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Managed Africanized honey bees and native stingless bees increase Arabica coffee yields in southeastern Brazil

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ABSTRACT: Using managed pollinators to supplement the contributions of wild pollinators is a promising means to increase crop production and rural livelihoods sustainably. However, evidence of the efficacy of managed pollinators must be provided for many crops, especially in tropical regions. Herein, we introduced managed colonies, including Africanized honey bees (*Apis mellifera*) and native stingless bees (*Scaptotrigona* spp.), in 23 coffee fields across a gradient of native forest cover in southeastern Brazil. We found coffee yield per bush increased by 16 % in coffee fields near managed colonies compared to more distant control fields. We detected positive effects for both managed bee species, though with higher variability for the native bee species due to low replication. Our study provides robust evidence that supplementing coffee farms with managed bee colonies can increase coffee yields and should stimulate further research and investment in bee supplementation.

Keywords: *Apis mellifera*, Apini, Meliponini, crop pollination, pollinator supplementation

Introduction

Animal-mediated pollination is an ecosystem service that is critical to global agriculture and enhances crop yield and/or quality in three quarters of global crops (Klein et al., 2007; Klatt et al., 2014; Potts et al., 2016). However, in many regions, wild pollinators are threatened by human activities, including (semi-) natural habitat loss and fragmentation, use of pesticides, spread of invasive species and pathogens, and climate change (Dicks et al., 2021). Thus, there is an urgent need to provide farmers with clear guidance on how to safeguard pollination services (Kleijn et al., 2019).

Where wild pollinators are scarce, crops can be supplemented with managed pollinators, typically honey bees (*Apis mellifera* L.) (Artz and Nault, 2011; Sáez et al., 2019). However, growing concern over agriculture's dependence on a single species (Aizen and Harder, 2009; Mashilingi et al., 2022), allied with emerging evidence on the efficacy of non-*Apis* bees (Garibaldi et al., 2013), has increased academic interest in alternative pollinators (Isaacs et al., 2017). In tropical and subtropical regions, this includes the honey bee's relatives, the stingless bees (Apidae: Meliponini) (Slaa et al., 2006).

Arabica coffee (*Coffea arabica* L.), while not being essentially dependent on biotic pollination due to its autogamous ("self-pollinating") breeding system, has an average yield increase of 18 % in the presence of pollinators (Moreaux et al., 2022; Escobar-González et al., 2024). Despite this benefit, management protocols for pollination services remain poorly developed compared to other external variables that affect coffee production (DaMatta et al., 2007). Furthermore, most of the recent evidence on coffee pollinators has focused on actions aimed at conserving wild pollinators (e.g., native habitat cover) (Vergara and Badano, 2009; Saturni et al., 2016; González-Chaves et al., 2022), rather than managed pollinators such as honey bees and stingless bees, which dominate coffee pollinator assemblages in Neotropical regions.

To understand the contributions of managed pollinators to coffee yields, managed colonies of Africanized honey bees (*A. mellifera*) were introduced into 20 coffee plantations across a gradient of native forest cover in southeastern Brazil. Alongside honey bee experiments, as a primer for research on native pollinators, stingless bees (*Scaptotrigona* spp.) were introduced in three additional plantations. We hypothesize that colonies and native habitat cover have complementary effects on coffee yields, as mediated by increases in pollinator densities during coffee flowering.

