ASIAN JOURNAL OF AGRICULTURE
Volume 10, Number 1, June 2026
Pages: 13
E-ISSN: 2580-4537
https://doi.org/10.13057/asianjagric/g100157

Responses of *Tetragonula sapiens* and *T. clypearis* to biotic and abiotic factors in Central Lombok, Indonesia

LUTFI ANGGADHANIA[1], KANTI DEWI RIZQIANI[2,♥], KRISNAWATI[2], EKA NOVRIYANTI[2], YELIN ADALINA[2]
[1]Research Center for Applied Microbiology, National Research and Innovation Agency. Jl. Raya Jakarta-Bogor Km. 46, Cibinong, Bogor 16911, West Java, Indonesia
[2]Research Center for Applied Botany, National Research and Innovation Agency. Jl. Raya Jakarta-Bogor Km. 46, Cibinong, Bogor 16911, West Java, Indonesia. Tel.: +62-811-1064-6793, ♥email: kant001@brin.go.id

Manuscript received: 4 December 2025. Revision accepted: 26 April 2026.

Abstract. *Anggadhania L, Rizqiani KD, Krisnawati, Novriyanti E, Adalina Y. 2026. Responses of* Tetragonula sapiens *and* T. clypearis *to biotic and abiotic factors in Central Lombok, Indonesia. Asian J Agric 10 (1): g100157. https://doi.org/10.13057/asianjagric/g100157. Tetragonula* spp. meliponiculture in Indonesia's dry tropical regions faces significant challenges from biotic and abiotic variables. This comparative study evaluated the responses of *Tetragonula sapiens* and *T. clypearis* to temperature, humidity, food availability, and pest occurrence in Central Lombok, Indonesia. Seventy colonies (35 per species) were monitored monthly for five months (July-November 2018) in two shaded demonstration blocks under managed conditions. Colony weight change (ΔW) was quantified as a proxy for colony development, while ambient temperature, relative humidity, and floral abundance were recorded concurrently. Multiple Linear Regression (MLR) analyses explored associations between ΔW and environmental variables at the block level (n = 5 monthly means per species), and separate simple regressions were fitted for each species. Colony weight change showed species-specific associations with environmental variables. Across both species, ambient temperature exhibited a stronger statistical association with ΔW than relative humidity. However, these relationships were based on a very small number of monthly observations and should be interpreted as exploratory. *T. clypearis* showed steeper negative associations with increasing temperature and decreasing relative humidity than *T. sapiens*, suggesting greater sensitivity to microclimatic variation within the observed range. In contrast, food availability was more strongly associated with colony weight dynamics in *T. sapiens* (R^2 = 0.819) than in *T. clypearis* (R^2 = 0.496). Pest inspections identified Psocoptera (*Tapinella* sp.) in the hives, marking the first documented case of this species in Central Lombok, associated with propolis discoloration and fungal growth. Within the limitations of the small dataset and the block-level design, microclimate and food availability were strongly associated with colony development in *Tetragonula* spp., during the dry season. These results highlight the importance of integrated floral, microclimate, and pest management for sustainable meliponiculture in Central Lombok.

Keywords: Abiotic factors, biotic factors, colony growth, meliponiculture, *Tetragonula* spp.

INTRODUCTION

The Meliponini (stingless bees) comprise approximately 500 species within the Apidae family (Herwina et al. 2023). These eusocial bees, which lack a functional sting apparatus, function as essential pollinators in tropical and subtropical ecosystems and provide valuable hive products to both rural and commercial beekeepers (De Moura et al. 2022). Indonesia harbors 46 native stingless bee species, distributed across Sumatra, Kalimantan, Java, Timor, Sulawesi, Maluku, and Papua (Janra et al. 2020; Suderajat et al. 2021; Salatnaya et al. 2023). Among these, *Tetragonula sapiens* and *T. clypearis* are widely cultivated for their honey, propolis, bee pollen, and bee bread products, which have been documented to have therapeutic properties including antioxidant, antibacterial, and anti-inflammatory effects (Ávila et al. 2018; Rozman et al. 2022).

