Agriculture, Ecosystems and Environment 377 (2025) 109258

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Bee pollination affects coffee quality, yield, and trade-offs within them

Natalia Aristizábal[a,b,*], Silvia E. Mora-Mena[c], Alejandra Martínez-Salinas[d], Adina Chain-Guadarrama[d], Danny Castillo[e], Juan B. Murillo[f], Jimmy Porras[g], Taylor H. Ricketts[a,b]

[a] Gund Institute for Environment, University of Vermont, Burlington, VT 05405, United States
[b] Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, United States
[c] Universidad de Costa Rica, Sede del Atlántico, Turrialba, Costa Rica
[d] CATIE – Centro Agronómico Tropical de Investigación y Enseñanza, Cartago, Turrialba 30501, Costa Rica
[e] El Fermentista, Tarrazú, Costa Rica
[f] TEC – Tecnológico de Costa Rica, San Carlos, Costa Rica
[g] CoopeTarrazú, San Marcos, Costa Rica

A R T I C L E I N F O

Keywords:
Agroecology
Biodiversity
Coffea arabica
Crop quality
Cup profile
Ecosystem services
Nature contributions

A B S T R A C T

Bees provide valuable pollination services by increasing crop yields. However, pollination services to crop quality – which often determines nutritional and financial value – have been less studied, particularly in tropical commodities such as coffee. Understanding how pollination affects coffee quality is critical because high-quality coffee on the specialty market fetches higher prices, which can potentially benefit farmers more than just focusing on yield alone. This study aimed to test the effects of bee pollination on coffee yield and quality and to evaluate possible trade-offs within them. We conducted bee-exclusion experiments on 30 coffee plants in the Tarrazú region of Costa Rica, controlling for several factors associated with coffee quality. At the end of the growing season, we harvested the berries and compared yield (that is, fruit set and weight) and quality (that is, the cup profiles of certified coffee tasters) among treatments. Our results indicate that bee pollination can lead to trade-offs in coffee production. Bee pollination significantly increased final fruit set by 9 % and the desired aroma scores by 2 %. However, these fruits weighed 7 % less than self-pollinated berries and displayed more body but less balance in their cup profiles. This is one of the first experimental studies to evaluate pollination services for coffee, considering not just yield but also its cup profile. We provide early evidence suggesting bee pollination improves coffee aroma, a critical quality attribute in specialty coffee. Our research emphasizes the importance of protecting or restoring bee habitats in coffee farms, which can not only improve income for coffee producers but also conserve biodiversity. Integrating these ecological insights into initiatives like 'bee-friendly' coffee production presents an innovative approach for stakeholders in the coffee supply chain and can serve as a strategic nexus of agricultural, economic, and ecological interests.

1. Introduction

Human food systems depend on pollinators. Animal pollination, the process of transferring pollen grains between flowers within and among individuals of the same species, enables reproduction in the vast majority of wild and managed plants (Klein et al., 2007; Ollerton, 2017). About 75 % of crops worldwide benefit from cross pollination by animals (i.e. bees, flies, bats, moths, wasps, birds, and other insects and mammals) (Potts et al., 2016), and bee pollination is beneficial to more than half of the leading global crops (Klein et al., 2007; Roubik, 1995). These pollination services also safeguard wild plant communities and contribute to cultural values, farm-based livelihoods, and food security (Potts et al., 2016).

Most research on crop pollination has focused on how it affects productivity metrics, such as fruit set, seed size, and yield. Fewer studies have evaluated pollination impacts on quality attributes (i.e., aroma, flavor, form, chemical composition), but growing evidence shows that pollination by bees can influence crop nutritional and commercial value (Bartomeus et al., 2014; Georg et al., 2012; Klatt et al., 2014). For instance, in strawberry crops, pollination by bees can reduce

* Corresponding author at: Gund Institute for Environment, University of Vermont, Burlington, VT 05405, United States.
E-mail address: naristizabalu@gmail.com (N. Aristizábal).

https://doi.org/10.1016/j.agee.2024.109258
Received 12 November 2023; Received in revised form 17 July 2024; Accepted 20 August 2024
Available online 30 August 2024
0167-8809/

malformations, improve commercial grade, and increase shelf life (Georg et al., 2012; Klatt et al., 2014). Pollination by bees and other insects has been shown to improve physical (i.e. shape, firmness) and chemical properties (i.e. acidity, moisture) in apple, macadamia, oil seed rape, buckwheat, and tomato crops (Atmowidi et al., 2022; Bartomeus et al., 2014; Bashir et al., 2018; Garratt et al., 2014; Kämper et al., 2021; Samnegård et al., 2019). Additionally, pollination by wild bees can also increase the uniformity of blueberry and coffee, another aspect of crop quality (Martínez-Salinas et al., 2022; Nicholson and Ricketts, 2019).

The mechanisms linking pollination and fruit quality are poorly understood, but several pathways are plausible. Adequate pollination, the amount and quality of pollen grains, can affect a plant's reproduction processes and outcomes (Stavert et al., 2020). Pollination studies in apples show that reducing pollinator diversity and visits decreases pollen tube growth, which negatively affects not only yield but also the desired shape (Grab et al., 2019; Stavert et al., 2020). Also, recent gas chromatography studies reveal that roasted coffee beans release different volatile compounds associated with sensory attributes such as aroma and flavor depending on the presence or absence of bee pollinators (Meireles et al., 2022).

Trade-offs between crop yield and quality have been documented for some crops (Culp and Harrell, 1975; Cusser and Jha, 2021). A study found that cotton plants producing more fiber had lower quality (Culp and Harrell, 1975), and apple orchards with higher crop loads had more incidences of bitter pit (Ferguson and Watkins, 2019). In coffee, studies to date have found mixed results. In Costa Rica, no trade-offs were found between coffee yield and quality at varying distances from the forest (Ricketts et al., 2004) or fertilizer applications (Castro-Tanzi et al., 2012). However, one study in Ethiopia found that coffee under the forest canopy produced better quality of roasted beans, although these less intensive practices tend to yield less (Geeraert et al., 2019). Because crop yield and quality outcomes depend on a variety of factors, it is critical to understand the role pollination plays in potential trade-offs between crop yield and quality.

Coffee is one of the most valued and studied crops, making it an ideal system for investigating the relationships between pollination, yield, and quality. In the two most commercialized coffee varieties, self-compatible *Coffea arabica* and self-incompatible *Coffea canephora*, pollination by managed honeybees and wild bees are well known to increase yield (Chain-Guadarrama et al., 2019). In shaded coffee systems, diverse bee communities have reported an increase in yield of up to 95 % in *C. canephora* (Klein et al., 2003). Even in large and conventionally managed farms, forest-based wild bees have been shown to enhance *C. arabica* yields by 11 % and up to 20 % (González-Chaves et al., 2020; Martínez-Salinas et al., 2022; Ricketts et al., 2004). However, none of these studies has tested whether these yield benefits from bee pollination come with a trade-off in the quality of the coffee beans.

