Seasonal correlation between rainfall and honey production by *Tetragonisca angustula* (Latreille 1811) in a meliponiculture system in the Peruvian Amazon †

[Correlación estacional entre la precipitación pluvial y la producción de miel de *Tetragonisca angustula* (Latreille 1811) en un sistema de meliponicultura en la Amazonía peruana]

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SUMMARY

Background: *Tetragonisca angustula* is the most abundant stingless bee in meliponaries of the Peruvian Amazon, especially in the Huallaga River valley. Its recent management has been conducted empirically, without scientific and technical guidance. **Hypothesis and objective**: Premised on the hypothesis that environmental conditions in seasonally dry forests affect the honey yield of *T. angustula* in technical meliponiculture this study aimed to evaluate variations in hive density and honey production patterns of this species in relation to the rainfall regime. **Methodology:** Between October 2019 and April 2023, a set of 36 'rational boxes' located in a meliponary was systematically evaluated for its longevity and honey production records. Likewise, information on the rainfall regime for the same period was systematized. **Results:** The longevity of the colonies was 2.25 ± 1.10 years. The total number of colonies and the number of unproductive colonies were strongly related, but they did not determine the honey production in the meliponary. The honey yield pattern showed the effects of the seasonal rainfall regime, probably related to a lower availability of floral resources. **Implications**: Under these ecological conditions, honey production is correlated with the number of productive hives but not with the total amount of hives in the meliponary, indicating competitive differences related to the combined effects of harvesting pressure and foraging capacity. **Conclusion**: Honey production by *Tetragonisca angustula* in a meliponiculture system responds to the seasonal rainfall regime in the Huallaga dry forest valley, in the Peruvian Amazon.

Key words: stingless bees; honey; meliponiculture; seasonal dry forest; Peruvian bees; time series analysis.

RESUMEN

Antecedentes. *Tetragonisca* angustula es la abeja sin aguijón más abundante en meliponarios de la Amazonía peruana, especialmente en el valle del río Huallaga. Su aprovechamiento se ha desarrollado de manera empírica, sin orientación científica ni técnica. **Hipótesis y objetivo**. En concordancia con la hipótesis de que las condiciones ambientales en los bosques estacionalmente secos afectan el rendimiento de miel de *T. angustula* bajo sistemas tecnificados de meliponicultura, la investigación tuvo por objetivo evaluar las variaciones en la densidad de

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colmenas y los patrones de producción de miel de esta especie en relación con el régimen de lluvias. **Metodología**. Entre octubre 2019 y abril 2023, la longevidad y los registros de producción de miel fueron sistemáticamente evaluados para un conjunto de 36 “cajas racionales” ubicadas en un meliponario. Asimismo, se sistematizó la información del régimen de lluvias para el mismo periodo. **Resultados**. Las colonias presentaron una longevidad de 2.25 ± 1.10 años. El número total de colonias y como de colonias improductivas estuvieron fuertemente relacionados, sin determinar la producción total de miel en el meliponario. El patrón de rendimiento de miel mostró los efectos del régimen estacional de lluvias, probablemente relacionado con una menor disponibilidad de recursos florales. **Implicaciones**. En estas condiciones ecológicas, la producción de miel está correlacionada con el número de colmenas productivas, pero no con la cantidad total de colmenas en el meliponario, lo que indica diferencias competitivas relacionadas con los efectos combinados de la presión de cosecha y la capacidad de forrajeo. **Conclusión**. La producción de miel de *Tetragonisca angustula* en un sistema de meliponicultura responde al régimen estacional de precipitaciones en el valle del bosque seco del Huallaga, en la Amazonía peruana.

Palabras clave: abejas sin aguijón; miel; meliponicultura; bosque seco estacional; abejas peruanas; análisis de series de tiempo.

INTRODUCTION

Stingless bees (Hymenoptera: Apinae: Meliponini) constitute a vital resource for tropical peoples. Since time immemorial, American populations have used honey, pollen, wax, resin, brood combs and propolis for nutrition, health care, handicrafts and rituals (Araújo *et al*., 2023). However, there is no clear evidence of domestication or systematic management, except for the well-documented breeding of *Melipona beecheii* by the Maya (Quezada-Euán, 2018).

Nowadays, the modern management of stingless bees, known as meliponiculture (Nogueira-Neto, 1953), has gained considerable momentum and undergone significant technological development. This expansion poses new challenges for updating current knowledge on ecology and productive responses of these bees in different ecosystems. Among these ecosystems, seasonal dry forests are of particular interest due to their wide distribution, the high degree of threat they face in the Neotropics, and the close link between their conservation and the persistence of stingless bee populations (May-Itzá *et al*., 2022).