Meliponiculture represents a low-cost, sustainable livelihood option for rural communities in Indonesia. In Lombok, the growing market demand for stingless bee products has spurred the rapid expansion of cultivation practices, particularly in areas with diverse flora and a suitable microclimate. However, this expansion has been constrained by production challenges, including colony abandonment, food scarcity, disease outbreaks, and pest infestations (Pangestika et al. 2018; Buchori et al. 2022). Understanding the comparative responses of different *Tetragonula* species to environmental stressors remains poorly documented in the Indonesian dry tropical context, suggesting the possibility of species-specific differences in stress responses, and thereby limiting evidence-based management recommendations for local beekeepers.

Food availability has a critical influence on colony survival and productivity in managed stingless bee systems. Stingless bees depend on nectar (carbohydrates), pollen (protein, lipids, vitamins), and resin (propolis precursors) from flowering plants throughout the growing season (Tahir et al. 2021; Rizqiani et al. 2025). Suboptimal conditions (temperature >35°C or humidity <40%) are known to suppress flight activity and nectar processing efficiency in stingless bee colonies (Salatnaya et al. 2020; Erwan et al. 2023). During the July-November dry season in Central Lombok, ambient temperature typically ranges between approximately 25-33°C, with diurnal fluctuations that may approach higher values during midday periods, while relative humidity varies between approximately 42-85%, which reflects typical dry tropical microclimatic conditions. Within this range, both temperature and humidity are expected to modulate, rather than completely suppress, foraging activity and colony development.

Despite the economic importance of meliponiculture in Lombok, significant research gaps hinder the sustainable intensification of this sector. First, there is a lack of comparative data on the stress responses of *T. sapiens* versus *T. clypearis* under managed conditions in tropical dry-season environments. Most published research derives from other Indonesian regions (e.g., Sumatra and Java) or tropical wet environments, which differ substantially from Central Lombok's pronounced dry season (July-November precipitation <50 mm). To our knowledge, no previous study has quantitatively compared the responses of *T. sapiens* and *T. clypearis* to combined abiotic (temperature and humidity) and biotic (food availability and pests) stressors under managed dry-season meliponiculture conditions in Indonesia. Second, the pest fauna of stingless bee hives in Central Lombok remains poorly characterized. By documenting Psocoptera associated with stingless bee hives in Central Lombok, this study contributes baseline information on hive-associated pest diversity for the region and helps to fill this gap. Third, there is minimal quantitative evidence linking specific microclimate parameters to colony performance metrics in local Lombok varieties, limiting evidence-based management recommendations for regional beekeepers. These gaps leave farmers without scientifically grounded guidance on species selection, optimal environmental management, and pest control for the specific agroclimatic context of Central Lombok.

This study addresses critical gaps in our understanding of the responses of two commercially important species, *T. sapiens* and *T. clypearis*, to combined abiotic and biotic stressors in the Central Lombok dry-season context. Using a comparative field approach and regression-based analyses, we seek to elucidate the relationship between floral resource availability, microclimate, and colony weight dynamics. In the hot and dry climate of Central Lombok, we hypothesize that *T. sapiens* is expected to demonstrate a more sensitive response to microclimate dynamics and floral resource availability compared to *T. clypearis*, because *T. sapiens* is frequently found in cooler mountainous environments. This differential response may highlight the impact of specific environmental conditions on each species' performance and resource utilization. Notably, this research contributes to the field by documenting previously unreported hive-associated pests, thereby enriching the limited quantitative literature on stingless bee pests in Central Lombok. The findings will be beneficial for species-specific management strategies to enhance local meliponiculture practices.