Differentiating between the specialty and commodity markets, coffee quality can profoundly influence farmers' incomes, potentially more so than yields. For instance, in the commodity market, the average price for conventional *C. arabica* in 2021 was $4.51 per kg (World Bank, 2021). Conversely, in the specialty coffee market, coffee sold at the prestigious international auction, Cup of Excellence, fetches up to 20 times the price of the commodity–an average of $61.7 per kg and peaking at $1102.3 per kg (Fischer, 2021). Moreover, coffee prices are projected to increase by 19 % with each additional point in the cup profile score (Traore et al., 2018). The cup profile refers to the comprehensive sensory evaluation of coffee, including ten attributes such as cup balance, flavor, and aroma, which are assessed by expert tasters using standardized protocols. These attributes are crucial determinants of coffee quality and play a major role in consumer preferences and market prices (Gumecindo-Alejo et al., 2021). Therefore, when farmers can tap into these specialty markets, the emphasis on improving and maintaining coffee quality could be more beneficial to their income than focusing solely on yield (Gumecindo-Alejo et al., 2021, ICAFE, 2022).

To our knowledge, only one study has investigated the effects of pollination on coffee quality, providing preliminary evidence that pollination improved berry size and cup profile scores (Karanja et al., 2013; Torrez et al., 2023). Other studies have found higher coffee quality is associated with altitude, slope exposure, local shade, and management (Avelino et al., 2005; Castro-Tanzi et al., 2012; Decazy et al., 2003; Muschler R.G., 2001; Tolessa et al., 2017; Torrez et al., 2023). Since coffee is a crop that provides livelihood to an estimated 1.68 million farmers in Latin America and many millions worldwide (Harvey et al., 2021; Jha et al., 2011), it is critical to better understand the effects of pollination services by bees on coffee quality.

In this study, we examine the relationship between bee pollination services and coffee by evaluating fruit set, fruit weight, and the quality attributes of roasted coffee beans, including flavor and aroma. Using standard quality evaluations and controlling for other factors, we conducted the first rigorous and well-replicated field experiments to quantify the effects of bee pollination on coffee's cup profile and assess potential trade-offs in quality attributes and traditional yield measures. We test three hypotheses: 1) Bee pollination does not affect coffee production. 2) Bee pollination improves coffee yield and quality. 3) Bee pollination improves coffee yield but not quality.

2. Materials and methods

2.1. Study site

The study was carried out in Tarrazú, Costa Rica, a region known for its gourmet high-altitude coffee (Fig. 1). The average annual precipitation in the region ranges from 1953 to 2048 mm, and the average temperature is between 17.5 and 20 ° C. Unlike other coffee growing regions in Latin America, Tarrazú is prospering due to its high quantity and quality of production (ICAFE, 2022) and where coffee is mostly exported or sold in the specialty market. For example, in the last five years, several Tarrazú farms have placed first at the national Cup of Excellence. In 2018, a farm in this region auctioned a kilogram of its coffee for $662.3, setting a new national record (Daily Coffee News. Brown, Nick., 2018).

We established our field experiments on a 90-ha farm that belongs to CoopeTarrazú, Costa Rica's largest coffee cooperative, located 1400 m above sea level (9°39'46.4 "N, 84°02'02.4 "W). CoopeTarrazú, and its nearly 5000 associated farmers throughout the region, generate 15 % of the coffee produced in the country. CoopeTarrazú's farm grows different coffee varieties under similar shade types in about 50 % of its area. Our experimental plot, known as *El Tirrá*, is a 2.5 ha area dedicated solely to the growth of *C. arabica*, specifically the *Catuaí rojo* variety, managed under common practices for the region (Fig. S1). These practices include maintaining a simple shade made up of flowering plants from the *Musa* genus and *Erythrina poeppigiana*, also known as *poró*. Furthermore, management includes an annual treatment against root pests, three treatments per year for fungal diseases, and one application of calcitic lime.

By conducting these experiments on a single experimental farm, we were able to isolate pollination effects by controlling most other factors that may influence the quality, including coffee variety, cropping management, plant age, landscape factors, and elevation (Ahmed et al., 2021; Avelino et al., 2005; Castro-Tanzi et al., 2012; Decazy et al., 2003; Muschler R.G., 2001; Nicholson et al., 2017; Tolessa et al., 2017).

2.2. Pollination experiments

Before the 2021 flowering season, we selected 30 neighboring coffee plants in the middle of the *El Tirrá* plot, arranging them as replicates in six rows with five plants spaced every 5–10 m (Fig. 1). Each of these plants, aged about 15 years, exhibited similar health conditions. On every plant, we identified four comparable branches positioned 1.5 m above the ground and randomly assigned two of these branches as

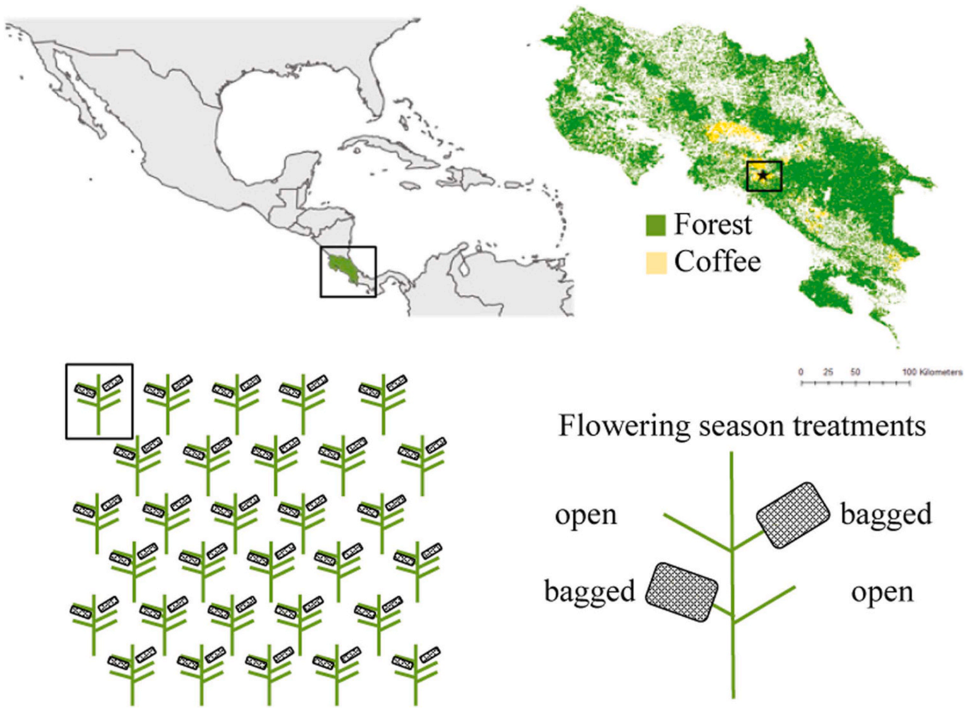

Fig. 1. Study site in Tarrazú, Costa Rica and experimental design involving 30 plants, two treatments, open or bagged, and two branches per treatment.

control and the remaining two as the exclusion treatment (Fig. 1). We counted the flowers on each branch before the onset of the main coffee bloom, which typically occurs between March and April depending on the elevation in the region.

