and its own fruit production was not included in any Yc or Yo value. Consequently, Edranol's baseline yield potential, whether higher or lower than that of Hass, does not directly enter into our comparisons, since every reported value in this study reflects Hass fruit production specifically. Both the self-pollination and open control treatments used two Hass trees, but the structural difference between them, rather than variety per se, is what matters for interpreting Yo: the two self-pollination trees were enclosed together within a single cage, so that pollen exchange was restricted exclusively between them, whereas the two open control trees were each individual, unnetted replicates exposed separately to whatever ambient pollinators and pollen sources were present in the orchard. Because commercial Hass orchards typically interplant a proportion of pollenizer trees such as Edranol, fruit set in these open controls plausibly reflects a mixture of self- and cross-pollination rather than either pollination mode in isolation. This contrasts with our self-pollination treatment, in which two Hass trees were enclosed together in a cage, completely excluding cross-pollen from any other variety, and with the native functional group and A. mellifera treatments, in which a Hass tree was deliberately paired with an Edranol pollenizer tree within the cage to enable cross-pollination by the introduced bees. Consequently, self-pollination was the only treatment in which fruit set could be attributed unambiguously to a single pollination mode (autogamous or close pollination within Hass), while Yo (the open-control denominator used for all PSI values) likely already includes some contribution from cross-pollination. If this is the case, the comparatively high PSI we observed for self-pollination is, if anything, a conservative estimate of how well Hass alone can sustain a fruit set relative to a baseline that may itself benefit from cross-pollen availability. A more limited concern that remains is a possible xenia effect, i.e., whether pollen arriving from Edranol itself alters the size or quality of the Hass fruit that develops, independent of pollinator identity (Kämper et al. 2021). We did not track individual pollen-donor identity and cannot test this directly, though xenia effects on fruit size and nutritional quality have been reported to be minor for Hass avocado in at least one comparable system (Kämper et al. 2021); however, any such effect would be shared equally by the native functional group and A. mellifera treatments, which all drew on the same paired Edranol source, and would not explain differences among those treatments. It remains a relevant distinction between those treatments and self-pollination, where no Edranol pollen was available.

Taken together, our findings highlight that functional trait diversity structures pollination services in Mediterranean agroecosystems rather

than by simple spatial proximity to semi-natural habitats. While landscape context remains an important driver of pollinator communities at broader scales (Kennedy et al. 2013; Tscharntke et al. 2012), our results indicate that, at fine spatial scales within orchards, functional identity governs the pathway through which pollinators influence reproductive success, consistent with trait-based frameworks of plant–pollinator interactions (Junker et al. 2013). These findings underscore the importance of maintaining functional diversity within pollinator assemblages, as different bee size classes contribute to distinct stages of the pollination process. Rather than a linear chain linking visitation to pollen transfer to fruit production, our study reveals a trait-mediated structuring of pollination services in which intermediate and final outcomes are differentially influenced by pollinator identity (Ne'eman et al. 2010; King et al. 2013). Such multidimensionality should be explicitly considered when designing management strategies aimed at sustaining crop pollination under increasing environmental variability.

Our study introduces a novel exclusion-based field approach to quantify pollen transfer and fruit production outcomes under realistic conditions. This method integrates exclusion treatments with pollen load quantification and visitation behaviour and provides a replicable framework for scaling up assessment of ecosystem services in other pollination-dependent systems (Delaplane et al. 2013). It could be promising in ecological contexts to isolate pollinator effects and improve comparability among taxa (King et al. 2013; Rader et al. 2016). The possibility to evaluate the landscape heterogeneity and proximity of crops to semi-natural vegetation may enhance the understanding about the ecological stability and resilience of pollination services, ultimately contributing to more sustainable crop yields. Such strategies are consistent with calls for integrated management approaches that consider both species diversity and habitat context to optimize pollination outcomes (Garibaldi et al. 2017; Martins et al. 2015).