MATERIALS AND METHODS

Study site and timeline

The research was conducted in a Specific Purpose Forest Area (SPFA) located in Pemepek Village, Rarung Sub-district, Central Lombok District, West Nusa Tenggara Province, Indonesia (8°33′35″S, 116°17′38″E, 404 m asl) (Figure 1). Field observations were carried out during the 2018 dry season (July to November). Data were recorded contemporaneously and preserved in structured field logs. Subsequent statistical analysis was conducted without modifying the original dataset. All interpretations refer strictly to environmental conditions recorded during the 2018 observation period. Accordingly, selected references published between 2023 and 2025 are cited to support contemporary interpretation of the findings and to reflect recent methodological developments in meliponiculture research.

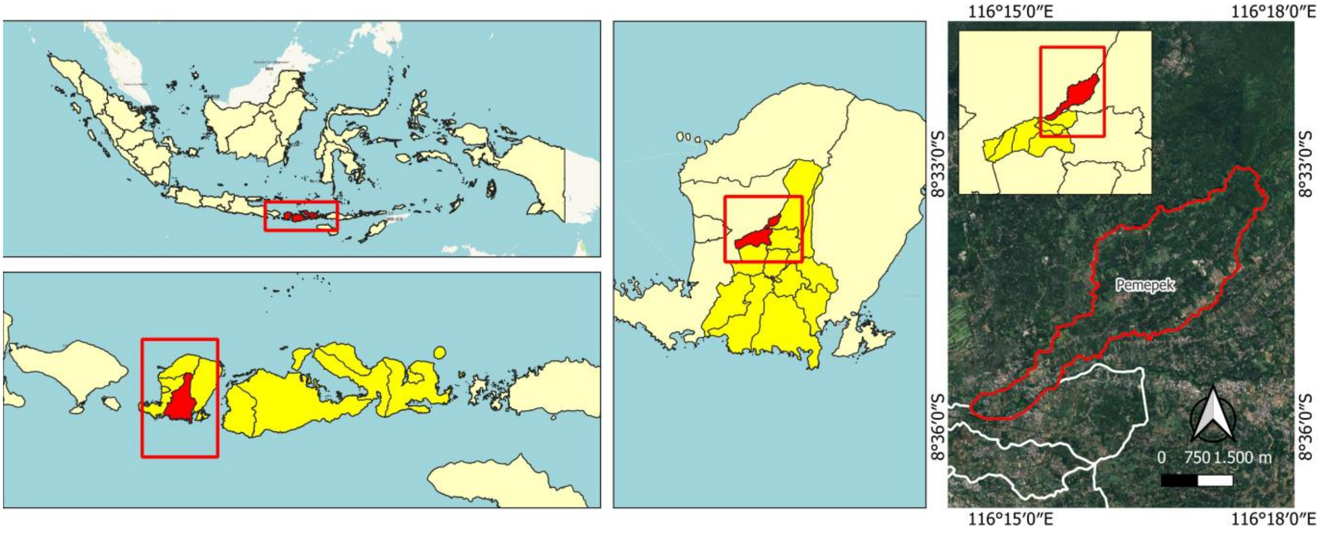

Figure 1. Map of the study location

Experimental design and bee management

The experiment consisted of two shaded demonstration blocks (12 m × 10 m × 5 m) assigned to a single species each. Before data collection, all colonies underwent a week of acclimatization period in shaded block environments. Bee colonies are moved to blocks A and B at night to avoid stress. During this period, colonies were allowed to adjust to the new spatial configuration and microclimatic conditions. It is recognized that stingless bees placed in enclosed or semi-enclosed environments may initially exhibit disoriented flight behavior, including collisions with enclosure structures, reduced foraging activity, and increased mortality. Therefore, data collection was initiated only after this initial acclimation phase to minimize the influence of early adaptation stress on colony performance measurements. "Block A" housed 35 colonies of *T. sapiens*, while "Block B" housed 35 colonies of *T. clypearis*. All colonies were maintained in identical wooden hive boxes (40 × 10 × 10 cm³) (Figure 3) following common meliponiculture box dimensions used for *Tetragonula* spp. management (Erwan et al. 2023; Salatnaya et al. 2023) (Figure 2). Each block was covered with black shade-net fabric to reduce direct solar radiation while maintaining natural airflow and ambient exposure, consistent with recommended stingless bee management practices in tropical environments (De Moura et al. 2022; Toledo-Hernández et al. 2022). The mesh structure allowed ventilation and minimized direct heat stress while preventing interspecific mixing. Colony placement density and hive orientation were kept consistent within each block to reduce microenvironmental heterogeneity, following standard comparative management approaches in stingless bee field studies (Jaffé et al. 2015; Buchori et al. 2022).