During the peak bloom period in the experimental plot, March 19–22, 2021, the control branches, hereafter referred to as *'open'*, were exposed to ambient pollination. In contrast, we used fine gauze bags with a 1 mm mesh to prevent bee pollination on the exclusion branches, hereafter referred to as *'bagged'*, following the methodology of Martínez-Salinas et al. (2022).

The gauze bags remained in place for one week while vital flowers were blooming. To assess whether our gauze bags deteriorated branch health, we counted the total number of leaves in all experimental branches before setting the gauze bags and a month after removing them (Fig. S2).

2.3. Measuring coffee productivity

To evaluate differences in productivity between pollination treatments, we harvested, counted, and weighed berries from all experimental branches between December 2021 and January 2022 when the berries reached peak ripeness. We calculated the final fruit set for each branch by dividing the number of fruits harvested by the initial number of flowers counted. Within 24 hours post-harvest, we combined all the berries from a single branch, weighed them as a collective group, and calculated the average fresh weight per berry for that branch.

2.4. Evaluating coffee quality

After measuring fruit set and fruit weight, we pooled the coffee berries from the 30 plants at the treatment level and manually peeled and sun-dried the berries, following a *honey* process (drying them with the pulp) (Poltronieri and Rossi, 2016). We monitored the berries daily and when the berries reached 10–12 % humidity, we divided them into the minimum roasting weight requirement at CoopeTarrazú's facilities (120 g), resulting in a total of four samples per treatment. We coded the experimental label of the samples and submitted them for blind quality evaluations by two CoopeTarrazú coffee cuppers certified by the Specialty Coffee Association of America (SCAA), who roasted, ground, and brewed all eight samples separately under identical conditions and scored quality attributes.

The SCAA coffee evaluations protocol involves a detailed sensory assessment where each cupper evaluates the coffee using a set scale to measure ten quality attributes. Specifically, for our study, each of the two certified cuppers evaluated four samples from each treatment. Consistent with the SCAA standards, they assessed each sample across five cups to ensure reliability and uniformity of results. The quality attributes are a combined score for dry fragrance and wet aroma (hereafter, aroma), flavor, aftertaste, acidity, body, balance, overall, uniformity, clean cup, and sweetness–contributing to an additive final score out of 100 (hereafter, final score) (SCAA, 2015). Higher scores for each attribute, and thus the final score, are more desired. Both cuppers evaluated the same samples independently to compare assessments across individuals and determine consistency in scoring. To avoid any bias in the tasting process, the arrangement of bee-pollinated and self-pollinated coffee samples was coded (blind evaluations) and randomized among the cuppers. This approach allowed each sample to be assessed twice, providing four independent replicates for each treatment. Additionally, the cuppers evaluated qualitative descriptor notes from the coffee taster's flavor wheel that contains 85 notes (e.g., chocolate, herbal). For our analyses (details next), we used seven of the sensory attributes, the final score, and qualitative descriptors to compare the quality of the coffee between treatments.

2.5. Data analysis

We compared productivity measures between treatments by performing generalized linear mixed models using the 'lme4' package R version 1.1–27.1 (Bates et al., 2015). We modeled the effect of pollination on the final fruit set using a binomial distribution with the 'glmer' function and on the average fruit weight using a Gaussian distribution with the 'lmer' function. In both models, we used treatment as the only fixed effect and "plant ID" as a random effect to control for treatment replicates ($n = 30$). For the models explaining quality traits, we also used treatment as the only fixed effect and "plant ID" as a random effect to control for treatment replicates (n = 8). We tested incorporating "cupper ID" as a second random effect, but these models yielded consistent results without it. Consequently, we retained the most parsimonious model that only included "plant ID" as a random effect. To assess differences between the cuppers, we conducted an analysis of variance using the 'aov' function from the 'stats' package in R (version 4.0.3). No significant differences were detected between the cuppers for any variable.

To analyze quantitative quality metrics, we performed an analysis of variance with the 'aov' function of the 'stats' package R (version 4.0.3). Additionally, we used a Multiple Factor Analysis (MFA) with the FactoMineR R package (version 2.7) to understand and visualize the differences between pollination groups (Le et al., 2008). The seven quality scores included in the MFA were aroma, flavor, aftertaste, acidity, body, balance, overall, and final score.

Next, we transformed qualitative descriptors (eg, "caramel" or "chocolate" notes) into count data based on the frequency that each term was used during cupping. We used an MFA to test for differences in this count data between groups. The descriptors included in the MFA were "caramelo," "chocolate," "dulce," "citrico," "herbal," "miel," "semillas," "cacao," "almendras," "hojas verdes," and "tapa dulce."

3. Results

3.1. Final fruit set and fruit weight

Bee pollination significantly increased the final fruit set from 0.39 to 0.43 (representing an increase of 8.5 %, $P < 0.001$) (Fig. 2a) and decreased the average fruit weight from 1.60 g to 1.49 g (representing a decrease of 7.4 %, $P = 0.04$) (Fig. 2b).

