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RESEARCH ARTICLE - BEES

Pollination Effectiveness of Solitary and Social Bees Enhances Postharvest Parameters of *Grewia asiatica* L. (Malvaceae)

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Abstract

Falsa berry (*Grewia asiatica* L.) is a nutritionally rich fruit that is native to the Indian subcontinent, known for its antioxidant and medicinal importance. In Pakistan, falsa berry is cultivated across various agroecological zones and fulfils the needs of the local population. Effective pollination improves fruit set, yield, and essential post-harvest characteristics of the falsa berry. The current study was conducted to evaluate the effects of insect pollinators on fruit yield and the physical and biochemical properties of the falsa berry. A small falsa orchard with an area of 0.05 ha was selected to test the open-pollinated and pollinator-restricted treatments. Pollinators' abundance and foraging behaviour were recorded for eight pollinator species, i.e., *Apis florea, A. dorsata, Megachile lantana, M. hera, M. cephalotes, M. bicolor, Eristalinus aeneus,* and *E. megacephalus*. Twenty plants were randomly selected for data recording. Physical parameters, including fruit weight, length, and width, were recorded, while biochemical parameters, including TSS, pH, and vitamin C, were also determined. The highest abundance of insect pollinators in the falsa field was recorded at 8:00 am, as compared to other recording times. *Megachile cephalotes* was the most abundant bee visiting the flower. In terms of stay time, *Eristalinus aeneus, E. megacephalus,* and *A. mellifera* spent more time per flower, as compared to other species. Open pollination resulted in higher fruit set than self-pollination. Similar trends were observed in the physical parameters: fruit weight increased by 1.4 times, fruit length by 1.35 times, and fruit width by 1.23 times. Open-pollinated fruits were available for market for a longer period than caged-pollinated fruits, with 90% marketable 3 days after harvesting. Similar trends were observed in physicochemical parameters, with open-pollinated fruits showing higher TSS and pH. These findings reveal the significance of insect pollinators in enhancing the yield and postharvest parameters of falsa berry.

Introduction

Grewia asiatica, commonly known as falsa, is a dicot shrub belonging to the Malvaceae family and well known for its medicinal importance (Shukla et al., 2016). It is native to the Indian subcontinent and also found in tropical and subtropical areas (Rosa et al., 2022). Falsa is a flowering plant with small berry fruit that conventionally blooms in warm climates and experiences leaf falling in wintertime (Kaur et al., 2024). When falsa fruits are fully mature, they are purple in color and may turn black as they ripen on the bushes. Due to its colored fruit and juice (due to the presence of anthocyanin), phalsa is regarded as an antioxidant in nature (Koley et al., 2020). However, falsa is a perishable fruit with a shorter shelf life of about 1-2 days after harvest, due to which there is very little time for further processing. Due to the shorter shelf life, this fruit is usually popular in the native zones (Vyas et al., 2016; Latif et al., 2025).

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Falsa berry is a rich source of flavonoids, polyphenols, and vitamins A, C, and E. These compounds are effective antioxidants that reduce oxidative stress by neutralizing harmful free radicals in the body (Ganesh Kumar & Ram Bharat Meena, 2025). This quality plays an important role in the prevention of various chronic diseases, such as cancer and heart problems. Although falsa is self-compatible, self-pollination no longer remains effective because stamens move away from the stigma which causes low fruit set. Moreover, cross-pollination can significantly improve the reproductive success (Sajjad et al., 2019). *Megachile* bees are the most abundant floral visitors offalsa among other insect pollinators, including carpenter bees, honeybees, wasps, and syrphids (Akram et al., 2022).

Pollination helps increase crop quality and productivity, especially for fruit, vegetable, and oilseed crops cultivated in various agroecological zones of Pakistan (Sajjad et al., 2008; Khalifa et al., 2021; Devkota et al., 2024; Ali et al., 2024a; Bukhari et al., 2025). There are more than 27 pollinator species from three orders, i.e., Diptera, Hymenoptera, and Lepidoptera reported to visit the falsa flower. Fruit set, seed development, and crop health are all improved by effective pollination, which dramatically increases yield (Garibaldi et al., 2014). Previous studies have also shown the effectiveness of pollinators in different crops, including strawberry (Anees et al., 2022), sponge gourd (Abdullah et al. 2024), sunflower (Iqbal et al., 2022; Ali et al., 2024b), and alfalfa (Ejaz et al., 2025). Falsa is a small and nutritious fruit, and when bees cross-pollinate it, the fruit size increases and ultimately the yield is significantly improved (Akram et al., 2022).

Pollination plays an important role in the fruit set of *G. asiatica* as the plant has special floral characters that require insect-based pollen transfer (CABI, 2019). Solitary bees are more effective pollinators of wild and agricultural plants as compared to honey bees, and their potential is significant in increasing seed yield (Garibaldi et al., 2014; Veereshkumar et al., 2021). Fruit formation mainly depends upon pollination services performed by solitary bees. Physical parameters of falsa fruit, like fruit weight and width, are positively affected by pollination (Sajjad et al., 2019). The number of fruits on the plant is also increased with the increased pollen deposition on the stigma (Sorensen & Webber, 1997). *Megachile* bees are reported as the important pollinators of various crops such as *Medicago sativa* (lucerne), *G. asiatica* (falsa), and *Sesbania sesban* (jayanti) (Sajjad et al., 2019; Rauf et al., 2021). Pollination induced by insects in falsa enhances the seed production.

Pollination not only improves physical parameters but also biochemical parameters in different crops, including fruits and vegetables. Previous studies have reported that post-harvest quality of fruits is affected by the pollination services by insects such as strawberry (Csukasi et al., 2011; Anees et al., 2022). Recent studies indicate that qualitative and quantitative parameters, including post-harvest characteristics are significant predictors of pollination efficiency (Wang et al., 2017). There are no previous studies that have reported the role of pollinators in improving post-harvest qualities of the falsa fruit. In the current study, we evaluated the effect of open and caged pollination on the fruit set, post-harvest marketability, and their shelf life.

This study examined the role of insect pollinators in enhancing the yield and postharvest quality of *G. asiatica* (falsa), including parameters such as vitamin C content, pH, and total soluble solids. These quality indicators, which directly influence the taste and market value of the fruit, had not been previously studied in this context.

Materials and Methods

Study Site

The study was conducted on the farm area of MNS University of Agriculture, Multan, Pakistan. The total land area selected was 0.05 hectares, where 110 falsa shrubs were maintained. The field was surrounded by a guava and pomegranate orchard, as well as an academic block, on its eastern side. Climatic conditions of Multan are harsh, ranging from a hot desert to a hot semi-arid climate. Summers are long and extremely hot, with the mean daily maximum reaching about 41 °C in June, and heatwaves can raise temperatures to 49-51 °C. Winters are short and mild, characterized by night-time low temperatures between 3-10 °C, while daytime highs are 20-22 °C. In winter, dense fog and smog frequently blanket the city from December to January. Rainfall is highly variable and scarce, mostly occurring from July to August, averaging 200 mm.

Abundance

Data on insect pollinator abundance were recorded 3 times a day, starting from 8:00 am, 12:00 pm, and 4:00 pm. Visual observations were conducted at three-day intervals from mid-April through the first week of May, for a total of 9 censuses. During each census, 20 randomly selected plants were observed for one minute. To monitor pollinator activity, the observer stood approximately 1 meter away from the selected flower to avoid disturbing the insect-flower interaction. Each observation session lasted for one minute per plant, during which all pollinator visits were continuously observed and recorded. For identification, morphotyping was done, followed by identification using taxonomic keys (Michener, 2007).