In tropical dry forests, variations in rainfall regimes are closely associated with the availability and quality of floral resources for bees (Hubbell and Johnson, 1977; Domínguez and Dirzo, 1995; Maia-Silva *et al*., 2015; Marques *et al*., 2018; Flórez-Gómez *et al*., 2020; Vossler, 2021). Additionally, meliponiculture introduces new ecological conditions through the spatial arrangement and density of colonies in managed areas “meliponaries” (FAO *et al*., 2021), which may lead to increased competition and behavioral changes among bees.

Tetragonisca angustula (Latreille 1811) is a small stingless bee (approximately 5 mm in length) widely distributed from Mexico to Argentina. It occurs in a variety of environments, including preserved and fragmented forests and urban areas (Moreno and Cardozo, 2002; Copa-Alvaro, 2004), as well as in meliponiculture systems (Vit, 2009; Flores and Sanchez, 2010; Fierro, 2011; Vit *et al*., 2016; Contreras *et al*., 2020; Marconi *et al*., 2020; Nates-Parra *et al*., 2021; Adler *et al*., 2023; Torres *et al*., 2023). In the Peruvian Amazon, this species is also commonly managed in meliponiculture systems (Rasmussen and Castillo, 2003; Marconi *et al*., 2020, 2022), particularly in the seasonal dry forest of the Huallaga River Valley, an ecosystem characterized by exceptional biological richness and uniqueness (Linares-Palomino *et al*., 2022). In this region, the species is locally known as “ramichi”.

The breeding of *T. angustula* in the Huallaga dry forest remains largely empirical, as there is currently little scientific or technical guidance available to support its management. Considering the biological characteristics of this species—such as its maximum foraging range of 621–951 m (Araújo *et al*., 2004), its non-aggressive behaviour, and its high tolerance to colony aggregation (Slaa, 2006)—maintaining a stable density of highly aggregated colonies in meliponaries may represent a challenge under dry forest conditions, where floral resources are both seasonal and limited.

The objective of this study was to evaluate the variation in the number of hives and the patterns of honey production of *Tetragonisca angustula* in a technical meliponiculture system under the environmental conditions of the seasonal dry forest of the Huallaga basin in the northeastern Peruvian Amazon.

MATERIALS AND METHODS

The study was conducted in a meliponary (6°39′27.33″S - 76°16′5.33″W, elevation 480 m) near the village of Utcurarca (30 km from the city of Tarapoto, Peru). The area represents a fragmented habitat, typical of the seasonal dry forest of the Huallaga River valley, with annual accumulated precipitation close to 1,088 ± 91 mm and temperatures ranging from a minimum of 21.19 ± 0.95 to a maximum of 33.49 ± 0.95 °C (see supplemental material).

The meliponary (Figure 1) was installed in January 2016 with five hives of *T. angustula* which had spontaneously occupied some empty boxes. The population increased by natural colonization of empty rational boxes in the surrounding area, reaching 16 hives at the beginning of the study and a peak of 34 hives during the evaluation phase (27 October 2019 - 29 April 2023). The colonies were placed in rational wooden boxes - INPA model (Rovira *et al*., 2005): 2-cm thick, 12 cm x 12 cm and up to 25 cm high, with interconnected subdivisions arranged in a main brood chamber (h = 10 cm) at the bottom of the box, and 1 to 3 additional chambers (h= 5 cm each) at the top.

Confirmation of the taxonomic identity of *T. angustula*

In March 2020, five workers of *Tetragonisca angustula* were collected from 30 rational boxes in the meliponary and four additional workers were obtained in the nearest town (6°39′47.58″S, 76°17′9.82W, 205 m elevation). Three of the specimens from each sample were mounted on #00 pins for morphological study and the one or two remaining individuals were preserved in 96% ethanol to confirm their taxonomic identity. For this purpose, DNA was extracted from the middle legs of each sample using the Dneasy® Blood and Tissue Kit (Qiagen, Germany) according to the manufacturer's instructions.

PCR reactions for COI barcoding were performed in a total reaction volume of 25 µL, containing 0.5 pmol of the universal barcoding primers LCO 1490 and HCO 2198 (Folmer *et al*. 1994), 10 mM Tris-Cl, pH 8.3 and 50 mM KCl, 1.5 mM MgCl2, 2.5 mM dNTPs, 2 µL of the DNA template, and 1 unit of Taq DNA Polymerase (Promega). PCR cycling conditions were an initial denaturation of 3 min at 94 °C followed by 35 cycles of 30 s at 96 °C, 30 s at 50 °C, and 1 min at 72 °C, with a final elongation step of 10 min at 72 °C. PCR products were visualised on a 1% agarose gel stained with ethidium bromide and sent to the sequencing facility of GenoScreen (Lille, France). COI sequences were edited and aligned using the Staden package 2.0.0b11-2016 (http://staden.sourceforge.net, 29 March 2022). The identity of the collected specimens to *T. angustula* was checked using the identification tool in Bold System (http://www.boldsystems.org/index.php/IDS_OpenIdEngine, 1 April 2022). Sequences were deposited in GenBank (Acc. OR483880 to OR483936).