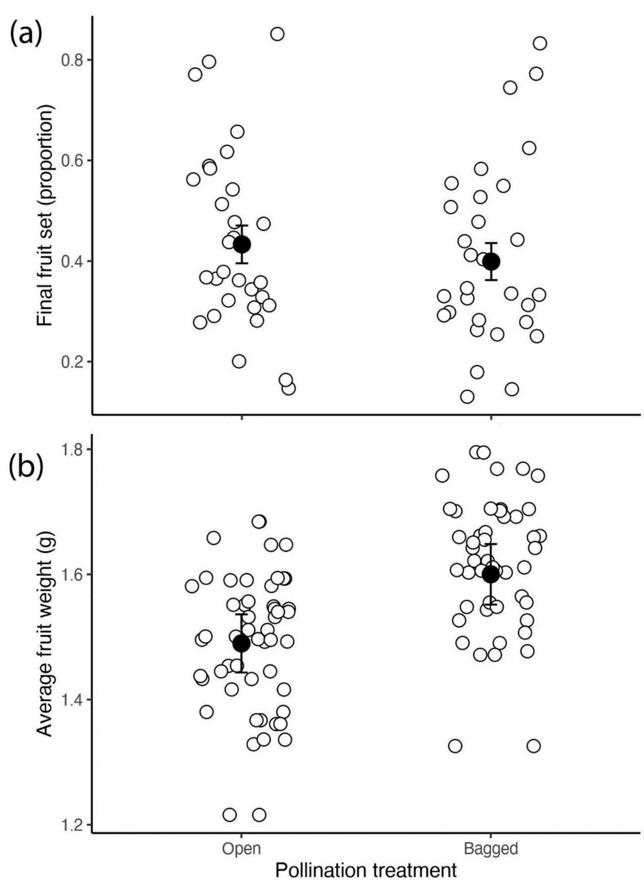

Fig. 2. Differences between treatments (open vs bagged) (n = 30) in (a) final fruit set – the proportion of initial flowers that became harvestable berries ($P < 0.001$) and (b) average fresh weight per branch ($P = 0.04$). The means are represented by black dots, and the standard errors are represented by bars.

3.2. Quality metrics

All eight samples tested for quality yielded a final cup profile score ranging from 80 to 82, which the SCAA classifies as 'very good – specialty coffee'. The analysis of variance highlighted quantitative differences in the aroma and balance scores (P = 0.04, Fig. 3a-b). We found that bee pollination enhanced coffee aroma by 2 % (P = 0.04, Fig. 3a) and reduced the cup's balance by 2 % (P = 0.04, Fig. 3b). However, all other quality attributes showed no differences between the groups (Fig. 4c-h).

In addition, the Multiple Factor Analysis (MFA) showed that bee pollination was significantly and positively correlated with aroma and body ($P = 0.02$), while negatively correlated with balance ($P = 0.02$, Fig. 4a-b). The MFA explained 64 % of the quantitative quality data; Dim1 (44 %) was correlated with the final score ($P < 0.001$), aftertaste ($P < 0.001$), and the aroma ($P < 0.001$, Fig. 4c), and Dim2 (20 %) was correlated with the balance ($P < 0.001$), aroma ($P < 0.05$), and the body ($P < 0.01$, Fig. 4d) of the cup profiles.

For the qualitative descriptors, the MFA did not show any significant groupings (Fig. S3). The frequency of descriptive words was comparable between treatments. Words associated with positive notes such as chocolate and caramel were the most common for both groups. However, bee pollinated samples had one-third the number of low-quality descriptors like 'herbal' and 'green leaves' (Fig. S4).

4. Discussion

For the first time in a replicated field experiment, our results demonstrate that bee pollination significantly impacts both the production and quality of roasted coffee. Specifically, we observed tradeoffs both among yield metrics and among quality profile attributes. Bee-pollinated coffee plants produced more fruits with higher quality scores for aroma and body, but they weighed less and scored lower on balance.

Coffee quality, as assessed by certified cuppers, exhibited comparable scores across bee pollinated and self-pollinated coffee, except for aroma, body, and balance. Our experiments suggest that bee pollination may play a role in shaping aroma—a desired coffee quality attribute. Bee pollinated coffee exhibited a 2 % enhancement in the aroma of roasted beans but showed a 2 % decline in balance within the cup profile. These subtle shifts in aroma and balance have significant implications for producers in the specialty market, potentially increasing prices by up to 6.5 % for desired aromas and decreasing them by 3 % for imbalanced profiles (Traore et al., 2018; Wilson and Wilson, 2014).

As shown by our findings and prior studies (Karanja et al., 2013; Meireles et al., 2022a), the presence of bees significantly enhances specific coffee quality attributes, such as aroma and balance. This finding aligns with a study in Ethiopia wherein coffee cultivated under forest canopy exhibited higher quality attributes such as flavor, body, and final score, among others (Geeraert et al., 2019). Forests foster more diverse bee habitats near coffee farms, which in turn support diverse bee communities (Geeraert et al., 2019b) and lead to higher coffee yields (González-Chaves et al., 2022). While these studies focus on pollination, it is important to recognize factors that influence coffee production and quality beyond bee pollination such as local environmental conditions and agricultural practices could also play influential roles (Avelino et al., 2005; Castro-Tanzi et al., 2012; Decazy et al., 2003; Muschler R.G., 2001; Tolessa et al., 2017; Torrez et al., 2023).

A critical component of assessing coffee quality beyond quantitative scores is identifying the symbolic attributes that characterize the coffee's geographic origins (Traore et al., 2018). According to Coope-Tarrazú's cuppers, the symbolic attributes of a Tarrazú-origin coffee are high acidity, medium body, and well-balanced flavors of caramel and