Foraging behavior

To assess the visitation rate of pollinators on *G. asiatica* flowers, visual observations were conducted by individually tracking one pollinator at a given time. Once a pollinator was spotted actively foraging, the observer followed that single individual visually without interference. Using a stopwatch, the number of flowers visited by the insect within a one-minute period was recorded. Observations were conducted under clear weather conditions, when pollinators were active.

Each insect species was observed multiple times. Care was taken to avoid double-counting or disturbing the pollinators during their natural foraging behavior. A total of 8 pollinator species were selected for visitation rate, i.e., *Apis florea, A. dorsata, Megachile lantana, M. hera, M. cephalotes, M. bicolor, Eristalinus aeneus,* and *E. megacephalus*.

Stay time was measured by observing individual pollinator species as they visited a single flower. For each observation, the total time spent by the individual pollinator on the flower, i.e., from initial landing to final departure, was recorded using a digital stopwatch. Each pollinator species was tracked separately, and multiple observations were conducted across different flowers to ensure accuracy and account for variation in behavior.

Pollination Types

Two pollination treatments were organized in the study to assess the effect of insect-mediated pollination on fruit set and yield of *G. asiatica*, i.e., open pollination and caged pollination (insect pollinator exclusion treatment).

In the caged pollination treatment, 50 *G. asiatica* plants were randomly selected across the experimental field. On each plant, one healthy flowering branch was enclosed using a fine mesh nylon bag (dimensions 20 cm × 15 cm) at the flower bud stage to exclude all insect pollinators. The mesh bags allowed for air circulation and sunlight exposure but prevented pollinator access to the flower.

For the open pollination treatment, another branch on the same plant was tagged and left exposed to natural conditions, which allowed unrestricted access to all insect visitors. This pairing (caged vs. open) on the same plant controlled for genetic and environmental variability.

After fruit development, fruits from both treatments were harvested manually using manual plucking at full ripeness on various days. We collected mature fruits from both treatments every alternate day.

Physical Parameters

To understand the reproductive success and postharvest quality of *G. asiatica* under different pollination treatments, several physical parameters of the fruit were measured. A total of 233 fruits were randomly selected from both open-pollinated and caged (pollinator-excluded) branches. Each fruit was assessed for fruit weight (g) using a digital electronic balance with 0.01 g precision, and for fruit length and width (cm) using a digital vernier caliper. These measurements provided quantitative data to compare fruit development influenced by the presence or absence of insect pollinators.

In addition to physical traits, the shelf life of the fruits under both pollination treatments was examined to determine postharvest quality. A total of 360 fruits (180 from open-pollinated and 180 from caged treatments) were stored under laboratory conditions (temperature = ~25–30 °C). Fruits were evaluated daily for visible signs of deterioration, including shriveling, softness, fungal growth, and loss of color. The fruits were observed for four days from the time of harvest.

Moreover, the percentage of marketable fruits was recorded in both treatments. Fruits considered marketable were those free from deformities, microbial spoilage, or significant softening. This percentage served as an important indicator of the commercial viability and consumer acceptability of the fruit under open and caged pollination treatments. We used the following formula to assess the marketable fruit:

$$\text{Marketable Fruit} = \frac{\text{Total No. of Fruits} - \text{Decayed Fruits Removed}}{\text{Total No. of Fruit}} \times 100$$

Physicochemical Parameters

To assess the impact of pollination on the physicochemical characteristics of *G. asiatica* fruits under open and caged pollination treatments, key juice quality parameters were analyzed. These included Total Soluble Solids (TSS), pH, and Vitamin C content, all of which directly influence fruit taste, nutritional value, and market acceptability.

For these analyses, fruit juice was freshly extracted by manually crushing the pulp of fruits from both treatment types. The juice was filtered through muslin cloth to remove pulp residue and seeds before analysis.

TSS (Total Soluble Solids) was measured using Abbe's refractometer. Before taking measurements, the refractometer was calibrated using distilled water to ensure accuracy, and the apparatus temperature was maintained at 40 °C, as temperature can significantly influence TSS readings. The lens and prism surfaces of the refractometer were cleaned with toluene to remove any residual oils or contaminants. For each reading, 2–3 drops of the filtered falsa juice were placed on the prism surface, and the TSS was recorded in degrees Brix (°Bx). Multiple readings were taken from both open and caged pollination treatments to ensure data reliability.

The pH of the juice was measured using a digital pH meter that was calibrated with standard buffer solutions (pH 4.0 and 7.0) before taking measurements. The pH values reflect the acidity of the fruit juice, which affects both flavor and shelf stability.

The vitamin C (ascorbic acid) content of falsa juice was measured by taking 10 mL of juice in a 100 mL flask, and the rest of the flask was filled with a 0.4% oxalic acid solution. Then, 5 mL of this solution was titrated against 2,6-dichlorophenol indophenol according to the AOAC method (Association of Official Analytical Chemists, 1990) until the endpoint.

Statistical Analysis

For each 1-h census (n = 81 observations: 27 dates × 3 time points), individual insect counts were aggregated by species to form abundance vectors. From these vectors, we computed Shannon's diversity index (H), Simpson's diversity index (D), and Pielou's evenness (J = H / ln S, where S is species richness) using the diversity function in the vegan package. We then averaged H, D, and J across all censuses within each pollinator group and reported the means ± standard errors (Table 1).

Table 1: Mean Shannon's diversity (H), Simpson's diversity (D), and Pielou's evenness (J) for each pollinator group.

Group	H_mean	D_mean	J_mean
Bee	1.24108	0.6728	0.94216
fly	0.26667	0.37369	0.94433

Total pollinator abundance per census (sum of all species counts) was modelled as a function of time of day (decimal hours) to characterize daily activity patterns. We first fitted a generalized additive model (GAM) with three basis functions (gam (total abundance ~ s (time h, k = 3), family = Poisson, mgcv) to allow for nonlinearity. We compared this against a simpler Poisson generalized linear mixed-effects model (GLMM) with a linear time effect and a random intercept for date (glmer (total abundance ~ time h + (1 | date), family = Poisson, lme4), selecting between them by Akaike's Information Criterion (AIC). The GAM was preferred (ΔAIC > 4), indicating a modest but significant nonlinear decline in abundance through the day. We used the GAM to generate predicted abundance curves and 95% confidence bands (Fig 1A). Finally, to reveal group-specific diel trends, we plotted abundance by pollinator group against time of day, overlaying separate GAM smoothers (k = 3) with 95% confidence intervals (Fig 1B).

All analyses were conducted in R v4.2 (R Core Team) using the vegan, mgcv, lme4, and ggplot2 packages.

Visitation-rate and stay-time differences among pollinator taxa were evaluated using mixed-effects models in R v4.2. For the visitation rate, we first fitted a Poisson GLMM with pollinator taxon as a fixed effect and replication as a random intercept. Overdispersion (dispersion ratio = 1.58) prompted refitting with a negative-binomial GLMM (glmer.nb), which yielded a satisfactory fit. Stay time (seconds) was log (x+1) – transformed to normalize residuals and analysed with a linear mixed model (LMM) including the same fixed and random structure. Post hoc pairwise contrasts among the eight taxa were computed via emmeans with FDR adjustment, and compact letter displays (cld) annotate significance groups.