Materials and Methods

Study sites and experimental design

The study was conducted on 23 farms located in the states of São Paulo ("Alta Mogiana" region, 21°02′ S, 46°30′ W, 1004 m), Minas Gerais ("Cerrado Mineiro", 18°56′ S, 46°59′ W, 943 m; and "Sul de Minas" regions, 21°33′ S, 45°25′ W, 884 m), southeastern Brazil (Figure 1A-D). This area has a concentration of Brazil's most intensively managed coffee farms, where high productivity is associated with irrigation and agrochemicals. All farms produced Arabica coffee under full sun (i.e., no shade plants) and were located at elevations between 926 and 1123 m. Landscapes around coffee farms comprised crops (coffee, sugarcane), commercial timber plantations intermixed with remnants of the Atlantic Forest, the original native vegetation cover, savannah-type vegetation, restored forest habitats, and areas of natural regeneration (i.e., secondary forests). Importantly, Brazilian environmental law requires all landowners in this region to maintain at least 20 % of their properties as native vegetation cover (Soares-Filho et al., 2014). Mean annual temperatures for this region range between 18 and 23 °C (Bunn et al., 2014).

To test the effects of managed pollinators on coffee yields, between Sept and Oct 2020, we established an experimental pollination gradient on farms using colonies of two bee species groups, exotic Africanized honey bees (*A. mellifera*) and native stingless bees (*Scaptotrigona* spp.). We chose these bee taxa because of the evidence from previous studies on their effectiveness as *C. arabica* pollinators (Saturni et al., 2016; González-Chaves et al., 2020; Escobar-González et al., 2024), ease of management, and availability among local beekeepers. On individual farms, we introduced either *A. mellifera* (20 farms) or *Scaptotrigona* bee colonies (three farms, due to the low availability of colonies among local beekeepers) into plantations during bloom periods. We assessed the yield on coffee bushes at two distinct locations: 1) an area close to bee colonies (i.e., within 50 m, herein, "supplemented pollination"), and 2) a more distant "control" area (mean distance from colonies = 260 m, minimum = 120 m, maximum = 355 m). On all farms, control areas were established within the same plantation as bee colonies or in a neighboring plantation under similar conditions (e.g., soil type, cultivar, management protocols, height of coffee bushes, and distance to adjacent native vegetation). For exotic honey bees and native *Scaptotrigona* bees (SB), we used stocking densities of five and six managed colonies per hectare, respectively. To ensure that managed bees exhibited normal foraging behaviors during coffee flowering, colonies were introduced to the plantations at least ten days before flowering began. They remained *in situ* for the entire flowering period (3-5 days). To ensure that only healthy colonies were used in field experiments, all colonies were checked by trained beekeepers. Checks assessed colony food stocks, worker population size, the presence of an egg-laying active queen, and pest/pathogen incidence.

Land use cover

To characterize native vegetation cover in the surrounding landscape of study farms, we used publicly available land cover maps from the MapBiomas project (version 6), which annually provides maps of land use and land cover across the Brazilian national territory at a spatial resolution of 30 × 30 m. For each farm, using maps provided for the year 2020 (validated using aerial photography and field visits), we calculated native vegetation cover (sum of natural forest and savannah classes, excluding plantations, herein "forest cover") around centroids of each pollination treatment (assisted pollination and control) at buffers between 100 and 1000 m, at 100 m intervals, in QGIS software (version 3.16.16).