The alignments also included 14 *T. angustula* sequences previously deposited in Genbank: OP093485.1 and OP093484.1 (from Utcurarca, Peru), OP093483.1, OP093482.1, and OP093481.1 (from northern Peru), GBAH12042.15, GBAH12111.15, KF222902.1, KF890487.1, KF890530.1, and KF890711.1 (from Brazil), ASINH827.12 and ASINH829.12 (from Costa Rica) and MN344929.1 (from Venezuela). A maximum likelihood bootstrap consensus tree (K2P corrected distances) was obtained by using MEGA11 after 500 replicates. Initial trees for the heuristic search were automatically obtained by Neighbour-Join and BioNJ algorithms on a matrix of pairwise distances estimated by the MCL approach, and then the topology with the superior log-likelihood value was selected. The identity of the 30 DNA datasets and other subsequent from hives that arrived at the meliponary during the evaluation phase was complemented by morphological criteria based on taxonomic keys (Ayala, 1999; Silveira *et al*., 2002; Álvarez, 2015; Engel *et al*., 2023).

Honey sampling

Between October 2019 and April 2023, 22 bimestrial evaluations (every 60.95 ± 11.52 days) were carried out for each hive (n=36, coded from C_1 to C_{36}) in the meliponary. The honey yield of the surviving colonies was recorded by carefully opening the jars in the additional chambers of the rational boxes (above the main chamber) and extracting the honey with a hypodermic syringe. The rational boxes were then cleaned and the grooves between the box chambers were sealed with tape to prevent phorid infestation.

Data analysis

Methodological consideration: colonies were treated as independent observational units. However, natural colony multiplication through local swarming may lead to partial common ancestry among some colonies.

Correlation analyses were conducted for colony longevity (V1, in days), productive period (V2, in days), and average honey yield per colony (V3, in mL). Linear mixed-effects models were fitted to analyze V3 as response variable, with V1, V2, and the number of coexisting colonies (N) included as fixed predictors. Colony identity was included as a random intercept term to account for repeated measures within colonies. Models were fitted using maximum likelihood estimation to enable comparison among candidate models using the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). The model with the lowest AIC and BIC values (Sakamoto *et al*., 1986; Burnham and Anderson, 2002) was selected as the most parsimonious representation of the data. Prior to model fitting, collinearity among predictors was assessed using variance inflation factors (VIF) calculated with the R package *performance* (Lüdecke *et al*., 2021).

Figure 1. Meliponary (left) and details of the typical structure of the *Tetragonisca angustula* hive in a rational box (right). Top right: main chamber containing the brood cells protected by the involucrum (centre) and surrounded by honey pots. Bottom right: pots, plenty of honey, in a second chamber located at the top of the main comb.

To evaluate the consistency of the honey records *Y*, 11 colonies (C_2, C_5, C_6, C_7, C_8, C_{14}, C_{15}, C_{16}, C_{17}, C_{19}, C_{20}) were selected because they had at least 18 honey records collected on identical evaluation dates for all colonies, ensuring direct comparisons among colonies. These colonies also showed a higher ratio of colonies "with" ($Y > 0$) to "without" ($Y = 0$) honey records. A multiple regression analysis was carried out on this group of 11 colonies to build a model, taking the colony with the highest frequency of significant partial correlation indices (r_{yx}) as a function of the rest of the colonies (predictors). The best set of predictors was fitted using the Step algorithm {stats} (Hastie and Pregibon, 1992; Venables and Ripley, 2002), based on AIC and BIC.

After applying exploratory analyses (Shapiro-Wilk normality and Bartlett homoscedasticity tests) to the honey yield records, the data transformation was evaluated using the Box-Cox method (MASS in R) (Box and Cox, 1964; Venables and Ripley, 2002). Year (2020, 2021, 2022) and period factors were analysed separately. According to the preliminary results, analysis of variance and Tukey's mean separation test (crd {ExpDes} in R) were applied.

All data were converted to time series format (ts {TSA} in R) and log transformed as suggested by the Box-Cox function. The time series were analysed to test the statistical significance of the main attributes of linear trend (general macroscopic changes) and seasonality (cyclicity or changes at regular intervals) (Cryer and Chan, 2008; Haben *et al*., 2023). Linear regression models (lm {stats}) were run to assess the invariance of the mean overtime. Finally, Kruskal (kw {seastests}) and the F-seasonal dummies (seasdum {seastests} in R) tests (Ollech and Webel, 2020) were performed to examine seasonality.

The moving average curves of accumulated rainfall and honey records by bimestrial periods were compared using Pearson's correlation index. For this purpose, the honey records were previously adjusted to periods equally spaced at 60.83 days (365 days/ 6 periods), by interpolating between the points of delay for each register.