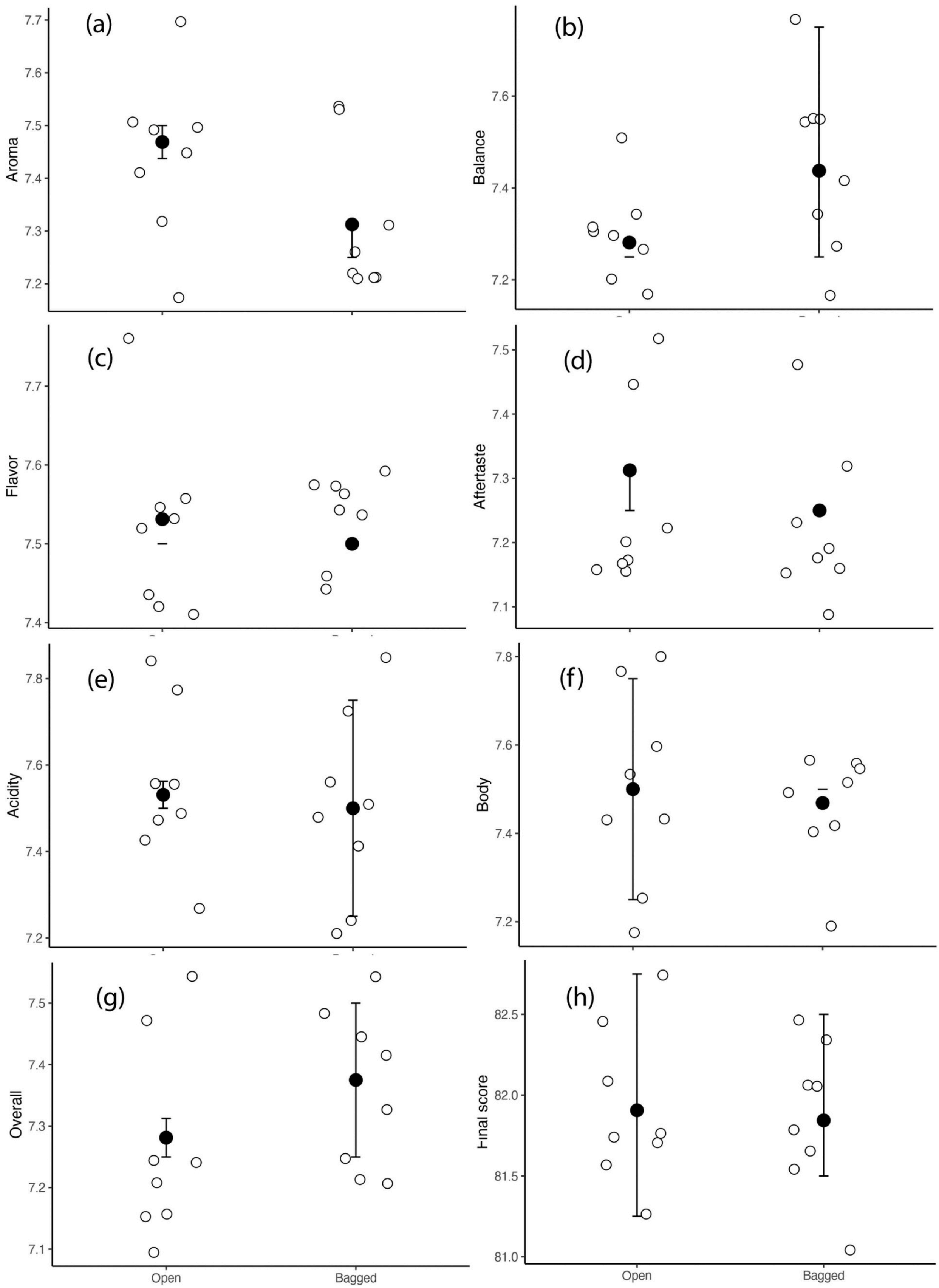

Fig. 3. Differences between pollination treatments (open vs baaged) for quantitative attributes of coffee quality. (a) aroma ($P = 0.04$), (b) balance ($P = 0.04$), (c) flavor, (d) aftertaste, (e) acidity, (f) body, (g) overall, and (h) final score. The black dots represent the means, the bars standard errors, and the asterisks $P < 0.05$. Each of the four samples was evaluated by two certified coffee cuppers, who scored each quality attribute between 0 and 10 (n = 8).

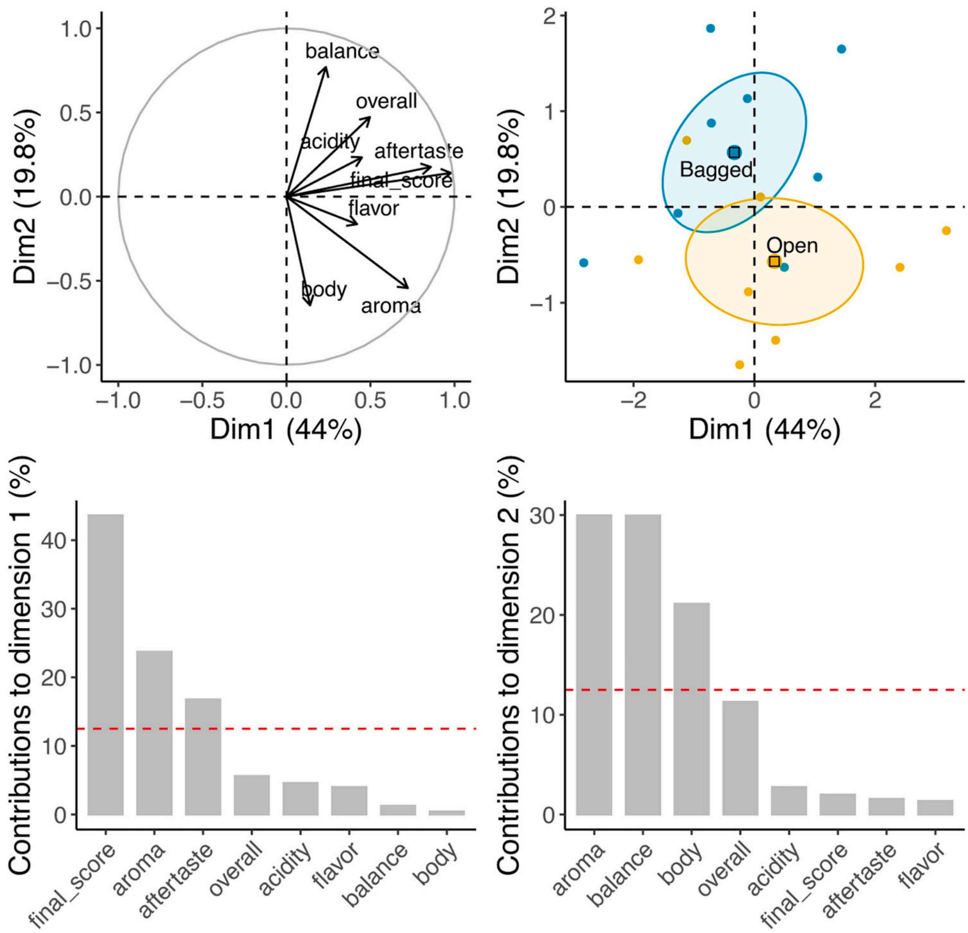

Fig. 4. Multiple factor analysis (MFA) describing the effect of bee pollination on quantitative scores of coffee quality. a) Correlations of quality attributes in MFA dimensions 1 and 2. b) Similarity of quality variables by treatment, in which more similar profiles are plotted closer together. The ellipses show 0.95 confidence intervals. The contributions of the quality attributes to the c) first and d) second MFA dimensions. The dashed line shows the expected average value if all attributes contributed equally.

chocolate. In our study, all samples were characterized with these flavor descriptors, but bee-pollinated samples had three times fewer descriptors associated with lower quality coffee. Specific qualitative aroma and flavor descriptors can influence auction prices and buyers' preferences more than other attributes of the cup profile attributes like aftertaste (Traore et al., 2018). For instance, fruity and floral notes increase prices by 40 % and 6.78 %, respectively (Traore et al., 2018). Understanding the effects of bee pollination on qualitative descriptors could provide new opportunities for farmers in these premium markets.