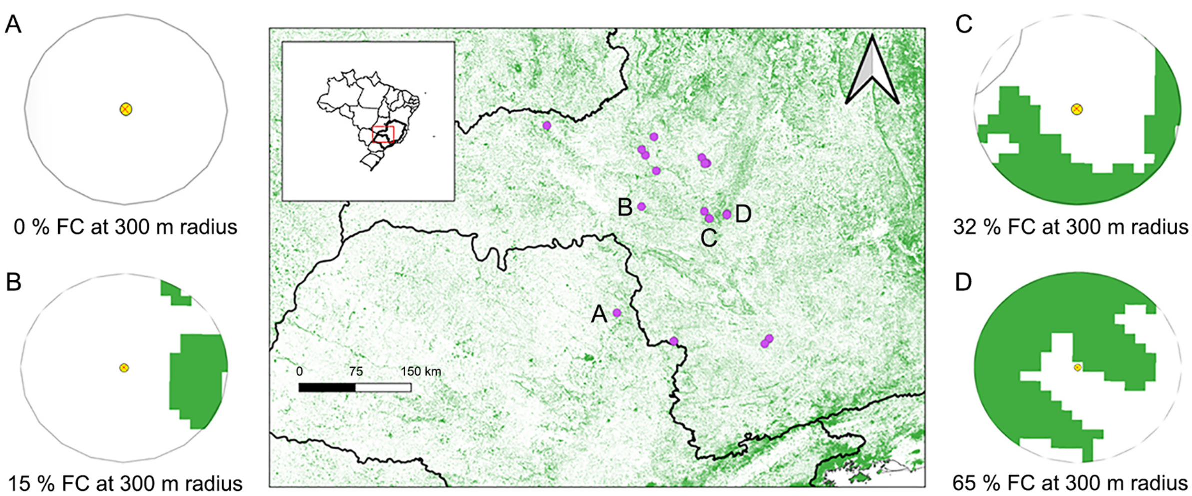

Figure 1 – Study region, state boundaries (Minas Gerais and São Paulo states, Brazil), coffee farms (n = 23), and natural vegetation cover (green areas, FC = forest cover) based on land use maps from MapBiomas project (see Land use cover, Materials and Methods). A-D) Farms are included as representative of our forest cover gradient at 300 m (range = 0-65 %). Inset shows study region in relation to Brazilian territory.

Coffee yield

Based on prior agreements with coffee producers, coffee production was assessed onsite at farms between June and July 2021 using two methods. On 20 farms, coffee berries were harvested manually, and on three farms, coffee was harvested mechanically. On 19 manual harvest farms, between two and eight plots were established in each pollination treatment area, using randomly generated coordinates on a handheld GPS. In individual plots, between 3 and 12 coffee bushes were manually harvested, with the total volume (in liters) of coffee berries recorded per bush. On the remaining farm, instead of discrete plots, a continuous area was manually harvested in each pollination treatment, with the number of bushes sampled and the total volume of harvested coffee berries noted. Finally, mechanical coffee harvesters sampled coffee bushes on three farms in treated areas until a predetermined volume of coffee berries had been collected (between 600 and 1000 L). Coffee producers provided information on planting density (bushes ha^{-1}) to estimate average berry yield per bush.

To convert coffee berry yield per bush into 60 kg bags ha^{-1}, the basic economic unit of coffee production, we calculated the average berry yield per bush and multiplied this value by planting density (bushes ha^{-1}, as provided by coffee producers). Based on the harvest timing, this value was then divided by the expected volume of coffee berries required to fill a single 60 kg bag. Plantations sampled during the optimum period ("cherry" period), have larger, heavier coffee berries, and thus require a lower total volume to fill a single bag (500 L). In contrast, plantations harvested after this period require a large volume (600 L) to fill a single bag as berries begin to dry on the bush. Importantly, treatment pairs ("control" and "supplemented pollination" plots) on individual farms were sampled on the same day to avoid potentially confounding the effects on yield estimates.

Statistical analyses

All analyses and figures were produced in the R statistical environment (R Core Team, 2021). To investigate the effects of managed bees and surrounding forest cover on coffee berry production on farms, we constructed linear mixed effects models of berry yield per coffee bush (log-transformed to normalize residuals) using the R package "lme4", with farm included as a random intercept to account for our nested experimental design. Preliminary analyses using more complex random effects structures, including sampling method (manual or mechanical harvest), did not explain the additional variance in our data and were thus not considered in further analyses. Fixed effects in the full model included pollination treatment ("control" or "supplemented pollination"), forest cover (%), elevation (m), planting density (bushes ha^{-1}), and two-way interactions between treatment and forest cover, and treatment and planting density. We included elevation as a proxy for biotic and abiotic variables influencing coffee yields and covary with elevation (e.g., soil type, temperature, relative humidity) (DaMatta et al., 2007). The spatial radius of forest cover (100 to 1000 m, in 100 m increments) in fitted models was determined by comparing Akaike Information Criterion values, corrected for small sample sizes (AICc) of a full model without interaction terms using forest cover variables at different spatial scales. The model with the lowest AICc value was used in all subsequent analyses.