RESULTS

COI barcode sequences (BoldSystem similarity: 94.12%) and morphological characters confirmed the identity of *Tetragonisca angustula* (Latreille 1811) in the two populations sampled in the meliponary and in the town of Utcurarca.

The number of colonies (N), initially 16 (in October 2019), increased steadily to a peak of 34 colonies (August 2021), after which a progressive decline to 16 colonies at the end of the evaluations (April 2023) was observed (Figure 2, lower part). Except for one colony which was lost due to phorid attack (April 2023), no other cases of natural enemy predation such as by *Lestrimelitta* or other organisms were observed during the entire evaluation period.

A total of 44% of the 36 colonies studied was still alive at the end of the study (mean colony survival: 2.25 ± 1.10 years), while the mean lifespan of the colonies that had died before was approximately 1.31 ± 0.47 years. Honey production records (Y>0, see supplemental material) represented only 31.5 ± 38.8% of the total records per colony. The hives produced a total of 11.62 ± 1.13 liters of honey per year, yielding an annual average of 0.424 ± 0.075 liters per colony. There was no evidence of differences in survival (X^2: 0.0689, p-value: 0.7929) and in the rate of unproductive records (Kruskal-Wallis X^2: 0.3865, p: 0.5342) between the old and the young colonies.

Cross-correlation analysis showed a significant relationship between colony longevity (V1) and honey productivity variables: production period (V2) and honey yield (V3) (Table 1). The correlation indexes (r) were all highly significant ($r_{V1\text{-}V2}$: 0.752; $r_{V2\text{-}V3}$: 0.812; $r_{V1\text{-}V3}$: 0.431, p<0.001 for all). The mixed model V3~V1*V2+N+(1|Colony) which incorporated density (N ≈ coexistence) as an additional predictor, significantly improved model fit compared to simpler alternatives. The full model outperformed the trait-only model (V1*V2 interaction without density; $X^2(1)$: 11.65, p-value: 0.0006; ΔAIC: 9.7) and the density-only model (N + period without interaction; $X^2(6)$: 42.9, p-value: $1.22e^{-7}$; ΔAIC: 30.9). V1 and N were moderately correlated, and variance inflation factors for the interaction terms were relatively high (raw VIF up to 16.2). However, adjusted VIFs ($GVIF^{[1/(2\times Df)]}$) fell within acceptable limits (3.8–4.0), indicating that collinearity does not unduly affect the model. Both predictors significantly improved model performance, suggesting they capture different ecological dimensions.

Table 1. Summary of main statistics for hive longevity and honey productivity variables from 36 *Tetragonisca angustula* colonies during the period 27 October 2019 - 29 April 2023.

Variables	Statistics	
	Range	Mean ± SD[1]
V1 Longevity (days)	243.0 – 1,280.0	933.7 ± 325.7
V2 Productive period (days)	0.0 – 1,280.0	870.6 ± 429.4
V3 Average gross yield/ harvest (ml)	0.0 – 213.8	66.7 ± 59.7

[1] SD = standard deviation. [2] Significance codes: "*" to 5%, "**" to 1%, "***" to ≤0.1%.