The ecological mechanisms linking pollination to crop quality remain relatively unknown (see (Geeraert et al., 2019; Meireles et al., 2022). Research on plums has revealed that physiological (that is, pollen tube growth) and molecular (that is, gene expression and metabolic pathways) mechanisms affect fruit set and fruit quality characteristics (Deng et al., 2022). In macadamia orchards, pollen genotype has been shown to be more important than pollen quantity in improving nutritional quality (Kämper et al., 2021). In coffee, research has typically focused on the quality impacts of post-harvest factors such as roasting techniques and storage conditions (Farah and Donangelo, 2006; Waters et al., 2017). However, a recent study that used gas chromatography and mass spectrometry showed that bee pollination increases the number of desired volatile compounds in roasted coffee, specifically compounds perceived by the sense of smell like pyrazines, pyrroles, pyridines, alcohols and phenols, and sulfur (Meireles et al., 2022). These results are consistent with our findings of improved aroma with bee pollination. If pollination affects the volatile compounds of a plant and is perceived in the aroma of roasted coffee (Meireles et al., 2022), maintaining pollinator habitat can improve the quality of coffee and benefit farmers beyond the known increases in yield.

Our research highlights potential trade-offs within different yield and quality metrics from bee pollination in coffee. While bee pollinated coffee showed higher fruit set along with enhanced aroma and body, coffee berries weighed less and its cups scored lower in balance. Previous research on the effects of crop pollination on quantity and quality trade-offs is scarce (but see Bartomeus et al., 2014). However, another study exploring bee pollination's impact on coffee reported slightly different findings, suggesting bee pollinated coffee produced heavier berries in addition to better cup quality scores (Karanja et al., 2013). These contrasting results could indicate that depending on the degree of pollination or management, coffee plants may produce more berries with less balanced cup profiles or smaller berries with better aroma.

Although our findings indicate a significantly higher fruit set in bee-pollinated *C. arabica* plants, similar studies typically report fruit set increments between 9 % and 50 % (González-Chaves et al., 2020; Martínez-Salinas et al., 2022; Ricketts et al., 2004). Partly contrasting with our study, a previous experiment on Costa Rican coffee farms found that bee pollination increases not only fruit set but also fruit weight by 4.2 % (Martínez-Salinas et al., 2022). However, this study was conducted on less intensively managed farms. In our study, CoopeTarrazú's plot receives an abundance of four fertilizer applications a year, and perhaps these compensate for physiological, chemical, or molecular processes that would be otherwise catalyzed by bee pollination. According to the resource availability hypothesis for plant defense and reproduction (Gianoli and Salgado-Luarte, 2017; Tuller et al., 2018), a surplus of resources through frequent fertilization could mean that the effects of bee pollination on the fruit set would be masked or diluted.

Our study reveals previously unknown benefits of bee pollination for coffee quality, presenting a valuable angle for nature conservation. Bee pollination not only increases earnings for coffee farmers tapping into specialty markets but also elevates coffee quality for consumers and enhances nature conservation through bee habitat maintenance or restoration in and near coffee farms. Certifications like organic or fair-trade labels, which often lead to premium prices (Richards et al., 2016), may not significantly improve the economic conditions of smallholder farmers (Dietz et al., 2019). However, they are valued by consumers who are willing to pay up to 15 % more for certified coffee (Traore et al., 2018), indicating that environmental and social standards can potentially offset the costs associated with yield reductions or habitat restoration efforts. Unlike other certifications, a 'bee-friendly' label could further emphasize these values, enhancing consumer appeal. Continued research in this area is crucial, as promoting pollinator habitats could become a sustainable strategy for coffee stakeholders, balancing ecological benefits with economic gains. It remains essential to analyze the economic trade-offs between the benefits provided by bee pollination and the costs of achieving these standards to determine if the premiums can adequately compensate for any yield losses.

Future studies can build on our work in several ways to better define the effect of bee pollination on coffee quality. First, additional studies on *C. canephora*, which depends on cross-pollination by bees, are likely to show even stronger effects. Second, replicating these experiments on plots under different management types would help to clarify to what extent fertilizers could mask the effect of pollination on the development and quality characteristics of berries. Third, a promising avenue for further enhancing the robustness of our findings is to include more cuppers in the tasting panels. By incorporating a larger number of cuppers in a single cupping trial, we can achieve even more nuanced statistical differentiation between treatments. Moreover, although *honey* processes are preferred by buyers (Traore et al., 2018), CoopeTarrazú's coffee tasters suggested that a *washed* process could allow for clearer differentiation of quality. Therefore, conducting experiments with various processes might yield further insights. Additionally, future research should include an analysis of the economic impact of how yield-quality trade-offs might offset any potential yield reductions from sustainable practices, which would be essential to scale up the impact of certification schemes and help guide policy and farm management decisions (Verburg et al., 2019). Finally, a better understanding of the chemical signaling and other potential mechanisms linking pollination with fruit reproduction was beyond the scope of this study but an important next step.

Our results underscore the vital need to explore further the relationship between bee pollination and coffee production, moving beyond just yield metrics. It is essential to pay special attention to quality attributes with the potential to have a disproportionate effect on coffee prices such as aroma and flavor. Improving cup profile scores can enable coffee farmers to enter premium markets, thus boosting their profits. Therefore, more research is needed to understand the mechanisms involved in pollination efficiency and the biotic interactions influencing coffee yield and quality. These studies could continue to explore how bee pollination benefits coffee farm livelihoods and bee conservation, identifying pathways to achieve true integration of agricultural production and conservation goals.

Author contributions

Natalia Aristizábal, Alejandra Martínez-Salinas, Adina Chain-Guadarrama, Jimmy Porras, and Taylor Ricketts designed the research; Natalia Aristizábal, Silvia E. Mora-Mena, Danny Castillo, and Juan Bosco Murillo collected the data; Natalia Aristizábal analyzed the data and led the writing of the manuscript. All authors contributed significantly to the drafts and gave their final approval for publication. The team that conducted this study includes authors from Colombia, Costa Rica, Nicaragua, Mexico, and the United States, and it is made up of scientists, farmers, engineers, and agronomists in collaboration among the Gund Institute, CATIE, and CoopeTarrazú (coffee cooperative). All authors participated early in the process and efforts were made to include relevant needs of CoopeTarrazú in the study design.

Data archival

The data will be archived on figshare.