To determine the important predictors of coffee yields we used a multi-model inference approach to compare all possible combinations of fixed effects included in the full model, including a null model (no fixed effects) (Anderson and Burnham, 2002). Prior to model selection, all fixed effects were standardized using z-scores to allow for comparison of effect sizes and screened for collinearity using variance inflation factors in the "car" R package (Fox and Weisberg, 2019). We then used the 'dredge' function in the "MuMIn" package (Bartoń, 2024) to rank all candidate models using AICc values. All models with ΔAICc < 2 of the reference model (lowest AICc score) were included in our best model set. After this procedure, we compared standardized residuals of the best model to check for assumptions of normality and homoscedasticity. Parameter estimates and confidence intervals of fixed effects included in the best models were estimated using restricted maximum likelihood. Fixed effects with confidence intervals that did not cross the intercept were considered as important predictors of coffee berry yield.

Additionally, to investigate the effects of individual bee species (honey bees = HB, *Scaptotrigona* bees = SB) on coffee yield, we replaced the binary pollination treatment term in the best model with a categorical variable with four levels ("HB control", "HB supplemented", "SB control", "SB supplemented"). To test for significant differences in coffee yield between levels, we used Tukey's test (α = 0.05) for multiple comparisons in the "multcomp" R package (Hothorn et al., 2008). To investigate the effects of managed bees and forest cover on coffee yield at the hectare scale (60 kg bags ha^{-1}, log-transformed to normalize residuals), we constructed a linear regression model with the following predictor variables: pollination treatment ("control", or "supplemented pollination"), forest cover (percentage cover at an *a priori* determined spatial scale, see previous description), elevation, and the interaction between pollination treatment and forest cover. As before, predictor variables were standardized to allow for comparison of effect sizes and checked for collinearity before using the same model selection and parameter estimation procedures described for berry yield models.

Results

On 23 farms, 1132 L of coffee berries were harvested from 2,756 coffee bushes distributed over 172 plots. Mean coffee production per bush on farms was 6.74 ± 4.09 L (minimum = 1.2, maximum = 20.33). Coffee yield per bush responded to forest cover in the surrounding landscape at a spatial scale of 300 m (mean forest cover = 19 %, minimum = 0 %, maximum = 66 %).

The best models of coffee yield per plant included pollination treatment, elevation, forest cover, and the interaction between pollination treatment and forest cover (Table 1). In all models, pollination treatment positively affected coffee production, on average increasing berry yields by 16 % (Figure 2A). In contrast, elevation had a negative effect on coffee yield per bush (Table 1, Figure 2B). When we analyzed pollination treatments by individual bee groups, a significant difference between control and supplemented pollination treatments was observed only on farms with honey bees (n = 20 farms). However, farms with *Scaptotrigona* colonies (n = 3 farms) showed a similar yield increase (~15 %; Figure 3).

Considering the effects on coffee production at larger scales (60 kg bags ha^{-1}), the best models included the effects of elevation and pollination treatment (Table 2). However, only the negative effect of elevation had non-overlapping confidence intervals.