Conclusions

Our results highlight the important contribution of native bees to pollination processes and yield outcomes in avocado crops. Pollen transfer potential (Ept) differed among functional groups, with medium- and small-sized bees showing higher Ept than large bees; this pattern was driven primarily by higher per-capita pollen load rather than by differences in visitation frequency, indicating a greater overall contribution to pollen transfer at the tree level rather than greater efficiency on a per-visit basis. In contrast, individual fruit weight showed a treatment × year interaction rather than a consistent pattern across years, suggesting that different pollinator groups may shape distinct dimensions of reproductive output. These results reveal a partial, though statistically limited, decoupling between pollen transfer potential and fruit development outcomes, emphasizing that multiple functional components may shape pollination services. In particular, high pollen transfer potential in both small and medium bees was not consistently associated with a fixed fruit-weight outcome, since fruit weight itself varied by year, suggesting that pollen transfer potential alone does not determine fruit outcomes. Self-pollination and medium-sized bees achieved the highest Pollination Service Index (PSI), sustaining fruit numbers closest to the open control, yet neither showed a corresponding advantage in fruit weight, whereas small bees produced the heaviest individual fruit despite the largest reduction in fruit number relative to the open control. No single treatment excelled across all metrics we measured, reinforcing our conclusion that a functionally diverse pollinator assemblage, rather than any single pollination strategy, is best positioned to reliably sustain both fruit quantity and fruit quality. Our findings therefore highlight the importance of maintaining functionally diverse pollinator communities. Functional diversity among bees may promote complementary roles in the pollination process, potentially increasing the reliability of crop pollination under environmental variability, though larger studies with greater replication across functional groups (particularly for less commonly captured groups such as small-bodied native bees) would help confirm the generality of these patterns.

Overall, these results suggest that supporting a diverse assemblage of native pollinators may provide greater benefits for crop productivity and long-term agroecosystem sustainability than relying on a single dominant pollinator group.

Such insights support conservation and management strategies that promote native pollinators as key providers of pollination services in fruit crop systems such as avocado.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge financial support from grant DO210001 awarded to Laura C. Pérez-Giraldo and José M. Cerda-Paredes.

AUTHOR CONTRIBUTION

LPG and SR conceptualized the idea. LPG collected and analysed the data and led the writing, with support from JCP. LPG and SR collected data. SR financed the study. All authors contributed to and revised the manuscript.

DISCLOSURE STATEMENT

The authors report no potential conflict of interest.

GENERATIVE AI DISCLOSURE STATEMENT

Claude (Anthropic) was used solely for language editing (grammar, clarity, and readability). No scientific content, data analysis, or interpretation was generated by AI. All edits were reviewed and approved by the authors. who take full responsibility for the final text.

DATA AVAILABILITY STATEMENT

Data and code to support the results are available in the following GitHub repository: https://github.com/LAURACPEREZ/

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Estimation method of pollination services using cage of exclusion trees.

Appendix II. General description of the exclusion treatments in crops of *P.americana.*

Appendix III. Effect of distance to semi-natural vegetation on visitation rate and pollen transfer potential (GAM results).

Appendix IV. Estimated marginal means of pollen transfer potential (Ept) by pollinator functional group.

Appendix V. Estimated marginal means of fruit weight (g) by pollinator treatment and year.

REFERENCES

Aizen MA, Aguiar S, Biesmeijer JC, Garibaldi LA, Inouye DW, Jung C, et al. (2019) Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. Global Change Biology 25: 3516–3527. https://doi.org/10.1111/gcb.14736

Albrecht M, Schmid B, Hautier Y, Müller CB (2012) Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences 279:4845-4852. https://doi.org/10.1098/rspb.2012.1621

Alcaraz ML, Hormaza JI (2011) Influence of physical distance between cultivars on yield, outcrossing rate and selective fruit drop in avocado (*Persea americana*, Lauraceae). Annals of Applied Biology 158:354-361. https://doi.org/10.1111/j.1744-7348.2011.00469.x

Ashman TL, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85:2408-2421. https://doi.org/10.1890/03-8024

Bartomeus I, Potts SG, Steffan-Dewenter I, Vaissière BE, Woyciechowski M, Krewenka KM, et al. (2014) Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2:e328. https://doi.org/10.7717/peerj.328

Bartomeus I, Garratt MPD, Park MG, Reitan T, Steffan-Dewenter I, Winfree R (2016) On the inconsistency of pollinator species traits for predicting either response to agricultural intensification or functional contribution. Oikos 125:721-731. https://doi.org/10.1111/oik.02665

Blüthgen N, Klein AM (2011) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology 12:282-291. https://doi.org/10.1016/j.baae.2010.11.001

Can-Alonzo C, Quezada-Euán JJG, Xiu-Ancona P, Moo-Valle H, Valdovinos Núñez GR, Medina-Peralta S (2005) Pollination of 'criollo' avocados (*Persea americana*) and the behaviour of associated bees in subtropical Mexico. Journal of Apicultural Research 44:3-8. https://doi.org/10.1080/00218839.2005.11101138