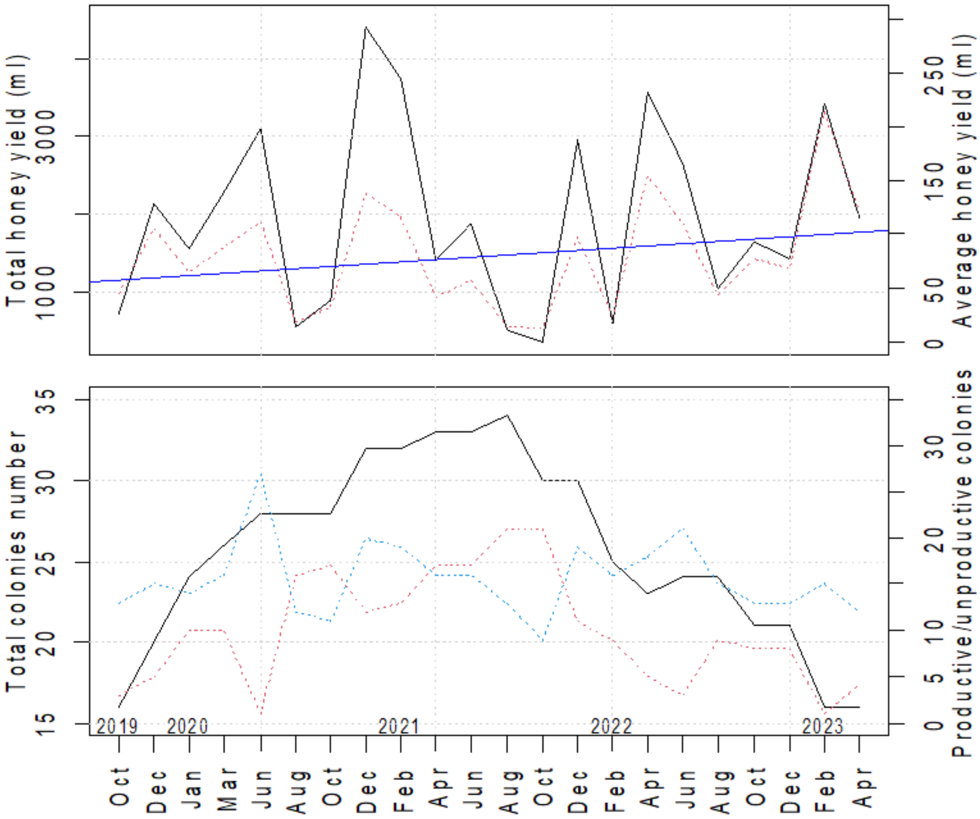

Figure 2. Honey production and number of colonies of *Tetragonisca angustula* over time (October 2019 - April 2023). Top: total honey production (ml) (black solid line) compared to average honey yield of colonies (ml) (red dashed line). The trend line is shown in blue. Bottom: number of colonies (black solid line) and frequency of productive (Y>0, blue dashed line) and unproductive colonies (Y=0) (red dashed line).

Honey production was not correlated with the number of colonies in the meliponary (F-statistic: 0.0079, p-value: 0.9299, R^2: 0.0004), but it was strongly correlated with the number of productive colonies (Y>0, F-statistic: 20.32, p-value: 0.0002, R^2: 0.4792). Total honey production and yield per colony (productivity) oscillated strongly around the mean according to time, with a slight increase but not significant trend (for average yields, F-statistic: 1.52, p-value: 0.23). The number of colonies *n* followed a quadratic polynomial ($n= -6.89\ t^2 - 23.6555\ t +25.64$), highly significant overtime *t* (F-statistic: 75.83, p-value: $8.767e^{-10}$, R^2: 0.88) (Figure 2).

The number of unproductive colonies was closely related to the total number of colonies (F-statistic: 30.96, p-value: $1.908e^{-5}$, R^2: 0.59), and it was strongly related to the decline in total honey production (r: -0.438, F-statistic: 4.75, p-value: 0.0414, R^2: 0.15) and productivity (r: -0.881***, F-statistic: 15.87, p-value: 0.0007, R^2: 0.41). No significant differences were found between old and new colonies in survival or frequency of unproductive records.

A total of 73% (n: 8) of the set of the most persistent colonies of *T. angustula* in the meliponary showed a similar honey production pattern ($C_{14}{\sim}C_2{+}C_5{+}C_6{+}C_8{+}C_{15}{+}C_{20}{+}C_{28}$, F-statistic: 25.05, p-value: $1.434e^{-5}$, R^2: 90.83%, $AIC_{n=8}$: 176.24 vs. $AIC_{n=11}$: 181.34).

Total honey production records (transformed data √x) were not statistically different by year (Kruskal-Wallis X^2: 2.23, p-value: 0.33), whereas bimestrial periods showed highly significant differences: P4 (9 to 12 August, dry season) recorded the lowest yield, and P6 (8 to 14 December) the highest one (F-statistic:10.29, p-value: $4.57e^{-9}$). This evidence of seasonality was confirmed by the seasonal model (Kruskal-Wallis X^2 =17.64, p-value: 0.0034), the Kruskal test statistic (kw: 16.22, p-value: 0.0062) and the "seasonal dummies" index (test statistic: 14.24, p-value: $3.0583e^{-5}$), coinciding with the dry season in the area (Figure 3). Moving averages (r: 3) of honey production and rainfall records showed a strong relationship (r: 0.6221, t: 3.371, p-value: 0.0034), demonstrating the variation of honey yield in response to climatic seasonality (Figure 4).