It is important to note that only one block per species was established. As a result, species identity is confounded with block, and species-level comparisons are effectively based on block-level responses rather than on fully replicated experimental units. All regression analyses, therefore, use block-level monthly means and should be interpreted as exploratory descriptions of species-specific patterns under the particular conditions of these two blocks, rather than as definitive, fully replicated tests of species effects. Data were analyzed to evaluate the associations between flower availability, air temperature, and relative humidity and colony weight change, and to provide descriptive comparisons between the two bee species.

Observation and data collection

Monthly assessments of colony development, flowering, and environmental parameters were conducted over a five-month study period, from July to November. Colony weight was used as an integrative indicator of colony development, reflecting combined changes in brood production, food storage, and structural growth. The use of hive weight as a non-destructive proxy for colony performance has been widely applied in managed bee studies (Meikle et al. 2018; Zacepins et al. 2022). Each hive box was initially weighed empty (W_0), and the total box weight (wooden box plus colony, brood, stored food, and propolis) was recorded monthly (W_n). The change in colony weight for each hive box (ΔW_n) was calculated as:

$$\Delta W_n = W_n - W_0 \quad [1]$$

In this definition, W_0 refers strictly to the empty box weight and does not include the initial colony mass at the start of the study. The ΔW_n values were first calculated at the individual hive level and subsequently averaged for each month of observation for each stingless bee species. As a result, five monthly mean values of ΔW_n, flower availability, air temperature, and relative humidity were obtained for each demonstration block. The effective sample size for regression analyses was therefore n = 5 monthly observations per species (n = 10 observations in total across both species).

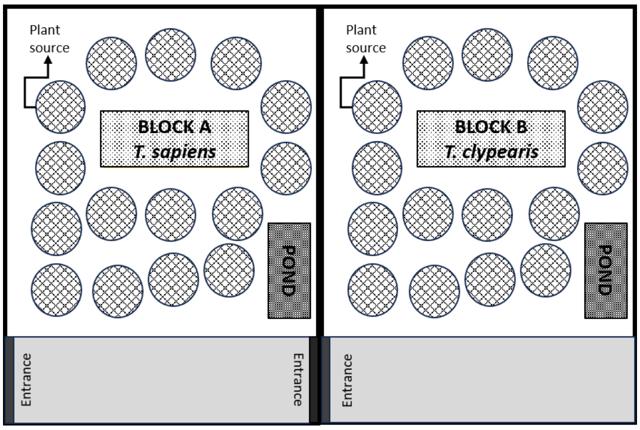

Figure 2. The demonstration blocks of *T. sapiens* and *T. clypearis* meliponiculture in Rarung, Central Lombok, Indonesia

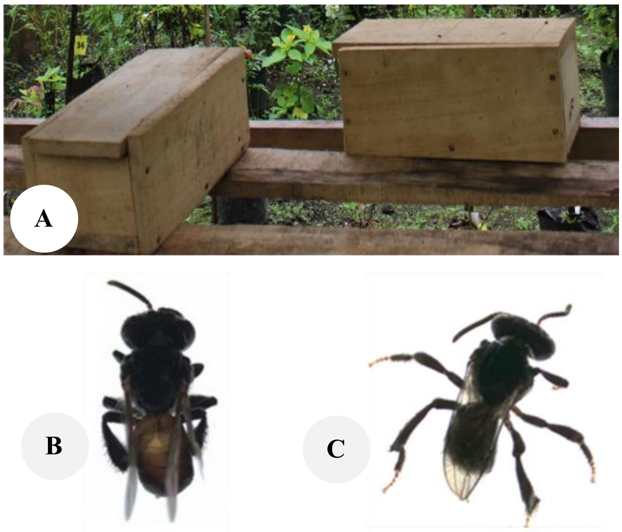

Figure 3. Experimental hives and stingless bee species were examined in this study. A. Standardized wooden hive boxes used to maintain and monitor stingless bee colonies, B. Worker of *T. clypearis*, C. Worker of *T. sapiens*