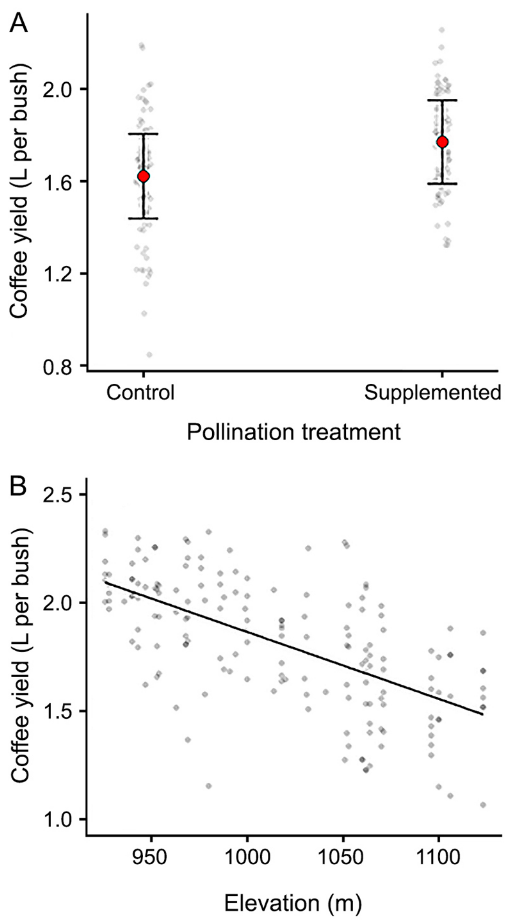

Figure 2 – A) Effects of pollination treatment and B) elevation on log-transformed coffee berry yield (in liters) per bush. Colored points, lines and error bars show parameter estimates and 95 % confidence intervals, respectively, and grey points show raw data.

Table 1 – Effects of supplemented pollination (SP), elevation, and forest cover at 300 m spatial radius (Forest300) on coffee berry yield per bush. Models were ranked by Akaike Information Criterion corrected for small sample sizes (AICc) and support for individual models was determined using Akaike weights (Wgt). Predictor variables with 95 % confidence intervals that do not overlap the intercept are shown in bold.

Model	Supplemented pollination	Elevation	Forest300	SP: Forest300	AICc	ΔAICc	Wgt
1	**0.15**	**–0.37**	–0.22		86.82	0.00	0.39
2	**0.16**	**–0.41**	–0.18	0.12	86.98	0.16	0.36
3	**0.17**	**–0.31**			87.71	0.88	0.25

Table 2 – Effects of supplemented pollination and elevation on coffee berry yield. Models were ranked by Akaike Information Criterion corrected for small sample sizes (AICc) and support for individual models was determined using Akaike weights (Wgt). Predictor variables with 95 % confidence intervals that do not cross the intercept are shown in bold.

Model	Supplemented pollination	Elevation	AICc	ΔAICc	Wgt
1		**–0.45**	80.76	0.00	0.63
2	0.19	**–0.47**	81.84	1.08	0.37

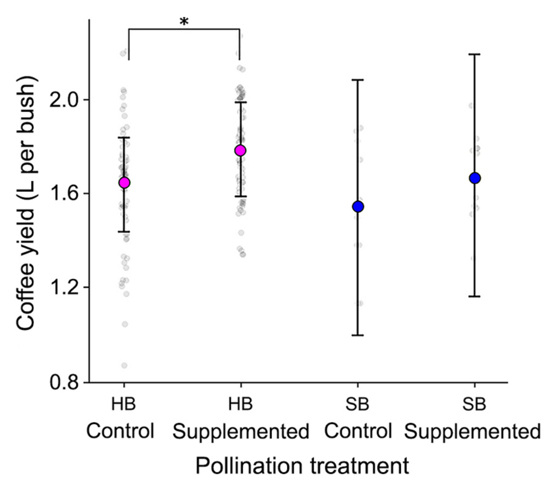

Figure 3 – Effects of pollination treatment on log-transformed coffee berry yield (in liters) per bush on farms with honey bees (HB, n = 20) and native bees (*Scaptotrigona* bees, SB, n = 3). Significant differences between treatment levels are noted with lines and asterisks. Colored points and error bars show parameter estimates and 95 % confidence intervals, and grey points show raw data.