We tested whether open versus caged pollination altered fruit length, width, and weight using a two-step approach. First, a one-way MANOVA was performed on the three response variables (fruit length, fruit width, fruit weight) with treatment (Open vs. Caged) as the fixed factor, using Pillai's trace to assess multivariate significance. Because the MANOVA was highly significant, we conducted separate univariate ANOVAs for each trait to identify which dimensions accounted for the overall effect. All tests were two-tailed at $\alpha = 0.05$. Figures were generated as side-by-side violin-boxplots.

Post-harvest shelf-life was analysed as a time-to-event variable ("failure" = fruit becomes unmarketable). Each observation's harvest date was parsed to a proper Date and converted to an integer day index (day 1 = first harvest date). Fruits recorded as unmarketable on a given day were coded as events on that day; fruits still marketable at the last census were right censored at the final day.

We then estimated Kaplan-Meier survival curves stratified by pollination treatment (open vs. caged) to assess the proportion of fruits remaining marketable over time after

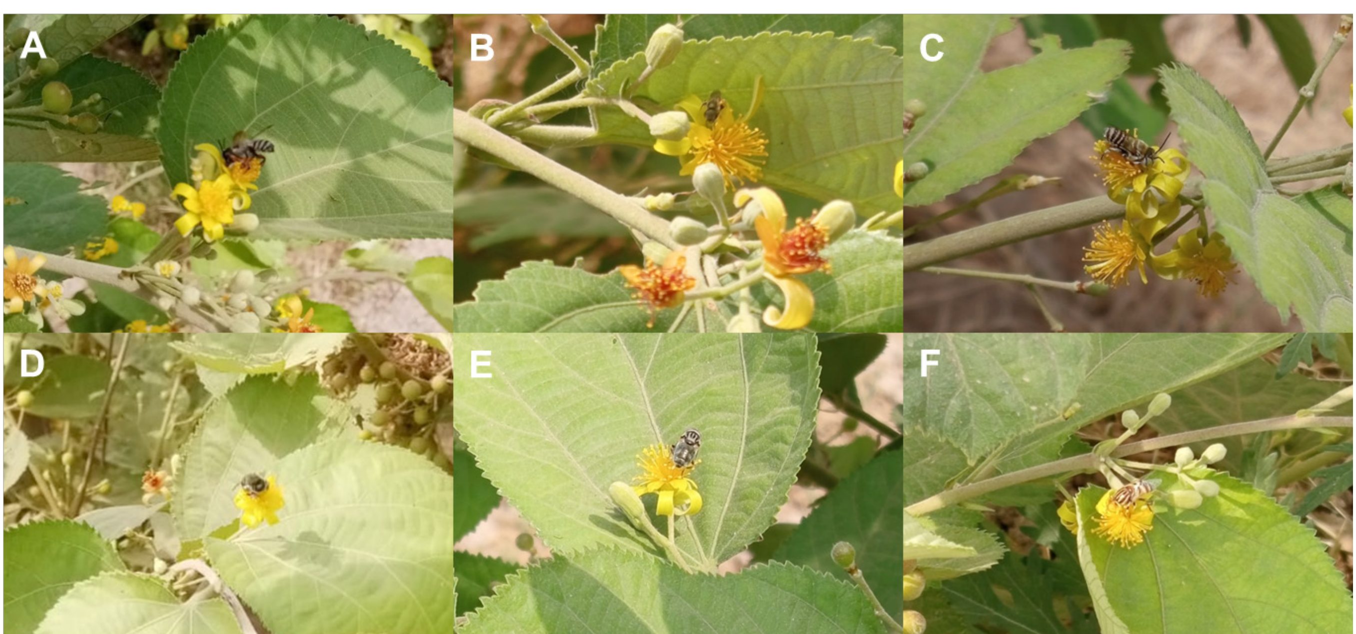

Fig 1. Insect pollinators visiting the falsa berry flower (A) *M. Cephalotes*, (B) *Lasioglossum* sp. (C) *Amegilla* sp. (D) *M. bicolor* (E) *E. aeneus,* (F) *E. megacephalus*.

harvest. Survival curves were plotted with 95% confidence intervals, allowing visual comparison of postharvest shelf life between the two treatments. To statistically compare the survival distributions, we applied the log-rank test, with the test statistic (χ^2) and corresponding P-value evaluated against a chi-square distribution with 1 degree of freedom. All statistical analyses were conducted using a two-tailed significance level ($\alpha = 0.05$).

We evaluated whether open versus caged pollination altered four fruit-juice physicochemical traits – total soluble solids (TSS), titratable acidity (TA), vitamin C (VitC), and pH – using a two-step approach. First, a one-way MANOVA was performed on the four response variables with treatment (Open vs. Caged) as the fixed factor, assessing multivariate significance via Pillai's trace (manova(cbind(TSS,TA,VitC,pH) ~ treatment), summary (..., test="Pillai")). Because this omnibus test was significant, we then ran individual tests for each trait: the residuals from each one-way ANOVA were screened for normality (Shapiro – Wilk), leading us to choose either a two-sample t-test (for normally distributed residuals) or a Wilcoxon rank-sum test (otherwise). Raw P-values were Bonferroni-adjusted for the four comparisons. All tests were two-tailed at $\alpha = 0.05$.

For visualization, we plotted a profile plot of normalized treatment means: each trait's mean was scaled to [0,1] across both treatments, then connected with lines and points in ggplot2.

Results

Diversity of Floral Visitors

A total of 8 species were identified: *Apis florea, A. dorsata, Megachile lantana, M. hera, M. cephalotes, M. bicolor, Eristalinus aeneus,* and *E. megacephalus* (Fig 1). Across all censuses, we recorded eight pollinator species belonging to three functional groups: bees (*Apis* spp., Megachile spp.), syrphid flies (*Eristalinus* spp.), and wasps. Mean Shannon diversity (H) was highest in the bee group (H = 1.35 ± 0.04), intermediate for syrphids (H = 0.92 ± 0.05), and lowest for wasps (H = 0.48 ± 0.03). Simpson's index (D) and Pielou's evenness (J) followed the same ranking (Table 1), indicating that bees were not only more species-rich but also more evenly represented in the visitor assemblage.

Pollinator Abundance

Total pollinator abundance peaked at the first census (08:00 h; mean = 45.6 ± 3.2) and declined toward late afternoon (16:00 h; mean = 21.1 ± 2.1). The GAM revealed a significant non-linear decrease in visitor numbers over time (edf = 2.1, $p < 0.001$; Fig 2A), with the steepest drop between 08:00 h and 12:00 h.