Methodological limitation

The use of total hive box weight as a proxy for colony growth integrates multiple biological components, including population growth, food storage (honey and pollen), and structural development such as brood comb formation. While this metric provides a practical and non-destructive field-based assessment, it does not separately quantify brood area, adult bee population size, or stored food mass. Future studies should employ more specific metrics such as direct brood cell counts, adult bee enumeration by frame sampling, or separation of stored resources from biomass. However, for comparative assessment across species under identical conditions, the consistency of this measurement approach provides valid relative comparisons between *T. sapiens* and *T. clypearis* responses to environmental factors.

Environmental monitoring equipment and calibration

Ambient temperature and relative humidity were measured using calibrated digital thermometer-hygrometers (HTC-1 model), with an accuracy of ±1°C for temperature and ±5% for relative humidity. Devices were positioned 1.5 m above ground level and centrally within each shaded block to represent the microclimate conditions experienced by foraging bees. Instruments were calibrated against a certified standard (NIST-traceable reference hygrometer) before the study and checked weekly for accuracy. The measurements were recorded once per month at approximately 10:00 AM local time during hive-box weighing to standardize observations and minimize diurnal bias during field visits, coinciding with peak bee foraging activity in tropical conditions (Faqih et al. 2024; Hadimani et al. 2024; Vignesh et al. 2024). A limitation of this approach is that single-time-point measurements at ~10:00 AM do not capture the full daily or intra-monthly variation in temperature and humidity; future studies should employ continuous data loggers to obtain more representative microclimate profiles.

The total number of floral resources was quantified using a direct visual count. Each month, two trained observers independently conducted a 20-minute walking survey within each 12 m × 10 m block, recording all visible open flowers, defined as flowers at reproductive maturity with exposed anthers or pistils. Any large discrepancies between the two observers were checked and reconciled in the field to enhance the reproducibility of the flower counts. Counts were averaged between observers and recorded as the total flower availability per block. This approach follows commonly applied apidological survey methods (Herwina et al. 2023) and provides a practical field-based estimate of nectar and pollen resources. Floral abundance was additionally categorized using a semi-quantitative ranking system (+++ very abundant, ++ abundant, + sparse, — not flowering), based on overall flowering intensity observed during the survey. A similar protocol has been applied in a previous study assessing floral availability for insect pollinators (Szigeti et al. 2016).

Pest identification

Pest infestations were inspected monthly during the box weighing. Insect specimens observed on propolis or within hive structures were collected using sterile instruments, preserved in 70% ethanol, and examined under stereo and light microscopy. Morphological identification was based on diagnostic characters including wing venation, body size, tarsal segmentation, and antennal morphology, following established keys for Psocoptera (Ramel 2020; Toineno et al. 2012).

Statistical analysis

Multiple Linear Regression (MLR) was performed to examine associations between colony weight change (ΔW) and environmental predictors (total monthly flower abundance, monthly temperature, and monthly humidity). Analyses were conducted at the block level using monthly mean values, yielding five observations per species ($n = 10$ in total). Given this very small sample size and the absence of true replication at the block level, all results are interpreted as exploratory associations rather than causal relationships or definitive predictive models.