CRediT authorship contribution statement

Alejandra Martínez-Salinas: Writing – review & editing, Resources, Investigation, Conceptualization. **Silvia Elena Mora-Mena:** Writing – review & editing, Methodology, Investigation. **Danny Castillo:** Writing – review & editing, Methodology. **Adina Chain-Guadarrama:** Writing – review & editing, Resources, Investigation, Conceptualization. **Jimmy Porras:** Writing – review & editing, Resources, Conceptualization. **Juan Bosco Murillo:** Writing – review & editing, Methodology. **Taylor H Ricketts:** Writing – review & editing, Supervision, Resources, Investigation, Conceptualization. **Natalia Aristizábal:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

We thank CoopeTarrazú for allowing us to conduct research on their farm and cupping facilities. Special thanks to CoopeTarrazú's coffee tasters, Jairo Rojas and Jesús Elizondo Valerio, and the entire team at CeDAO (Centro para el Desarrollo de Alternativas Orgánicas) for intellectual and logistical support. We also thank our two anonymous reviewers as well as Sarah Cusser for reviewing an earlier version of this manuscript, Sergio Vilchez Mendoza for statistical assistance, Mariluz Fuentes and Aura Alonso-Rodríguez for field assistance, and CATIE for institutional support. This work was supported by an Apis Fund award from the Gund Institute for Environment at the University of Vermont. N.A. was supported by the NSF Quantitative and Evolutionary STEM Training (QuEST) Program (DGE-1735316) and the Gund Institute for Environment.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109258.

References

Ahmed, S., Brinkley, S., Smith, E., Sela, A., Theisen, M., Thibodeau, C., Cash, S.B., 2021. Climate change and coffee quality: systematic review on the effects of environmental and management variation on secondary metabolites and sensory attributes of coffea arabica and coffea canephora. Front. Plant Sci. *12*, 1–20. https://doi.org/10.3389/fpls.2021.708013.

Atmowidi, T., Prawasti, T.S., Rianti, P., Prasojo, F.A., Pradipta, N.B., 2022. Stingless bees pollination increases fruit formation of strawberry (Fragaria x annanassa Duch) and melon (Cucumis melo L.). Trop. Life Sci. Res 33 (1), 43–54. https://doi.org/