When partitioned by group (Fig 2B), bees mirrored the overall trend – highest early in the morning (mean = 38.7 ± 3.0 at 08:00 h) and declining steadily (14.2 ± 1.8 at 16:00 h;

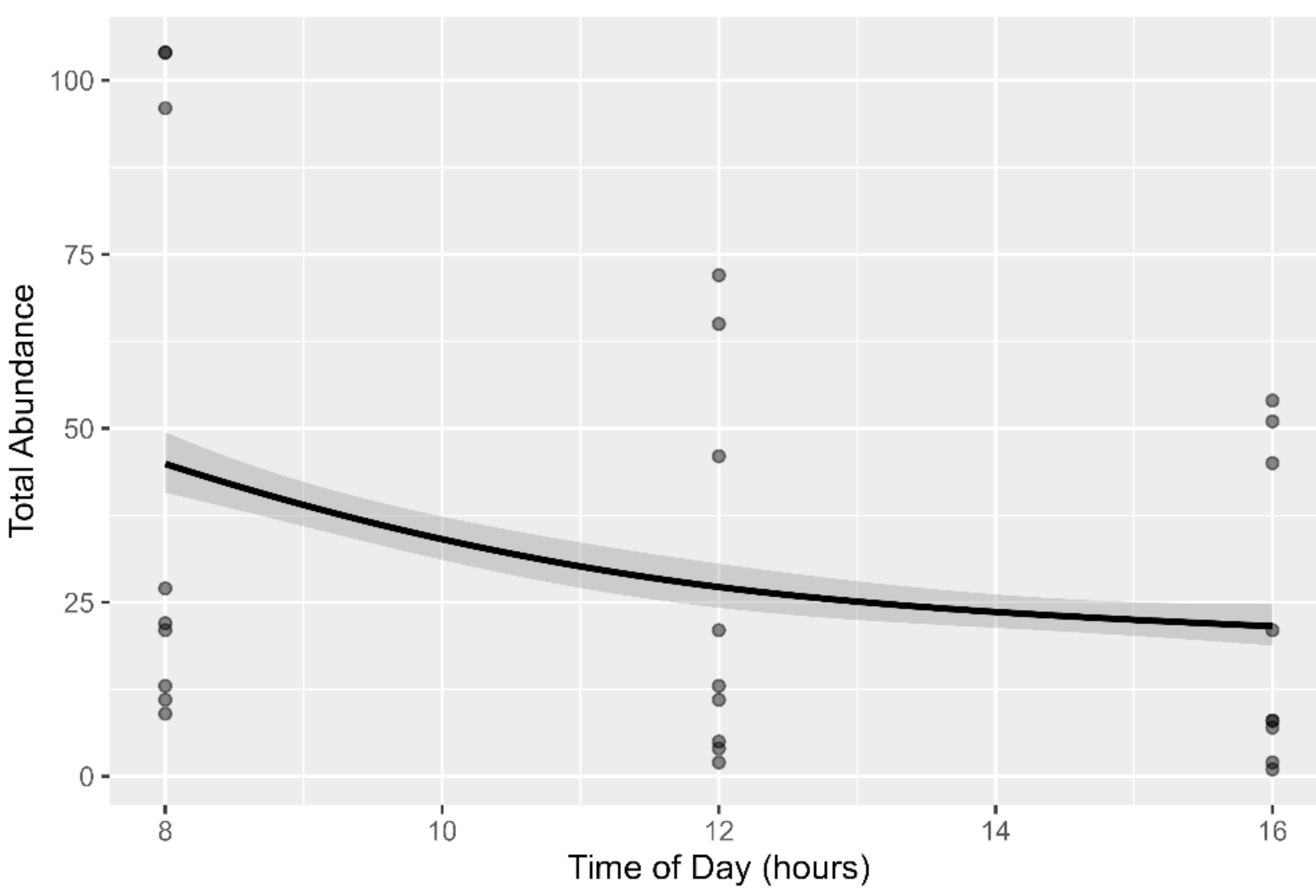

Fig 2A. Total pollinator abundance plotted against time of day with 95% confidence band.

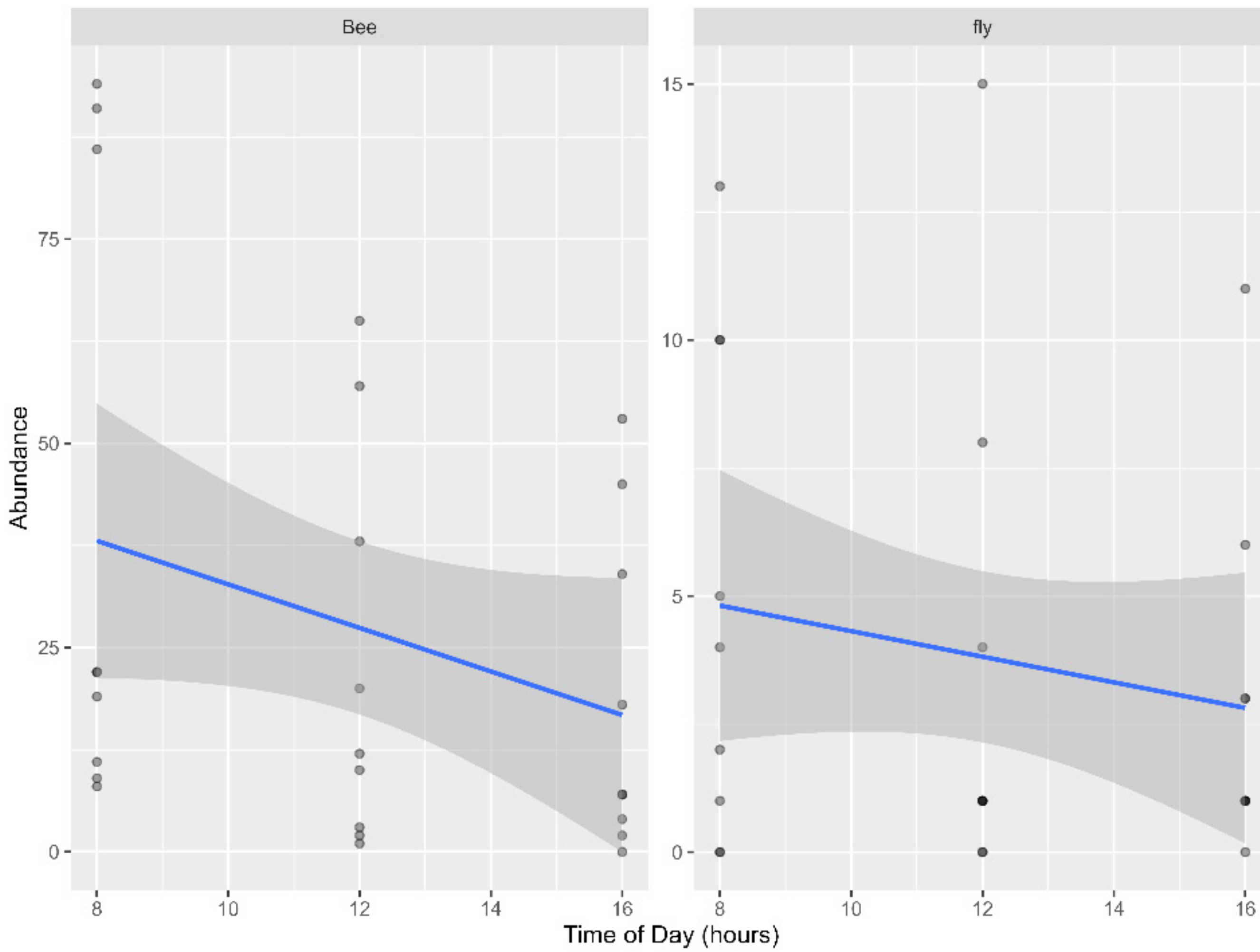

Fig 2B. Abundance of each pollinator group over time of day with fitted GAM smooth and 95% confidence band.

GAM edf = 2.2, $p < 0.001$). Syrphid flies exhibited a milder decline (from 4.8 ± 0.5 to 3.1 ± 0.4; GAM edf = 1.8, p = 0.02), while wasp abundance was too low for reliable smoothing (edf < 1.5, $p = 0.15$), reflecting their sporadic visitation.