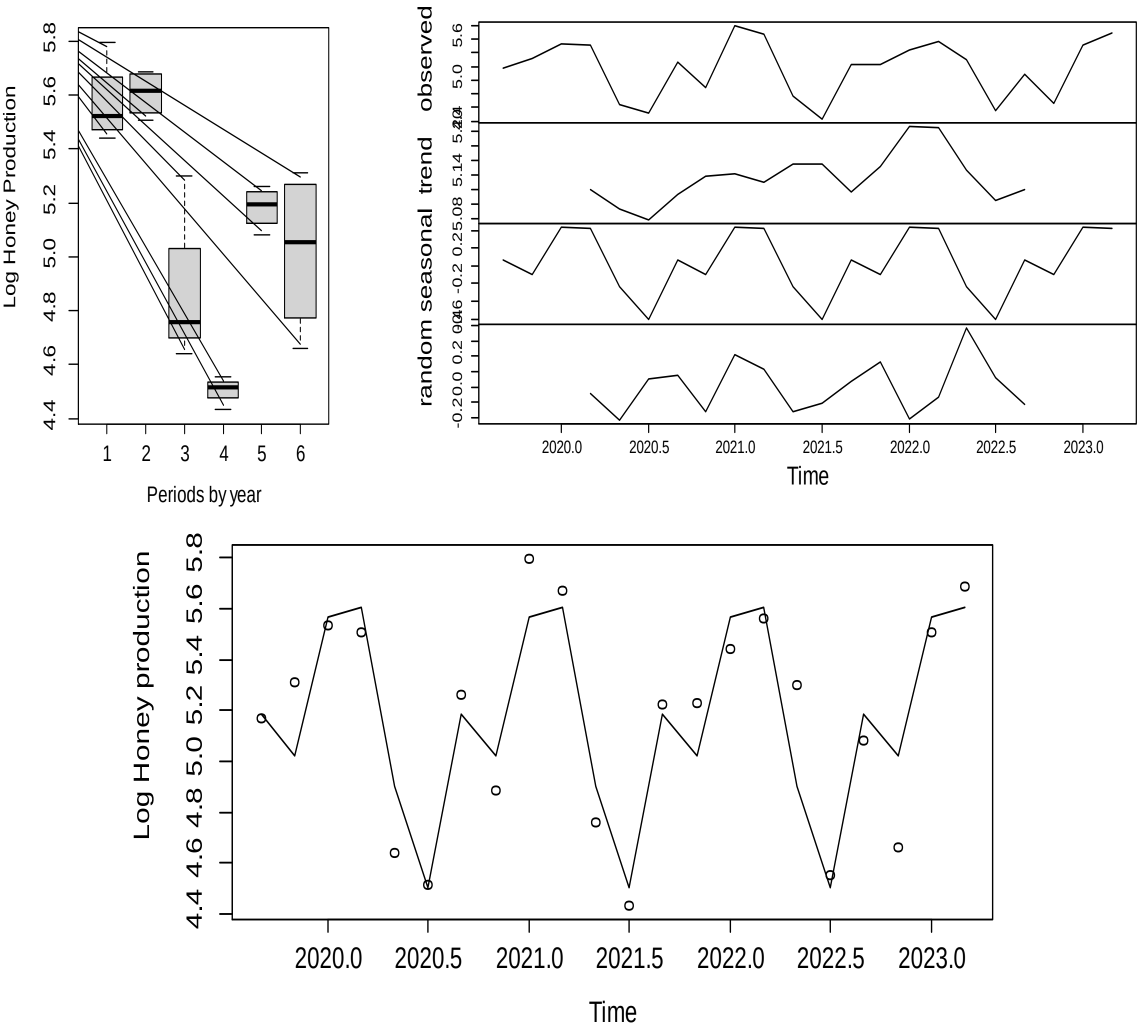

Figure 3. Analysis of honey production time series (log data) between September 2019 and April 2023. Top left: distribution of yields (log data) by bimestrial periods. Top right: time series components. Bottom: seasonal simulated curve of *Tetragonisca angustula* honey production (solid line) and observed records (dots) over time.

Figure 4. Comparison between mobile averages (r= 3) of bimestrial accumulated rainfall (black solid line) and honey production of *Tetragonisca angustula* (red dashed line), for the period September 2019 - April 2023.

DISCUSSION

Sequences obtained from specimens in this work (n: 56) and a previous study (n: 2; Marconi *et al*. 2022) were all identical, but differed from individuals from other sites in Peru, Brazil, Venezuela and Costa Rica (obtained from Genbank) for two fixed mutations at positions 513 (A→G) and 525 (A→G), respectively. The K2P-corrected tree with the highest log likelihood (-1103.77) is shown (Figure 6). This small genetic difference at the intraspecific level suggests a probably very recent geographic and ecological isolation of the Utcurarca populations, which should be investigated further.