10.21315/tlsr2022.33.1.3. Epub 2022 Mar 31. PMID: 35651645; PMCID: PMC9128655.
Avelino, J., Barboza, B., Araya, J.C., Fonseca, C., Davrieux, F., Guyot, B., Cilas, C., 2005. Effects of slope exposure, altitude and yield on coffee quality in two altitude terroirs of Costa Rica, Orosi and Santa María de Dota. J. Sci. Food Agric. *85* (11), 1869–1876. https://doi.org/10.1002/jsfa.2188.
Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Bommarco, R., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ (1), 1–20. https://doi.org/10.7717/peerj.328.
Bashir, M.A., Alvi, A.M., Khan, K.A., Rehmani, M.I.A., Ansari, M.J., Atta, S., Tariq, M., 2018. Role of pollination in yield and physicochemical properties of tomatoes (Lycopersicon esculentum). Saudi J. Biol. Sci. *25* (7), 1291–1297. https://doi.org/10.1016/j.sjbs.2017.10.006.
Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 https://doi.org/10.18637/jss.v067.i01.
Castro-Tanzi, S., Dietsch, T., Urena, N., Vindas, L., Chandler, M., 2012. Analysis of management and site factors to improve the sustainability of smallholder coffee production in Tarrazú, Costa Rica. Agric., Ecosyst. Environ. *155*, 172–181. https://doi.org/10.1016/j.agee.2012.04.013.
Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., Ricketts, T.H., 2019. Ecosystem services by birds and bees to coffee in a changing climate: a review of coffee berry borer control and pollination. Agric., Ecosyst. Environ. *280*, 53–67. https://doi.org/10.1016/J.AGEE.2019.04.011.
Culp, T.W., Harrell, D.C., 1975. Influence of lint percentage, boll size, and seed size on lint yield of upland cotton with high fiber strength 1. Crop Sci. *15* (6), 741–746. https://doi.org/10.2135/cropsci1975.0011183x001500060001x.
Cusser, S., Jha, S., 2021. No tradeoff in fiber quality with increased cotton yield due to outcross pollination. Sustainability *13* (11), 6079. https://doi.org/10.3390/su13116079.
Daily Coffee News. Brown, Nick, 2018. Costa Rican Gesha Shatters Cup of Excellence Record at $300 Per Pound." https://dailycoffeenews.com/2018/07/11/costa-rican-gesha-shatters-cup-of-excellence-record-at-300-per-pound/ (Accessed November 2022).
Decazy, F., Avelino, J., Guyot, B., Perriot, J.J., Piñeda, C., Cilas, C., 2003. Quality of different honduran coffees in. J. Food Sci. 68, 2356–2361. https://doi.org/10.1111/j.1365-2621.2003.tb05772.x.
Farah, A., Donangelo, C.M., 2006. Phenolic compounds in coffee. Braz. J. Plant Physiol. https://doi.org/10.1590/S1677-04202006000100003.
Ferguson, I.B., Watkins, C.B., 2019. Crop load affects mineral concentrations and incidence of bitter pit in `cox's orange pippin' apple fruit. J. Am. Soc. Hortic. Sci. *117* (3), 373–376. https://doi.org/10.21273/jashs.117.3.373.
Fischer, E.F., 2021. Quality and inequality: creating value worlds with Third Wave coffee. Socio-Econ. Rev. *19* (1), 111–131. https://doi.org/10.1093/ser/mwz044.
Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C., Potts, S.G., 2014. Avoiding a bad apple: insect pollination enhances fruit quality and economic value. Agric. Ecosyst. Environ. *184*, 34–40. https://doi.org/10.1016/j.agee.2013.10.032.
Geeraert, L., Berecha, G., Honnay, O., Aerts, R., 2019. Organoleptic quality of Ethiopian Arabica coffee deteriorates with increasing intensity of coffee forest management. J. Environ. Manag. *231*, 282–288. https://doi.org/10.1016/j.jenvman.2018.10.037.
Georg, A., Maj, R., Smith, H.G., 2012. Organic farming improves pollination success in strawberries. PloS One *7* (2), e31599. https://doi.org/10.1371/Citation.
Gianoli, E., Salgado-Luarte, C., 2017. Tolerance to herbivory and the resource availability hypothesis. Biol. Lett. 13 https://doi.org/10.1098/rsbl.2017.0120.
González-Chaves, A., Carvalheiro, L.G., Garibaldi, L.A., Paul Metzger, J., 2022. Positive forest cover effects on coffee yields are consistent across regions. J. Appl. Ecol. 59, 330–341. https://doi.org/10.1111/1365-2664.14057.
González-Chaves, A., Jaffé, R., Metzger, J.P., Kleinert, A, de M.P., 2020. Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. Landsc. Ecol. 35, 1841–1855. https://doi.org/10.1007/s10980-020-01061-1.
Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science *363* (6424), 282–284. https://doi.org/10.1126/science.aat6016.
Gumecindo-Alejo, A.L., Sánchez-Landero, L.A., Ortiz-Ceballos, G.C., Cerdán-Cabrera, C. R., Alvarado-Castillo, G., 2021. Factors related to coffee quality, based on the "cup of excellence" contest in Mexico. Coffee Sci. *16* https://doi.org/10.25186/.v16i.1887.
Harvey, C.A., Pritts, A.A., Zwetsloot, M.J., Jansen, K., Pulleman, M.M., Armbrecht, I., Valencia, V., 2021. Transformation of coffee-growing landscapes across Latin America. A review. Agron. Sustain. Dev. *41* (5), 1–19. https://doi.org/10.1007/S13593-021-00712-0/TABLES/3.
ICAFE. Instituto del Café de Costa Rica. "El Mejor Café del Mundo." https://www.icafe.cr/nuestro-cafe/el-mejor-cafe-del-mundo/ (accessed November 2022.
Jha, S., Bacon, C.M., Philpott, S.M., Rice, R.A., Méndez, V.E., & Läderach, P. (2011). A Review of Ecosystem Services, Farmer Livelihoods, and Value Chains in Shade Coffee Agroecosystems. doi: 10.1007/978-94-007-1309-3_4.
Kämper, W., Trueman, S.J., Ogbourne, S.M., Wallace, H.M., 2021. Pollination services in a macadamia cultivar depend on across-orchard transport of cross pollen. J. Appl. Ecol. *58* (11), 2529–2539. https://doi.org/10.1111/1365-2664.14002.
Karanja, R.H.N., Njoroge, G.N., Kihoro, J.M., Gikungu, M.W., Newton, L.E., 2013. The role of bee pollinators in improving berry weight and coffee cup quality. Asian J. Agric. Sci. 5, 52–55. https://doi.org/10.19026/ajas.5.4841.
Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., Tscharntke, T., 2014. Bee pollination improves crop quality, shelf life and commercial value. Proc. R. Soc. B Biol. Sci. 281 https://doi.org/10.1098/rspb.2013.2440.
Klein, Alexandra Maria, Steffan-Dewenter, I., Tscharntke, T., 2003. Pollination of Coffea canephora in relation to local and regional agroforestry management. J. Appl. Ecol. 40, 837–845 https://doi.org/10.1046/j.1365-2664.2003.00847.x.
Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. *274* (1608), 303–313. https://doi.org/10.1098/rspb.2006.3721.
Le, Sebastien, Julie Josse, Francois Husson, 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25 (1), 1–18. https://doi.org/10.18637/jss.v025.i01.
Martínez-Salinas, A., Chain-Guadarrama, A., Aristizábal, N., Vilchez-Mendoza, S., Cerda, R., Ricketts, T.H., 2022. Interacting pest control and pollination services in coffee systems. Proc. Natl. Acad. Sci. U. S. A *119* (15), 1–7. https://doi.org/10.1073/pnas.2119959119/-/DCSupplemental.Published.
Meireles, D.A.L., Valdez, A.S.B., Boroski, M., Augusto, S.C., Toci, A.T., 2022. Effects of pollination on the composition of volatile compounds in Coffea arabica L. J. Sci. Food Agric. https://doi.org/10.1002/jsfa.11769.
Muschler, R.G., 2001. Shade improves coffee quality in a sub-optimal coffee-zone of Costa Rica. Agrofor. Syst. *85*, 131–139.
Nicholson, C.C., Koh, I., Richardson, L.L., Beauchemin, A., Ricketts, T.H., 2017. Farm and landscape factors interact to affect the supply of pollination services. Agric. Ecosyst. Environ. 250, 113–122. https://doi.org/10.1016/j.agee.2017.08.030.
Nicholson, C.C., Ricketts, T.H., 2019. Wild pollinators improve production, uniformity, and timing of blueberry crops. Agric. Ecosyst. Environ. *272*, 29–37. https://doi.org/10.1016/j.agee.2018.10.018.
Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation. annurev-ecolsys-110316-022919 Annu. Rev. Ecol. Evol. Syst. *48* (1). https://doi.org/10.1146/annurev-ecolsys-110316-022919.
Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588.
Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. Proc. Natl. Acad. Sci. USA *101* (34), 12579–12582. https://doi.org/10.1073/pnas.0405147101.
Roubik, D.W., 1995. Pollination of cultivated plants in the tropics. Agric. Serv. Bull. *118*.
Samnegård, U., Hambäck, P.A., Smith, H.G., 2019. Pollination treatment affects fruit set and modifies marketable and storable fruit quality of commercial apples. R. Soc. Open Sci. *6* (12) https://doi.org/10.1098/rsos.190326.
SCAA (2015) "Cupping specialty coffee." http:// www.scaa.org/?page=resources&d=cupping- protocols (accessed November 7, 2023).
Stavert, J.R., Bailey, C., Kirkland, L., Rader, R., 2020. Pollen tube growth from multiple pollinator visits more accurately quantifies pollinator performance and plant reproduction. Sci. Rep. *10* (1), 1–9. https://doi.org/10.1038/s41598-020-73637-5.
Tolessa, K., D'heer, J., Duchateau, L., Boeckx, P., 2017. Influence of growing altitude, shade and harvest period on quality and biochemical composition of Ethiopian specialty coffee. J. Sci. Food Agric. *97* (9), 2849–2857. https://doi.org/10.1002/jsfa.8114.
Torrez, V., Benavides, C., Johanna, F., Chinwe, J., Speranza, I., 2023. Ecological quality as a coffee quality enhancer. a review. Agron. Sustain. Dev. *43* (19), 1–34. https://doi.org/10.1007/s13593-023-00874-z.
Traore, T.M., Wilson, N.L.W., Fields, D., 2018. What explains specialty coffee quality scores and prices: a case study from the cup of excellence program. J. Agric. Appl. Econ. *50* (3), 349–368. https://doi.org/10.1017/aae.2018.5.
Tuller, J., Marquis, R.J., Andrade, S.M.M., Monteiro, A.B., Faria, L.D.B., 2018. Trade-offs between growth, reproduction and defense in response to resource availability manipulations. PLoS One 13. https://doi.org/10.1371/journal.pone.0201873.
Waters, D.M., Arendt, E.K., Moroni, A.V., 2017. Overview on the mechanisms of coffee germination and fermentation and their significance for coffee and coffee beverage quality. Crit. Rev. Food Sci. Nutr. 57, 259–274. https://doi.org/10.1080/10408398.2014.902804.
Wilson, A.P., Wilson, N.L.W., 2014. The economics of quality in the specialty coffee industry: Insights from the cup of excellence auction programs. Agric. Econ. (U. K) 45, 91–105. https://doi.org/10.1111/agec.12132.
World Bank. (2021). World Bank Commodities Price Data (The Pink Sheet). Description of Price Series: https://www.worldbank.org/en/research/commodity-markets (accessed February 6, 2023).