Capera-Aragones P, Cartar R, Foxall E, Tyson RC (2024) How can we enhance crops with flowers to increase pollination services and stop bee decline? Agriculture, Ecosystems & Environment 367:108964. https://doi.org/10.1016/j.agee.2024.108964

Dainese M, Martin EA, Aizen MA, Albrecht M, Bartomeus I, Bommarco R, Carvalheiro LG, Chaplin-Kramer R, Gagic V, Garibaldi LA, Ghazoul J, Grab H, Jonsson M, Karp DS, Kennedy CM, Kleijn D, Kremen C, Landis DA, Letourneau DK, et al. (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5:eaax0121. https://doi.org/10.1126/sciadv.aax0121

Davenport TL (1992) Pollination habit of avocado cultivars in South Florida. In: Lovatt CJ, Holthe PA,

Arpaia ML (eds) Proceedings of the Second World Avocado Congress. University of California, Riverside and California Avocado Society, pp 169–172.

Davenport TL (2019) Cross- vs. self-pollination in 'Hass' avocados growing in coastal and inland orchards of Southern California. Scientia Horticulturae 246:307-316. https://doi.org/10.1016/j.scienta.2018.10.051

Delaplane KS, Dag A, Danka RG, Freitas BM, Garibaldi LA, Goodwin RM, Hormaza JI (2013) Standard methods for pollination research with *Apis mellifera*. Journal of Apicultural Research 52:1-28. https://doi.org/10.3896/IBRA.1.52.4.12

Devkota K, dos Santos CF, Blochtein B (2021) Higher richness and abundance of flower-visiting insects close to natural vegetation provide contrasting effects on mustard yields. Journal of Insect Conservation 25:1-11. https://doi.org/10.1007/s10841-020-00279-3

Dicks LV, Breeze TD, Ngo HT, Senapathi D, An J, Aizen MA, Basu P, Buchori D, Galetto L, Garibaldi LA, Gemmill-Herren B, Howlett BG, Imperatriz-Fonseca V, Johnson SD, Kovács-Hostyánszki A, Kwon YJ, Lattorff HMG, Lungharwo T, Seymour CL, et al. (2021) A global-scale expert assessment of drivers and risks associated with pollinator decline. Nature Ecology & Evolution 5:1453-1461. https://doi.org/10.1038/s41559-021-01534-9

Eilers EJ, Kremen C, Smith Greenleaf S, Garber AK, Klein AM (2011) Contribution of pollinator-mediated crops to nutrients in the human food supply. PLoS ONE 6:e21363. https://doi.org/10.1371/journal.pone.0021363

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Martin JL (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14:101-112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Földesi R, Howlett BG, Grass I, Batáry P (2020) Larger pollinators deposit more pollen on stigmas across multiple plant species – a meta-analysis 58: 699–707. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.13798

Fründ J, Dormann CF, Holzschuh A, Tscharntke T (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94:2042-2054. https://doi.org/10.1890/12-1620.1

Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, et al. (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14:1062-1072. https://doi.org/10.1111/j.1461-0248.2011.01669.

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608-1611. https://doi.org/10.1126/science.1230200

Grab H, Blitzer EJ, Danforth B, Loeb G, Poveda K (2017) Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Scientific Reports 7:45296. https://doi.org/10.1038/srep45296

Greenop A, Woodcock B, Pywell R (2023) Using functional traits to predict pollination services: a review. Journal of Pollination Ecology 35:194-206. https://doi.org/10.26786/1920-7603(2023)735

Hapuarachchi NS, Kämper W, Hosseini Bai S, Ogbourne SM, Nichols J, Wallace HM, Trueman SJ (2024) Selective retention of cross-fertilised fruitlets during premature fruit drop of Hass avocado. Horticulturae 10:591. https://doi.org/10.3390/horticulturae10060591

Harder LD, Barrett SCH (1996) Pollen dispersal and mating patterns in animal-pollinated plants. In: Lloyd DG, Barrett SCH (eds) Floral biology: studies on floral evolution in animal-pollinated plants. Chapman & Hall, New York, pp 140-190.

Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B: Biological Sciences 275:2283-2291. https://doi.org/10.1098/rspb.2008.0405

Jaboor SK, Buke da Silva CR, Kellermann V (2022) The effect of environmental temperature on bee activity at strawberry farms. Austral Ecology 47:1470-1479. https://doi.org/10.1111/aec.13228

Junker RR, Blüthgen N, Brehm T, Binkenstein J, Paulus J, Schaefer HM, Stang M (2013) Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. Functional Ecology 27:329-341. https://doi.org/10.1111/1365-2435.12005

Kämper W, Ogbourne SM, Hawkes D, Trueman SJ (2021) SNP markers reveal relationships between fruit paternity, fruit quality and distance from a cross-pollen source in avocado orchards. Scientific Reports 11:20043. https://doi.org/10.1038/s41598-021-99394-7

Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, et al. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16:584-599. https://doi.org/10.1111/ele.12082

Khalifa SAM, Elshafiey EH, Shetaia AA, El-Wahed AAA, Algethami AF, Musharraf SG, AlAjmi MF, Zhao C, Masry SHD, Abdel-Daim MM, Halabi MF, Kai G, Al Naggar Y, Bishr M, Diab MAM, El-Seedi HR (2021) Overview of bee pollination and its economic value for crop production. Insects 12:688. https://doi.org/10.3390/insects12080688

King C, Ballantyne G, Willmer PG (2013) Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. Methods in Ecology and Evolution 4:811-818. https://doi.org/10.1111/2041-210X.12074

Klatt BK, Holzschuh A, Westphal C, Clough Y, Smit I, Pawelzik E, Tscharntke T (2014) Bee pollination improves crop quality, shelf life and commercial value. Proceedings of the Royal Society B: Biological Sciences 281:20132440. https://doi.org/10.1098/rspb.2013.2440

Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein AM, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM, Adamson NL, Ascher JS, Báldi A, Batáry P, Benjamin F, Biesmeijer JC, Blitzer EJ, Bommarco R, Brand MR, Bretagnolle V, Button L, et al. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communications 6:7414. https://doi.org/10.1038/ncomms8414

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303-313. https://doi.org/10.1098/rspb.2006.3721

Klein AM, Boreux V, Fornoff F, Mupepele AC, Pufal G (2018) Relevance of wild and managed bees for human well-being. Current Opinion in Insect Science 26:82-88. https://doi.org/10.1016/j.cois.2018.02.011

Kremen C (2018) The value of pollinator species diversity. Science 359:741-742. https://doi.org/10.1126/science.aar7614

Lattorff HMG (2022) Increased stress levels in caged honeybee (*Apis mellifera*) (Hymenoptera: Apidae) workers. Stresses 2:373-383. https://doi.org/10.3390/stresses2040026

Lavín U, Martinez-Harms MJ, Celis-Diez JL, Francois JP, Aguirre Y, Martínez-Harms J (2024) Modelling pollination maps in agroecosystems of a Chilean biodiversity hotspot. Ecosystems and People 20:2358471. https://doi.org/10.1080/26395916.2024.2358471

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545-556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Layek U, Kundu A, Bisui S, Karmakar P (2021) Impact of managed stingless bee and western honey bee colonies on native pollinators and yield of watermelon: a comparative study. Annals of Agricultural Sciences. 66: 38-45. https://doi.org/10.1016/j.aoas.2021.02.004

Lázaro A, Alomar D (2019) Landscape heterogeneity increases the spatial stability of pollination services to almond trees through the stability of pollinator visits Agriculture, Ecosystems & Environment 279: 149-155. https://doi.org/10.1016/j.agee.2019.02.009

Liu R, Chen D, Luo S, Xu S, Xu H, Shi X, Zou Y (2020) Quantifying pollination efficiency of flower-visiting insects and its application in estimating pollination services for common buckwheat. Agriculture, Ecosystems & Environment 301:107011. https://doi.org/10.1016/j.agee.2020.107011

Martins KT, Gonzalez A, Lechowicz MJ (2015) Pollination services are mediated by bee functional diversity and landscape context. Agriculture, Ecosystems & Environment 200:12-20. https://doi.org/10.1016/j.agee.2014.10.018

Monzón VH, Avendaño-Soto P, Araujo RO, Garrido R, Mesquita-Neto JN (2020) Avocado crops as a floral resource for native bees of Chile. Revista Chilena de Historia Natural 93. https://doi.org/10.1186/s40693-020-00092-x

Ne'eman G, Jürgens A, Newstrom-Lloyd L, Potts SG, Dafni A (2010) A framework for comparing pollinator performance: effectiveness and efficiency. Biological Reviews. 85: 435-451. https://doi.org/10.1111/j.1469-185X.2009.00108.x