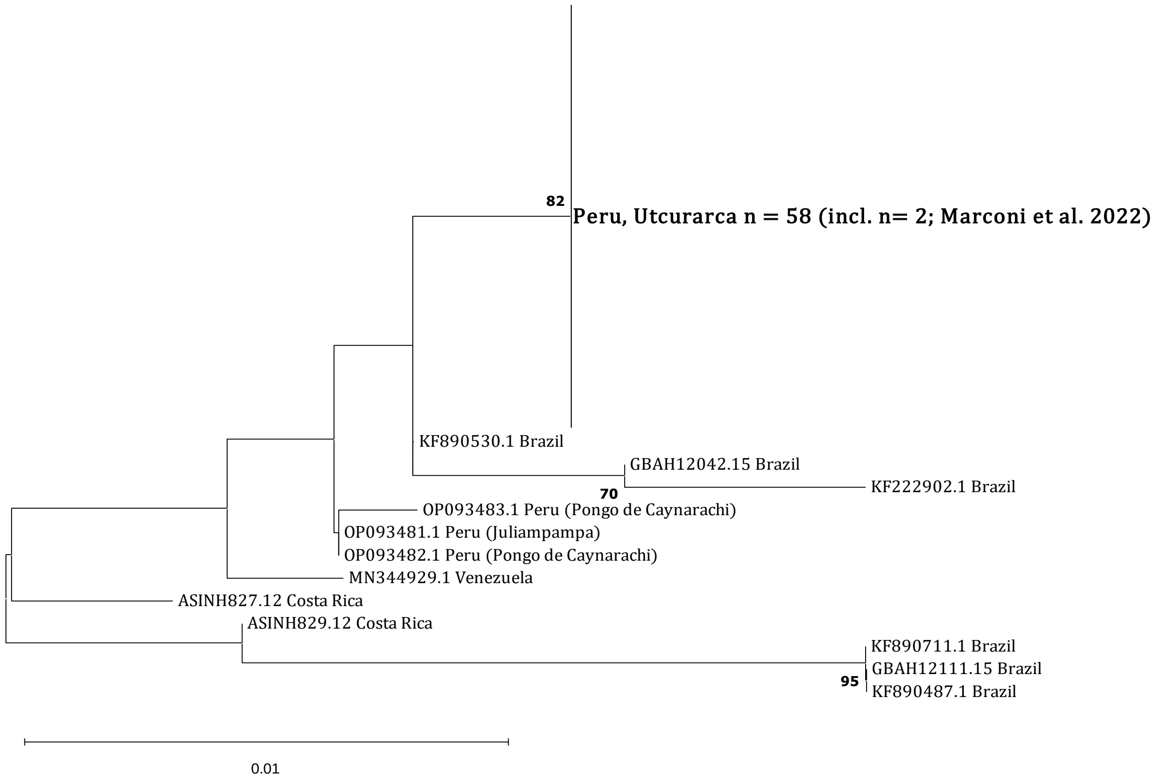

Figure 5. COI-based maximum likelihood phylogenetic tree of *Tetragonisca angustula*. Bootstrap values are shown next to the branches. The tree is drawn to scale, with branch lengths related to the number of substitutions per site. Description of 'Utcurarca', includes samples from the meliponary (n: 52), the nearest town (n: 4) and an additional sample collected by Marconi *et al*. (2022) from the same site.

The selected mixed model indicates that honey production was influenced by colony age, seasonal period, and colony density. The interaction between relative colony age and period suggests that the temporal pattern of honey production varies across seasons rather than remaining constant through time. This indicates that the effect of colony age on productivity is not uniform but depends on the seasonal context.

Colony density also improved model performance, indicating that competition among colonies for floral resources may influence individual colony productivity (Roubik, 1989; Seeley, 1995). Adding density to the trait-only model (which already included the colony age x period interaction) significantly improved model fit (ΔAIC: 9.7, $X^2(1)$: 11.65, p-value: 0.0006), demonstrating that density explains unique variation not captured by colony age and period alone.

Although colony age and density were moderately correlated (r: 0.431, p-value <0.001), both variables contributed to improving model fit, indicating that they are not redundant. Instead, they appear to represent different, but related, aspects of the ecological context in which colonies operate. Colony age may reflect intrinsic or functional characteristics (e.g., colony size), whereas density captures external biotic interactions such as resource competition and foraging pressure.

Together, these results suggest that honey production is shaped by the combined influence of internal colony traits and density-dependent processes, with a clear temporal component associated with seasonal conditions. The significant interaction between colony age and period further suggests that the relative advantage of older colonies may be contingent on seasonal resource availability.

These temporal dynamics are consistent with seasonal environmental variability, particularly rainfall regimes that regulate plant phenology in tropical ecosystems. Precipitation seasonality has been shown to influence the timing and intensity of flowering events in tropical forests (van Schaik *et al.*, 1993; Wright and van Schaik, 1994), which determines the temporal availability of nectar, pollen and plant resins used by bees. Consequently, fluctuations in floral resource availability across seasons may contribute to the observed variation in honey production. Field observations and previous studies support this relationship between climatic seasonality and bee productivity (Domínguez and Dirzo, 1995; Maia-Silva *et al.*, 2015; Marques *et al.*, 2018; Flórez-Gómez *et al.*, 2020; Prado *et al.*, 2021; Vossler, 2021; Thuma *et al.*, 2023).