A main-effects MLR model was fitted, including species (dummy variable: 0 = *T. sapiens*, 1 = *T. clypearis*), flower availability, temperature, and relative humidity as predictors. Model assumptions of linearity, normality of residuals, and homoscedasticity were evaluated using scatter plots, normal probability plots of standardized residuals, and inspection of residuals versus fitted values. Autocorrelation was assessed using the Durbin–Watson statistic. Multicollinearity was examined using tolerance values and Variance Inflation Factors (VIF), following established recommendations in applied regression and ecological modeling studies (Brien 2007; Dormann et al. 2013).

An initial exploratory model including interaction terms among species, flower availability, temperature, and humidity was also fitted. However, with only 10 observations, this interaction model was severely underpowered, showed strong multicollinearity and unstable parameter estimates, and had only 1 residual degree of freedom. Concerning the degrees of freedom and overfitting, the interaction model was not used for inference, and its detailed results are not presented. Subsequent interpretation focuses on the simpler main-effects model.

To further examine species-specific patterns, separate simple linear regressions were conducted for each species, relating ΔW to each environmental variable (flower availability, temperature, or relative humidity) individually ($n = 5$ per regression). For these models, coefficients of correlation (R), coefficients of determination (R^2), regression coefficients (B), and p-values for slope estimates were obtained. Because all separate regressions are based on only three residual degrees of freedom, statistical significance at $p<0.05$ is considered unstable and is interpreted cautiously. All analyses were conducted using IBM SPSS Statistics version 20, and the small-sample context is explicitly acknowledged when discussing R^2 and p-values. Given the limited sample size and the absence of true experimental replication, the regression analyses presented in this study do not imply causal relationships. Instead, they are intended to describe exploratory associations among variables. The potential for model overfitting and inflated coefficients of determination (R^2) is acknowledged. Future studies should employ larger sample sizes, replicated experimental designs, and alternative statistical approaches such as mixed-effects models or time-series analyses to better capture the complexity of these ecological interactions.

RESULTS AND DISCUSSION

Flora diversity supporting bee nutrition

A total of twenty plant species providing nectar, pollen, or resin resources were identified within the cultivation blocks during the observation period (Table 1). Several species, including *Helianthus debilis*, *Ageratum conyzoides*, *Lantana camara*, *Turnera subulata*, *Amaranthus* spp., *Impatiens balsamina*, and *Celosia* spp. exhibited continuous flowering from August to November, corresponding to the main flowering period during the dry season. Among these, *H. debilis* showed the highest and most consistent flowering intensity. Other species, such as *Jatropha integerrima* and *Euphorbia* spp. provided both pollen and nectar across most months. Overall floral availability showed seasonal variation, with higher abundance in August–September than in October–November.

It should be noted that the identification of floral resources was based on availability within the foraging range of the colonies rather than direct observation of bee visitation. Although many of the recorded plant species are well-documented sources of nectar, pollen, or resin for stingless bees, this study did not include direct foraging observations or pollen analysis. Therefore, the listed plant species represent potential rather than confirmed resources utilized by the colonies.

Dynamics of the relationships between food availability and environmental factors with the colony weight

The interpretation of colony weight dynamics should consider potential residual effects of acclimatization following colony relocation. Although a week adjustment period was implemented before measurement, early observations may still partially reflect ongoing adaptation processes rather than purely environmental influences. The total flower abundance declined progressively over the study period in both cultivation blocks (Table 2). Therefore, the first observation point may still partially reflect residual acclimatization effects. In block A (*T. sapiens*), the flower availability decreased from more than 6,000 at the beginning of the study to fewer than 4,000 by week 20. A similar decline was observed in Block B (*T. clypearis*), where flower numbers also dropped from more than 3,000 to approximately 1,000 over the same period. This reduction broadly followed the pattern of colony weight variation; however, this apparent similarity should be interpreted cautiously, particularly for early observations that may still reflect residual acclimatization effects (Table 2). These initial differences in flower counts between blocks reflect the specific planting design and spontaneous colonization by herbaceous and ornamental species in each block, rather than treatment effects imposed during the experiment. In contrast, both blocks showed an increasing trend in ambient temperature over the observation period, from ≈25°C in week 0 to ≈30°C in week 20. Meanwhile, relative humidity followed a similar trend to the number of flowers and colony weight (Table 2).