Ospina-Torres R, Montoya Pfeiffer PM, Parra-H A, Solarte V, Otero JT (2015) Interaction networks and the use of floral resources by male orchid bees (Apidae: *Euglossini*) in a primary rain forest from the biogeographic Chocó Region (Colombia). Revista de Biología Tropical 63(3): 647–658. ISSN 2215-2075

Page ML, Minahan N, González-Varo JP, et al. (2021) A meta-analysis of single-visit pollination effectiveness comparing bees and other pollinators. American Journal of Botany 108:1-17. https://doi.org/10.1002/ajb2.1764

Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R, Cunningham SA, Mayfield MM, Arthur AD, Andersson GKS, Bommarco R, Brittain C, Carvalheiro LG, Chacoff NP, Entling MH, Foully B, Freitas BM, Gemmill-Herren B, Ghazoul J, et al. (2016) Non-bee insects are important contributors to global crop pollination. Proceedings of the National Academy of Sciences 113:146-151. https://doi.org/10.1073/pnas.1517092112

Reese MA, Wilson RS, Nichols J, Trueman SJ (2025) Declining outcrossing rates inside orchard blocks of 'Maluma' and 'Shepard' avocado (*Persea americana* Mill.) trees: effects on fruit yield and quality. Plants 14:1218. https://doi.org/10.3390/plants14081218

Requier F, Pérez-Méndez N, Andersson GKS, Blareau E, Merle I, Garibaldi LA (2023) Bee and non-bee pollinator importance for local food security. Trends in Ecology & Evolution 38:196-205. https://doi.org/10.1016/j.tree.2022.10.006

Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, et al. (2008) Landscape effects on crop pollination services: are there general patterns? Ecology Letters 11:499-515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Robinson SV, Cartar RV, Pernal SF, Waytes R, Hoover SE (2023) Bee visitation, pollination service, and crop yield in commodity and hybrid seed canola. Agriculture, Ecosystems & Environment 347:108396. https://doi.org/10.1016/j.agee.2023.108396

Rodríguez S, Pérez-Giraldo LC, Vergara PM, Carvajal MA, Alaniz AJ (2021) Native bees in Mediterranean semi-arid agroecosystems: unravelling the effects of biophysical habitat, floral resource, and honeybees. Agriculture, Ecosystems & Environment 307:107188. https://doi.org/10.1016/j.agee.2020.107188

Ryan IC, Shutt JD, Dicks LV (2023) The importance of multi-year studies and commercial yield metrics in measuring pollinator dependence ratios: a case study in UK raspberries *Rubus idaeus* L. Ecology and Evolution 13:e10044. https://doi.org/10.1002/ece3.10044

Sagwe RN, Peters MK, Dubois T, Steffan-Dewenter I, Lattorff HMG (2022) Pollinator efficiency of avocado (*Persea americana*) flower insect visitors. Ecological Solutions and Evidence 3:e12178. https://doi.org/10.1002/2688-8319.12178

Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12:253-279. https://doi.org/10.1146/annurev.es.12.110181.001345

Trueman SJ, Nichols J, Farrar MB, Wallace HM, Hosseini Bai S (2024) Outcrossing rate and fruit yield of Hass avocado trees decline at increasing distance from a polliniser cultivar. Agronomy 14:122. https://doi.org/10.3390/agronomy14010122

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, et al. (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87:661-685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Turley NE, Biddinger DJ, Joshi NK, López-Uribe MM (2022) Six years of wild bee monitoring shows changes in biodiversity within and across years and declines in abundance. Ecology and Evolution 12:e9190. https://doi.org/10.1002/ece3.9190

Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J (2018) Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359:791-793. https://doi.org/10.1126/science.aao2117

Zhang KY, Li YY, Bao JY, He XN, Chen LF, Guo LL, Guo DL, Song CW, He CL, Hou XG (2025) Bee-mediated pollination enhances fruit set and seed yield in *Paeonia ostii* 'Fengdan': insights into physiological and molecular mechanisms. Horticulture Research 12:uhaf224. https://doi.org/10.1093/hr/uhaf224

Zou Y, Xiao H, Bianchi FJJA, Jauker F, Luo S, van der Werf W (2017) Wild pollinators enhance oilseed rape yield in small-holder farming systems in China. BMC Ecology 17, 6. https://doi.org/10.1186/s12898-017-0116-1

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