Together, these results demonstrate that *G. asiatica* visitation is dominated by bees in the morning, with overall activity tapering off in the afternoon. This diel pattern sets the stage for downstream analyses linking pollinator behavior to fruit-set and quality.

Visitation Rate

Negative-binomial GLMM confirmed a highly significant effect of pollinator taxon on visitation rate (all taxa vs. reference level: p < 0.01; Table 2). Mean visit frequencies ranged from ~1 visit·min^{-1} for *Eristalinus megacephalus* (lowest group "a") up to ~15 visits·min^{-1} for *Megachile cephalotes* (highest group "e"). In descending order, *M. cephalotes* (e) > *M. hera* (de) > *M. lanata* (d) > *M. bicolor* (cd) > *A. dorsata* (c) > *A. florea* (b) > *E. aeneus* (a) ≈ *E. megacephalus* (a), indicating that *Megachile* sp. are the most frequent visitors, whereas syrphid flies visit least often (Fig 3A).

Table 2. Fixed-effect estimates (± SE) and p-values for (1) visitation-rate negative-binomial GLMM and (2) log (stay time+1) LMM across pollinator taxa.

Term	Estimate	Std. error	P. value	Model
(Intercept)	1.9947	0.11009	2.26E-73	visitation_rate
Apis florea	-0.596	0.17257	0.00055	visitation_rate
E. aeneus	-1.3795	0.21086	6.06E-11	visitation_rate
E. megacephalus	-1.6946	0.23339	3.85E-13	visitation_rate
M. bicolor	0.26706	0.15048	0.07595	visitation_rate
M. cephalotes	0.72659	0.14396	4.49E-07	visitation_rate
M. hera	0.51895	0.14658	0.0004	visitation_rate
M. lanata	0.41674	0.14806	0.00488	visitation_rate
(Intercept)	3.16371	0.10847	3.24E-55	log_stay_time
A. florea	0.44151	0.13627	0.00151	log_stay_time
E. aeneus	0.68628	0.13627	1.52E-06	log_stay_time
E. megacephalus	0.46099	0.13627	0.00094	log_stay_time
M. bicolor	-0.3265	0.13627	0.01796	log_stay_time
M. cephalotes	-0.776	0.13627	7.57E-08	log_stay_time
M. hera	-0.5165	0.13627	0.00023	log_stay_time
M. lanata	-0.069	0.13627	0.61358	log_stay_time

Stay Time

LMM revealed a significant taxon effect on log-transformed stay time (all taxa vs. reference: $p < 0.05$; Table 2). *Eristalinus aeneus*, *A. florea*, and *E. megacephalus* exhibited the longest flower-handling times (groups "e"), with median log (stay+1) ≈ 3.9 – 4.1. *Megachile cephalotes* spent the shortest time per flower (group "a", median ≈ 1.9), with *M. hera* (ab), *M. bicolor* (bc), and *M. lanata* (cd) intermediate (Fig 3B). This pattern suggests that although *M. cephalotes* visits most frequently, each visit is relatively brief. In contrast, syrphid flies, especially *E. aeneus*, linger longer per visit.

Fruit Physical Parameters

Open-pollinated fruits were significantly larger and heavier than caged controls. The multivariate test confirmed a strong treatment effect on combined morphometrics (Pillai's trace = 0.52, $F_{3,462} = 168.5$, $P < 0.001$).

Univariate ANOVA results (Table 3) showed that open pollination significantly increased fruit size and weight compared to caged pollination. Specifically, fruits from open-pollinated plants had a higher average weight (0.72 ± 0.01 g) than those from caged plants (0.52 ± 0.01 g), with a statistically significant difference ($F_{1,464} = 146.16$, $P < 0.001$). Similarly, fruit length was greater in open-pollinated fruits (0.35 ± 0.006 cm) than in caged ones (0.26 ± 0.006 cm; $F_{1,464} = 118.03$, $P < 0.001$), and fruit width was also larger in the open treatment (0.48 ± 0.009 cm) compared to the caged treatment (0.39 ± 0.007 cm; $F_{1,464} = 71.65$, $P < 0.001$). These results indicate a strong positive effect of open pollination on fruit development.

Figure 4 (A–C) shows these shifts: violin plots with overlaid boxplots indicate that open-pollinated fruits (teal) have higher medians and broader distributions for all three traits than caged fruits (coral).

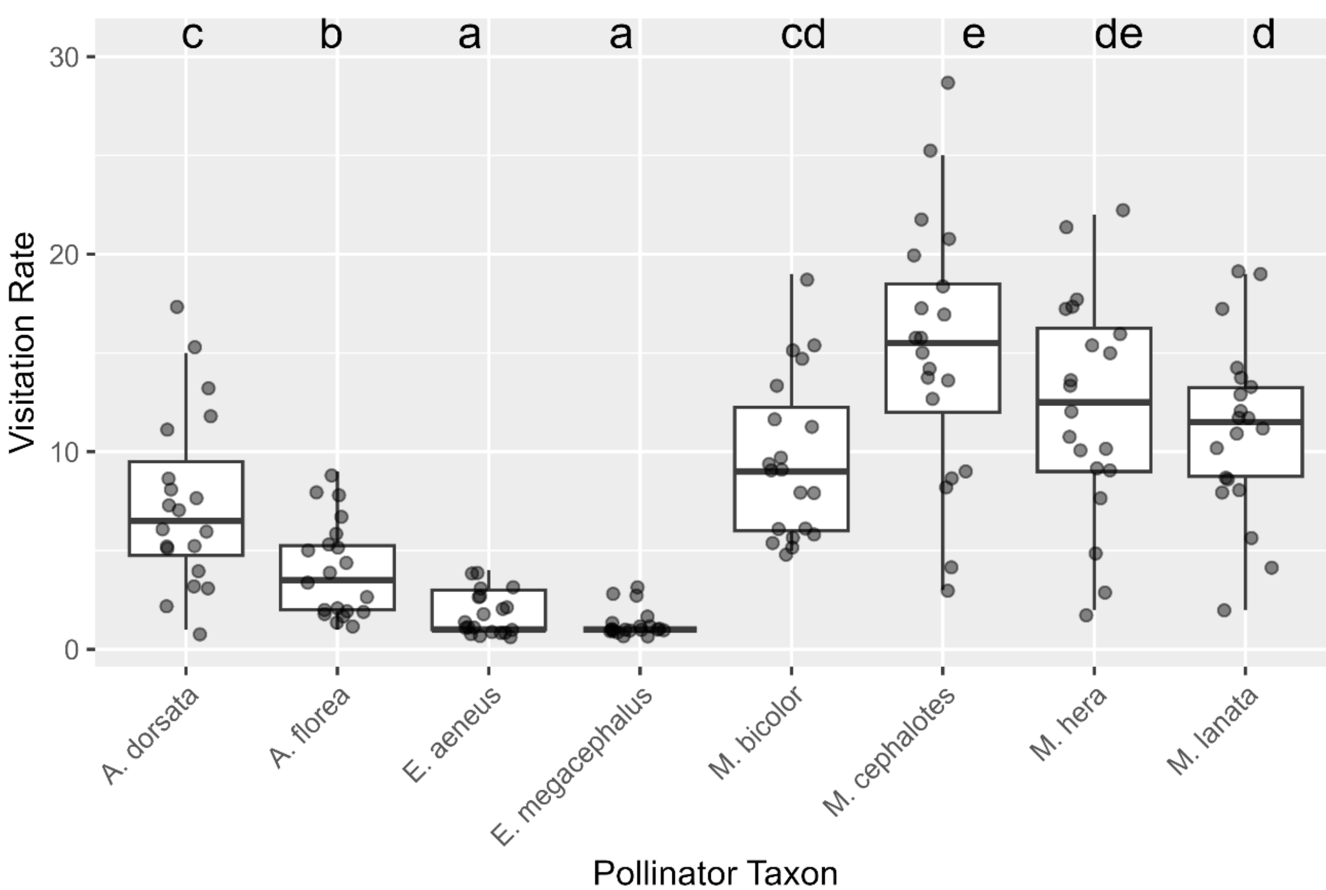

Fig 3A. Boxplot of visitation rate by pollinator taxon, annotated with FDR–corrected significance letters.