Discussion

Our results show that supplementation of coffee farms with managed colonies of Africanized honey bees or native stingless bees increased coffee yields per bush by an average of 16 %, independent of surrounding landscape composition. In many global production regions, wild bees are the primary pollinators of coffee plants, but these may be scarce in plantation areas isolated from native forests (Ricketts, 2004; Vergara and Badano, 2009; Klein, 2009; González-Chaves et al., 2022; Escobar-González et al., 2024), as characterized by the large open fields of many farms included in this study. Thus, supplementation with managed bee colonies can provide coffee growers an immediate and complementary means to increase yields alongside longer-term investment in native forest restoration programs (Pérez-Méndez et al., 2020).

Herein, we confirm the findings of previous studies that honey bees are effective pollinators of coffee flowers (Roubik, 2002; Saturni et al., 2016; Giannini et al., 2020), although our study is unique in that we manipulated bee colony densities in coffee plantations, rather than just report observed flower visitor densities. We also detected positive yield effects on coffee farms with native SB at similar stocking densities (4-6 colonies ha^{-1}), even though native stingless bee colonies contain approximately four times fewer workers (~10,000 vs 40,000) (Geslin et al., 2017; Grüter, 2020). While caution is required due to the small number of replicates, this was supported by a previous study that reported a higher efficiency of stingless bees as coffee pollinators over honey bees (Escobar-González et al., 2024). Several mechanisms may underpin this relationship, including better functional compatibility of smaller insects with coffee flowers, i.e., 'trait matching', *sensu* Garibaldi et al. (2015), flower handling behaviors (i.e., stigmatic contact) (Escobar-González et al., 2024), a greater tendency to move between coffee plants (Klein et al., 2003), and shorter foraging ranges (0.5 vs 1.5 km), concentrating foragers in crops rather than surrounding habitats (Couvillon et al., 2014; Campbell et al., 2019). Our results underline the promise of alternative managed pollinators to support honey bee pollination services in coffee plantations. The use of multiple pollinator species can improve yield stability and contribute to the overall resilience of agricultural systems to environmental or socioeconomic change (Isaacs et al., 2017). However, further studies with a higher number of replicates using native bees, while accounting for the effects of colony size and different combinations of bee species, are needed to unpick the effects of species traits and species abundance on coffee pollination services.

We found no significant effect of forest cover in the surrounding landscape on coffee yields. Numerous studies have reported positive effects of forest cover and forest proximity on wild pollinator abundance, richness, and diversity (Ricketts, 2004; Klein, 2009; Saturni et al., 2016; González-Chaves et al., 2020), but the effects on coffee yields are equivocal (Moreaux et al., 2022; González-Chaves et al., 2022). Several studies on bee communities in southeastern Brazil (Atlantic Forest and Cerrado biomes) have reported negative trends with overall forest cover or a scarcity of native bees in forested habitats (Ferreira et al., 2015; Montoya-Pfeiffer et al., 2020). These authors suggest that historic clearance and degradation of this region's native forests have significantly reduced resource availability (e.g., pollen and nectar sources, nest sites) in remaining fragments and connectivity at the landscape scale, limiting wild pollinator movement and dispersal among suitable habitat patches. Consequently, many forest habitats, including primary and restored forests, support depauperate pollinator communities dominated by generalist social bee species, including feral honey bees (Montoya-Pfeiffer et al., 2020; Garibaldi et al., 2021) and native *Trigona spinipes* Fabricius (Jaffé et al., 2016). This is supported by findings of a recent meta-analysis investigating the effects of pollinators and surrounding habitats on global coffee yields, which only detected positive effects of forest cover in landscapes with 'dense' forest cover (≥ 75 % closed canopy) (Moreaux et al., 2022). Alternatively, our results may be reflecting the negative impacts of introducing honey bees on more efficient wild pollinators (Badano and Vergara, 2011), masking the effects of surrounding forest cover on coffee yields. Further studies with additional controls (i.e., farms without bee colonies), classifying forests by habitat structure and ecological integrity, and accompanying pollinator surveys are required to unpick relationships between forest cover, wild pollinators, and coffee yields in this region.