The storage of pollen and honey in the hive is a strategy used by eusocial bees during flowering peaks, allowing colonies to buffer periods of food scarcity (Maia-Silva *et al.*, 2015; de Paula *et al.*, 2021). The quality and diversity of these food sources influence worker body condition and survival in both honeybees and stingless bees (Sawatthum and Kumlert, 2015; Oskay, 2021). Species formerly included in the genus *Trigona*, pollen and honey are also associated with caste differentiation processes within the colony (Amano *et al.*, 2000, Kwapong *et al.*, 2010).

In *Tetragonisca angustula*, the storage of essential food for brood development coincides with periods of maximum resource availability, when colonies accumulate reserves that sustain brood production and colony maintenance (van Veen and Sommeijer, 2000). In this species, honey appears to represent a larger proportion of stored resources than pollen, at least quantitatively. Although pollen storage was not systematically recorded in this study, only negligible amounts were observed in the hives. Despite the well-known adaptability of *T. angustula* to fluctuating resource availability, harvesting pressure may have affected the capacity of colonies to maintain adequate reserves for brood development and colony growth, particularly during the dry season. In this sense, honey extraction could act as an additional source of resource depletion within the hive.

The study also revealed that variations in rainfall regime were associated with changes in the number of productive colonies, with some hives failing to produce honey in certain periods. Under meliponiculture conditions, where colonies share the same landscape and foraging area, such variation may reflect the effects of seasonal resource limitation. Reduced food availability, combined with harvesting pressure, may favour stronger colonies that remain productive while weaker colonies become temporarily unproductive or decline.

However, the hypothesis that colony unproductivity was primarily driven by competitive asymmetries should be considered with caution. No clear differences were detected in survival or frequency of unproductive records between older and younger colonies, although older colonies could be expected to be more robust. Moreover, treating each hive as a fully independent biological unit may oversimplify the dynamics of meliponaries. Local swarming events generate mother–daughter relationships between colonies that may involve temporary dependence and resource sharing (van Veen and Sommeijer, 2000). Consequently, fluctuations in the number of productive or unproductive colonies could partly reflect swarming dynamics rather than direct competitive exclusion.

In addition to harvesting effects, competitive interactions may occur at the level of foraging resources or nesting sites. These interactions may involve the exploitation of nectar sources or territorial behaviour near resource patches. Due to the limited ecological data available in this study, it is not possible to distinguish the relative contribution of intra- or interspecific competition. Morphological studies suggest that some degree of co-adaptive niche differentiation may occur among stingless bees (Ramli *et al*., 2023). However, classical ecological studies emphasize that floral resource availability is the main limiting factor for bee populations, being strongly influenced by colony size and foraging range (Hubbell and Johnson, 1977).

The non-aggressive behaviour of *T. angustula* suggests that it does not rely on strong mechanisms of direct intraspecific competition for floral resources (Villa and Weiss, 1990; Biesmeijer and Slaa, 2004, 2006). Instead, this species shows considerable plasticity in its floral niche, ranging from selective resource use to seasonal overlap with other pollinators (Barth *et al*., 2013; Prado *et al*., 2021). Resource overlaps appear to occur more frequently with the honeybee *Apis mellifera* than with other stingless bees (Biesmeijer and Slaa, 2006).

Beekeepers in the vicinity of the meliponary reported that honey production by *Apis mellifera* reached 875 ± 230 L per year, with the highest yields occurring during the dry season (June–August) (unpublished data). In contrast to the pattern observed in *T. angustula*, this period coincides with peak activity of the honeybee. The larger body size, colony population and efficient recruitment behaviour of *A. mellifera* may increase its competitive advantage in exploiting floral resources (Biesmeijer and Slaa, 2006). Such differences could intensify competitive pressure on *T. angustula* colonies and potentially shift their foraging activity toward alternative niches.

At the nest level, interactions with conspecific colonies or with other stingless bees such as species of the genus *Lestrimelitta* may impose additional energetic costs through prolonged guarding or defensive behaviour (van Zweden *et al*., 2011; Balbuena *et al*., 2018). The relatively high density of colonies maintained in the meliponary may also modify natural spatial patterns of nest distribution, which in natural conditions tend to be random or aggregated in weakly aggressive bees (Hubbell and Johnson, 1977). However, recent evidence suggests that *Tetragonisca angustula* can tolerate relatively high nest densities in anthropogenic environments (Ushiñahua *et al*., 2026). Consequently, the high hive density observed in meliponary systems may not necessarily exceed the ecological tolerance of the species, although it could still intensify competitive interactions under conditions of seasonal resource limitation.

CONCLUSION

Honey production by *Tetragonisca angustula* in a meliponiculture system appears to be strongly influenced by the seasonal rainfall regime in the Huallaga dry forest valley of the Peruvian Amazon. Under these ecological conditions, total honey production was associated with the number of productive colonies rather than with the total number of hives maintained in the meliponary. This pattern suggests that seasonal resource availability, together with harvesting pressure and differences in colony foraging capacity, may influence the productivity of individual colonies and contribute to variation in honey yield within the meliponary.

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