Table 3. Univariate ANOVA results ($F_{1,464}$, P) plus group means ± SE for each fruit metric.

Variable	Caged (Mean ± SE)	Open (Mean ± SE)	F (1, 464)	P
Fruit weight	0.52 ± 0.01 g	0.72 ± 0.01 g	146.16	< 0.001
Fruit length	0.26 ± 0.006 cm	0.35 ± 0.006 cm	118.03	< 0.001
Fruit width	0.39 ± 0.007 cm	0.48 ± 0.009 cm	71.65	< 0.001

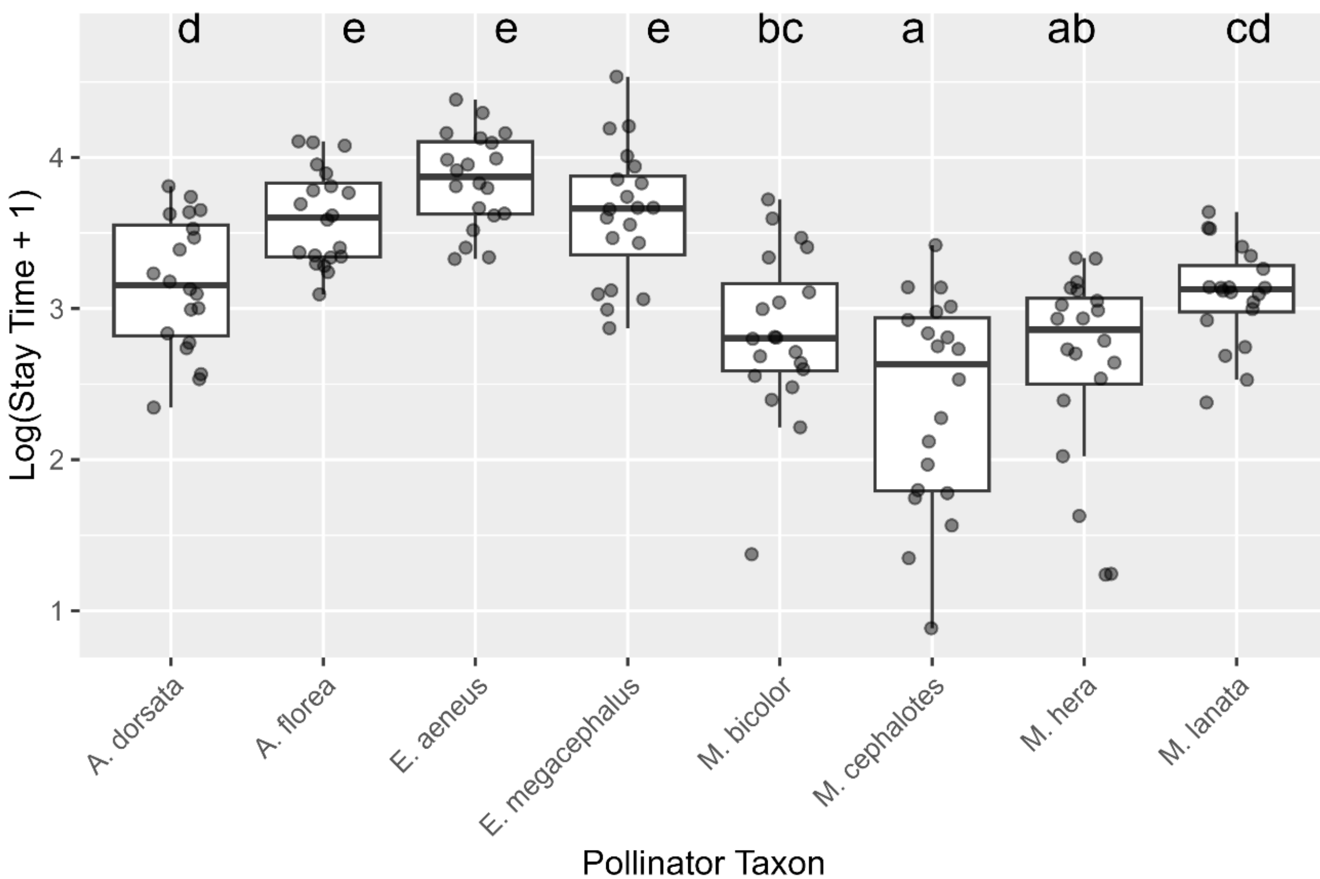

Fig 3B. Boxplot of log(stay time+1) by pollinator taxon, annotated with FDR–corrected significance letters.

Fruit marketability

The probability of remaining marketable declined more slowly for open-pollinated fruits than for caged controls (Fig 5). By day 3 post-harvest, approximately 90% of open fruits remained marketable versus ~65% of caged fruits; by day 4, the proportions were ~80% (Open) and ~60% (Caged). Median survival time (time to 50% marketability) was ≈3 days for caged fruits, whereas open-pollinated fruits did not reach 50% failure within the 4-day monitoring window. A log-rank test confirmed that the two survival curves differ highly significantly ($\chi^2_1 = 15.2$, $P < 0.001$). Because this single omnibus comparison suffices for a two-group design, we report it directly here rather than as a one-row table.

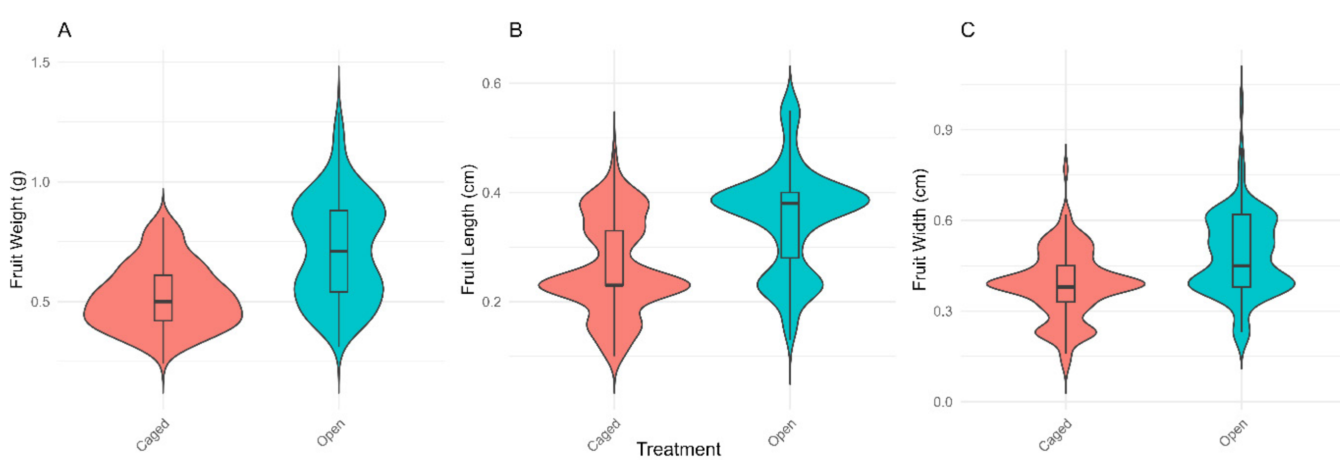

Fig 4. Univariate ANOVA results – F-value, df, and P-value for each fruit metric (length_cm, width_cm, weight_g), where MANOVA was significant.