A Multiple Linear Regression (MLR) analysis was used to explore the relationships among flower availability, ambient temperature, relative humidity, and colony weight across both species. Scatter plots and normal probability plots of standardized residuals indicated that, within the limitations of the small dataset, the assumptions of linearity and approximate normality were reasonably met (Figure 4).

The main-effects model, which included species (dummy variable), flower availability, temperature, and humidity as predictors, showed no strong evidence of multicollinearity among the independent variables: all tolerance values exceeded 0.1 and VIF values were below 10, and the Durbin-Watson statistic (1.526) indicated no serious autocorrelation (Table 3). In contrast, an exploratory interaction model that included multiple interaction terms among species and environmental variables exhibited extremely high VIF values, strong multicollinearity, and only one residual degree of freedom. Consistent with this, the interaction model was not statistically significant in ANOVA and was deemed unreliable for inference (Table 4). In line with the limited degrees of freedom, further interpretation is therefore restricted to the simpler main-effects model.

For the main-effects model, the coefficient of determination was high ($R^2 = 0.971$; see Table 5), but given the small sample size ($n = 10$), this value should be interpreted as an exploratory association rather than strong statistical power. The regression analysis indicated a negative association between temperature and colony weight across both species, with an unstandardized coefficient of approximately –0.552 g per °C increase ($p = 0.006$). The species dummy variable (representing *T. clypearis* relative to *T. sapiens*), flower availability, and relative humidity had smaller and statistically nonsignificant coefficients. Specifically, the coefficient for flower availability was near zero and slightly negative (approximately -4×10^{-3} g per flower; $p = 0.687$), and the coefficient for humidity was small and positive (= 0.022 g per % relative humidity; $p = 0.274$) (Table 6). These results suggest that, within the combined dataset, temperature showed the strongest statistical association with colony weight change. However, this pattern should be interpreted cautiously, given the potential influence of early-phase acclimatization. At the same time, the contributions of flower abundance and humidity were weaker and more uncertain.

Table 1. Food source plants of *T. sapiens* and *T. clypearis* in cultivation demonstration blocks, Pemepek Village, Central Lombok, Indonesia, July-November 2018

Scientific name	**Local name**	**Month**				**Pollen**	**Nectar**	**Resin**
		Aug	**Sept**	**Oct**	**Nov**			
Jatropha integerrima Jacq.	*Batavia*	+	+	+	+	√	√	
Euphorbia spp.	*Euphorbia*	+	-	+	-	√	√	√
Helianthus debilis Nutt.	*Matahari mini*	+++	+++	+++	+++	√	√	
Ageratum conyzoides L.	*Babandotan*	++	++	+++	++	√	√	
Lantana camara L.	*Tembelekan*	++	++	++	++	√	√	
Turnera subulata J.E.Sm.	*Bunga pukul 9*	++	++	++	++	√		
Orthosiphon aristatus (Blume) Miq.	*Kumis kucing*	+	-	+	-		√	
Amaranthus spp.	*Bayam*	+++	++	+	+	√		
Rosa spp.	*Mawar*	+	+	+	+	√		
Impatiens balsamina L.	*Pacar*	++	++	++	+	√		
Calliandra spp.	*Kaliandra*	+	+	-	-	√	√	
Euphorbia pulcherrima Willd. ex Klotzsch	*Kastuba*	++	++	-	-	√	√	√
Celosia spp.	*Bunga jengger*	++	+	+	+	√		
Oxalis barrelieri L.	*Belimbingan*	+	-	-	-	√		
Bougainvillea glabra Choisy	*Bougenvil*	+	++	+	-	√		
Citrus aurantiifolia (Christm.) Swingle	*Jeruk nipis*	-	+	+	-	√	√	
Eleutheranthera ruderalis (Sw.) Sch.Bip.	*Rumput liar*	-	-	+	-	√		
Stachytarpheta jamaicensis (L.) Vahl	*Pecut kuda*	-	+	+	-	√		
Dimocarpus longan Lour.	*Kelengkeng*	-	-	+	+	√	√	
Capsicum annuum L.	*Cabai rawit*	-	-	-	+	√	√	