Contrary to our expectations, elevation had a negative effect on coffee yields. A possible explanation is that elevation covaried with local management variables that influence coffee yields. For example, while all farms were under conventional management (e.g., fertilizers, pesticides, irrigation), input intensity may have been higher on lowland farms, where machine access is easier than on farms at high elevations with steep inclines, which limits machine accessibility. However, it is important to note that previous studies have found inverse relationships between management intensity (i.e., pesticide use) and coffee yield, as mediated by more diverse pollinator communities on low-impact farms (Hipólito et al., 2018; Escobar-González et al., 2024). Alternatively, Neotropical pollinator communities are known to be less abundant and diverse at high elevations (Perillo et al., 2021). However, in our study, this effect was not offset by the use of managed bee colonies (i.e., no interactive effect of elevation and pollinator supplementation). Further studies assessing pollination benefits under different management scenarios can establish how pollination and other input variables affect coffee yields to optimize management practices and increase agroecosystem sustainability (Tamburini et al., 2019).

In summary, our study provides clear evidence that managed bees boost fruit yields on coffee farms at the coffee bush level. The fact that we did not find similar findings at the hectare scale is likely due to the high variation in sampling methods, as protocols were developed in partnership with farmers to minimize disruption to farming activities (e.g., mechanical versus manual harvest, plot size, and number). Nonetheless, our findings should stimulate further research in bee management, mainly native stingless bees, which, despite their smaller colony population sizes, showed similar effects than more populous colonies of Africanized honey bees. However, the lack of trained beekeepers still hinders stingless bee management at commercial scales in southeastern Brazil (Jaffé et al., 2015). A possible solution to this shortfall is the use of mixed species assemblages, which introduce a small number of native bee hives alongside honey bees. This could promote functional complementarity among pollinator species and enhance pollination services in coffee fields (Viana et al., 2014; Campbell et al., 2022), while reducing reliance on honey bees, which are already suffering from several pressures including parasites and disease (Boncristiani et al., 2021). Finally, pollinator management, combined with native habitat restoration to enhance ecological connectivity at the landscape scale, is expected to become an increasingly important strategy for mitigating the effects of climate change on Brazilian coffee yields, as the widespread decoupling of wild pollinator occurrence and coffee production areas is anticipated in the coming decades (Giannini et al., 2017).

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Authors' Contributions

Conceptualization: Berretta AA, Rehder CP, Sousa GJG, Menezes C. **Investigation**: Almeida-Dias JMV, Moure-Oliveira D. **Methodology**: Almeida-Dias JMV, Moure-Oliveira D. **Project administration**: Berretta AA, Sousa GJG, Rehder CP, Almeida-Dias JMV, Moure-Oliveira D., Menezes C. **Data curation**: Campbell AJ. **Formal Analysis**: Campbell AJ, Alves DA. **Writing – original draft**: Campbell AJ, Alves DA, Almeida-Dias JMV, Moure-Oliveira D, Quenzer FCL, Ramos JD, Menezes C. **Writing – review & editing**: Almeida-Dias JMV, Campbell AJ, Moure-Oliveira D, Alves DA, Quenzer FCL, Ramos JD, Rehder CP, Sousa GJG, Berretta AA, Menezes C. **Funding acquisition**: Berretta AA, Rehder CP, Menezes C.

Conflict of interest

The first and third authors were fellows from FAPESP and FINEP, respectively, and were employed by AgroBee after the conclusion of the project (PAPPE/PIPE). The seventh, eighth, and ninth authors opened the Startup AgroBee after the approval of the resources with FAPESP and FINEP for the realization of the project and pollination services based on the data available in the scientific literature and as a consequence of all the scientific results obtained during the period of resources support (2018-2021). The remaining authors have no conflicts of interest to declare.

Data availability statement

All data used in this manuscript will be available from the corresponding author upon request.

Declaration of use of AI Technologies

The authors declare that no AI technologies were used to produce this manuscript.

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