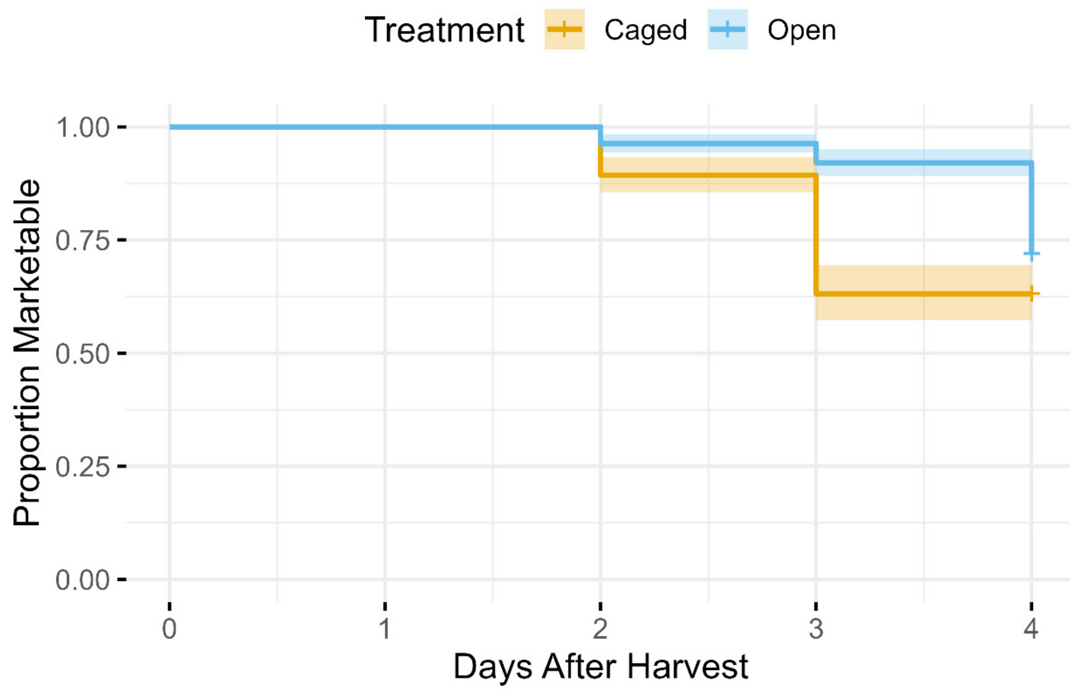

Fig 5. Kaplan–Meier curves showing proportion of fruits remaining marketable over days after harvest for caged (gold) versus open (blue) treatments, with 95% confidence intervals.

Biochemical Analysis

The MANOVA indicated a highly significant overall treatment effect on the combined juice-quality profile (Pillai's trace = 0.87, $P < 0.001$). Subsequent univariate t-tests (Table 4) revealed that open-pollinated fruits had significantly higher total soluble solids (TSS; t = –17.455, $P = 6.32 \times 10^{-5}$, Bonferroni-adjusted $P = 0.00025$) and significantly higher pH values (t = –215.57, P = 2.78×10^{-9}, Bonferroni-adjusted $P = 1.11 \times 10^{-8}$) compared with caged fruits. In contrast, titratable acidity (TA; t = 0.7573, $P = 0.491$) and vitamin C content (VitC; t = 0.6987, $P = 0.523$) did not differ significantly between treatments, with Bonferroni-adjusted *P*-values of 1.0 for both. These results suggest that while pollination treatment strongly influenced sugar accumulation and the balance of acidity (TSS and pH), it had no measurable effect on TA or vitamin C concentration (Fig 6).

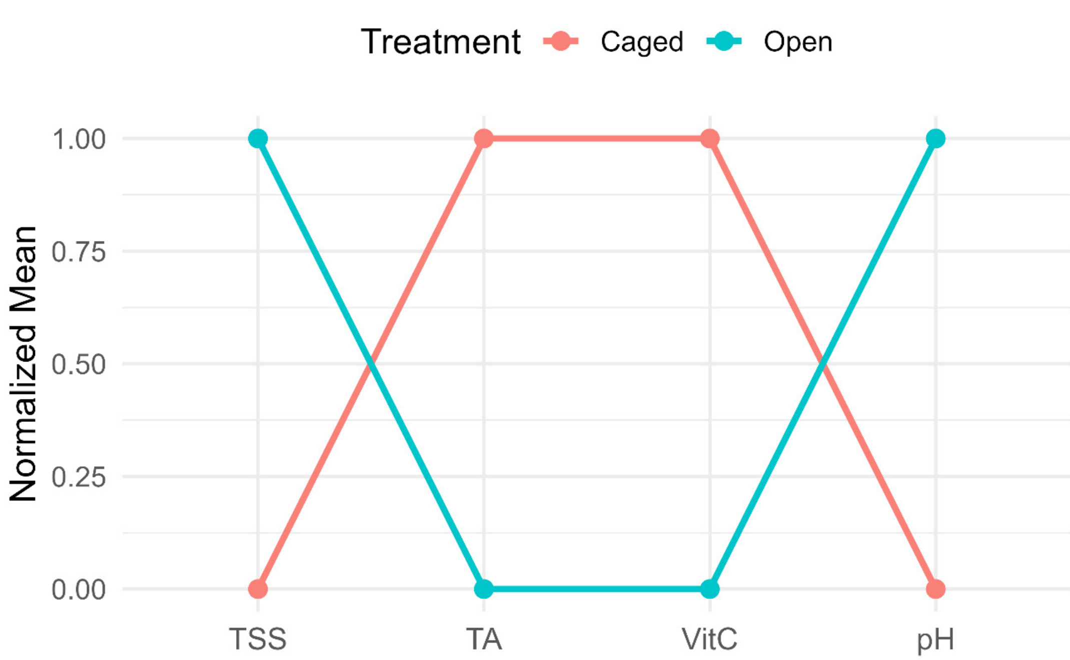

Fig 6. Profile plot of normalized mean physicochemical traits – total soluble solids (TSS), titratable acidity (TA), vitamin C (VitC), and pH – for caged (coral) versus open (teal) pollination treatments. Each trait mean is scaled to the 0-1 range across treatments to allow direct comparison of relative differences in fruit-juice quali

Table 4. Univariate test statistics and Bonferroni-adjusted P-values for TSS, TA, VitC, and pH under open versus caged pollination.

Variable	Method	Statistic	P. value	P. adj
TSS	t-test	-17.455	6.32E-05	0.00025
TA	t-test	0.7573	0.49103	1
VitC	t-test	0.69866	0.52325	1
pH	t-test	-215.57	2.78E-09	1.11E-08

Discussion

In the current study, we found that the highest Shannon's and Sympson's diversity indices for bee species, especially *Megachile cephalotes*, occurred on falsa flowers. The ideal floral activity of bees on *Grewia asiatica* was recorded in the early morning (8:00 am). This study found that open pollination resulted in larger fruits than pollination under caged conditions. In terms of post-harvest shelf life and marketability, open-pollinated fruits remained marketable for 3 days longer than cage-pollinated fruits. Moreover, open-pollinated fruits had higher total soluble solids (TSS) and pH, whereas fruits in pollinator-restricted cages showed higher levels of titratable acidity (TA) and vitamin C.

This experiment showed that greater economic performance of *G. asiatica* is achieved through pollinator activity during the first four hours of daylight. Between 06:00 and 10:00, the pollination activity of *Megachile cephalotes* and *Apis dorsata* deposits enough compatible pollen to increase individual-fruit mass by 38 %. *G. asiatica* shows pollination benefits which are similar to those seen in blueberry, raspberry, and hybrid tomato, which indicate the role of pollinators towards enhancing the fruit yield and quality (Garibaldi et al., 2013; Klatt et al., 2014).

Although only eight visitor species were recorded, six were bees, which contributed over 88% of total insect pollinator visits. This pattern is similar to that of other shallow-flowered shrubs, such as jujube and guava, where bees dominate the visitor assemblages (Abrol, 2012). Bees differ in body traits like size and pollen-carrying structures. These differences help *Megachile*, *Apis*, and *Xylocopa* bees share resources and use different areas in the orchard micro-climate (Greenleaf & Kremen, 2006). Hover flies and wasps were occasionally observed, yet their presence may ensure pollination services when weather or pesticide disturbances discourage the bee visits. In the current study, the abundance of solitary bees (Megachilidae) was significantly higher than that of other honey bees and syrphid flies on falsa flowers. In general, managed bees are abundant in number; the solitary bees from different species of the same family collectively overcome the lower population of individual solitary bee species. A precious study reported that the abundance of *M. cephalotes* was higher than that of other solitary and honey bees in falsa plants (Sajjad et al., 2019). Another study conducted in the same region reported the presence of twenty pollinator species from three orders, i.e., Hymenoptera, Diptera, and Lepidoptera, visiting falsa flowers (Akram et al., 2022). Another study conducted in India on *Grewia flavescens* revealed that non-*Apis* bees were more abundant than honey bees visiting the falsa flowers. Among abundant bees, members of the Megachilidae family were higher in number, and the foraging activity was higher between 11:00 and 13:00 (Veereshkumar et al., 2021). It also reflects that pesticide applications can be moved to late afternoon without affecting pollination services, a practice that has been reported to improve the farm-gate profits in other bee-dependent crops (Morandin & Winston, 2006).

In addition to these regional reports, the observed community structure of pollinators as found on falsa could also be explained through an ecological and trait-based perspective. The shallow, open floral structure of *G. asiatica* could also support small- to medium-bodied cavity-nesting bees, such as *Megachile cephalotes*, through its morphology, as its compact body and rapid foraging behavior enable efficient pollen transfer at early-morning temperatures. In contrast, crops with deeper or tubular corollas, such as certain solanaceous or leguminous species, often attract larger or long-tongued bees (e.g., *Xylocopa* or *Bombus* spp.) that can access concealed nectaries and ensure stigma-anther contact (Stang et al., 2009; De Luca et al., 2019). This shift in dominance from small- to large-bodied pollinators reflects a fundamental ecological rule of trait matching, where flower morphology determines the most efficient functional groups (Greenleaf & Kremen, 2006; Naghiloo et al., 2021). Thus, the differences between our findings and those of other regional crops are possibly due to differences in floral architecture rather than true inconsistencies in pollinator assemblages. Recent evidence also shows that variation in corolla depth, reward accessibility, and floral color spectra strongly correlates with pollinator body size and the number of pollinator visits per plant (Erickson et al., 2022). Therefore, assessing the correlation between floral morphology and pollinator body size is important for predicting pollination efficiency and ensuring sustainable crop yield and quality in diversified agroecosystems.

The solitary bee, *Megachile cephalotes*, showed a higher visitation rate (15 visits per minute) but spent less time per flower (2 seconds). This finding is consistent with the fast-foraging behavior seen in other cavity-nesting Megachilids (Bosch & Kemp, 2002). On the other hand, *Apis dorsata* visitation rates were intermediate, while syrphid flies stayed much longer on flowers but made fewer than 5% as many visits. A similar pattern of visitation rate and stay time has been observed in crops such as raspberry and avocado (Chacoff et al., 2012). In our study, visitation rates of different bee and fly species on *G. asiatica* showed significant differences. *Megachile cephalotes* was the most frequent bee visiting the falsa flower and was significantly higher than other bee species, including *M. hera*, *A. dorsata,* while syrphid flies had the lowest visitation rate.

Larger fruits were produced through open pollination, with increased weight, length, and width compared to caged pollination (Ozga & Reinecke, 2003; Dorcey et al., 2009). Added calcium and polyamines delivered by pollen tubes may further stiffen cell walls and delay softening. In the same region, Akram et al. (2022) reported that the maximum yield was obtained under open pollination. *M. bicolor* pollinated flower fruit weight was greater than that of other *Megachile* sp. bees (Akram et al., 2022). Another study reported that seed set increased with greater pollen deposition on the flower (Sorensen & Webber, 1997).

By day three of post-harvest, 90% of open-pollinated fruit remained marketable, compared to 65% of caged controls. Compared to caged fruit, open fruit contained 18% more soluble solids, had a 0.3-unit higher pH, and 22% lower titratable acidity. These shifts are similar to those reported in open-pollinated strawberry and apple (Klatt et al., 2014). Higher vitamin C in cage fruit reflects stress-induced antioxidant responses, which are common when seed set is low (Smirnoff, 2000).

This study was conducted in a single orchard over one growing season, providing only a limited view of a landscape where bee populations can change significantly across years (Kennedy et al., 2013). Future studies should aim to use hand-pollination at different levels to better understand how fruit size and quality respond to pollination, track bee visits using RFID tags, and measure pollen deposition to compare pollination efficiency among species, and also test shelf life under cold storage, including microbial quality and consumer preferences. Additionally, considering floral morphological data with pollinator body-size could lead to a better understanding of the trait-matching and its consequences for pollination success. Moreover, AI-based insect tracking models could also be used to determine the seasonal variation in different insect pollinator groups on a particular crop (Hakim et al., 2025). Future studies should also investigate the effect of providing artificial nesting sites and establishing conservation or floral strips near falsa orchards on overall pollination success (Haider et al., 2024; Khan et al., 2024). Overall, our findings show that early-morning visits by cavity-nesting bees, especially *Megachile* sp., lead to better-quality falsa fruit that also remain marketable for an extra day. Steps for pollinator management, including installing reed nests, avoiding pesticide sprays during bee activity times, and planting flowering plants beneath trees, could increase income per unit area.

Authors' Contributions

A.I.J.: Methodology, investigation, data curation, writing-original draft.
M.A.: Conceptualization, methodology, validation, resources, writing-original draft, project administration, funding acquisition.
F.Z.A.K: Formal analysis, writing-original draft, writing-review and editing, project administration.
A.H.: Visualization.
T.H.A.: writing-review and editing, funding acquisition.
S.A.M.: Software, Formal analysis.

All authors have read and agreed to the published version of the manuscript.

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