Note: +++: Very abundant, ++: Abundant, +: Sparse, —: Not flowering (Szigeti et al. 2016). The following references in parentheses verify whether the species provides pollen, nectar, and resin: (Prasad and Sunojkumar 2013; De Lima et al. 2019; Priawandiputra et al. 2020; Mularz 2021; Anita et al. 2022; Erwan et al. 2022; Santoso et al. 2022; Wahyuningsih et al. 2022)

Table 2. The average of colony weight, number of flowers, ambient temperature, and relative humidity in the block of *T. sapiens* and *T. clypearis* at Pemepek Village, Central Lombok, Indonesia

Species	**Week**	**Number of flowers**	**Temperature (°C)**	**Humidity (%)**	**Colony weight (*10^{-2} (g))**
T. sapiens	0	6146	25.5	85	9.95
	4	5591	26.4	76	9.91
	8	4056	29.8	42	7.07
	12	4094	29.5	58	8.12
	20	3926	33	51	5.89
T. clypearis	0	3401	25.8	85	10.09
	4	3025	27.9	70	8.50
	8	2973	31.2	47	6.18
	12	2416	29.8	67	6.91
	20	1896	30.7	58	6.51

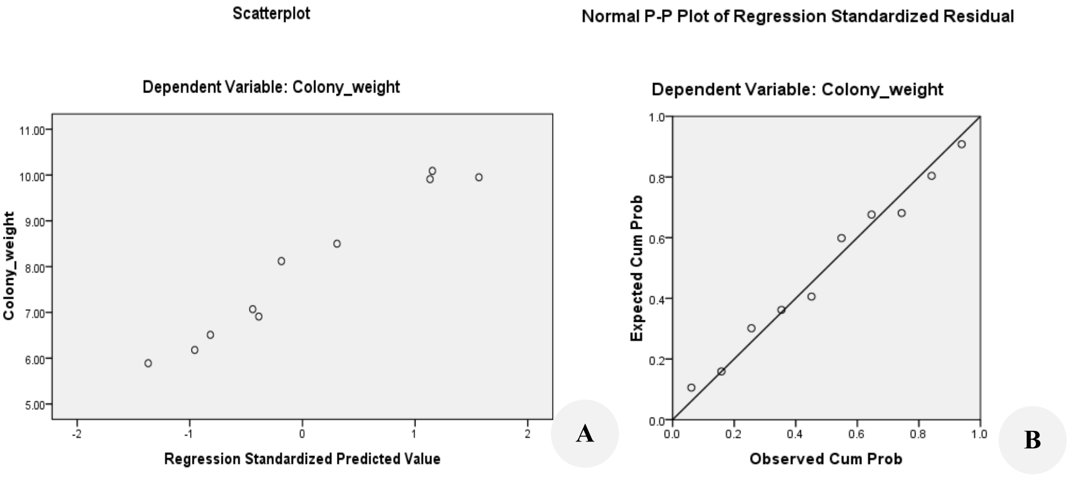

Figure 4. A. Scatter plot and B. Normal P-P plot for data on the number of flowers, ambient temperature, and relative humidity in the cultivation block of *T. sapiens* and *T. clypearis*

Table 3. The multicollinearity and autocorrelation of the independent variables (number of flowers, temperature, and humidity) to colony weight

Model	Independent variable	Collinearity statistic		Durbin-Watson (DW)
		Tolerance	VIF	
Main	Species_dummy	0.135	7.387	1.526
	Flowers availability	0.678	1.475	
	Temperature	0.194	5.154	
	Humidity	0.234	4.281	
Interaction	Species_dummy	0.003	312.496	2.795
	Flowers availability	0.002	454.190	
	Temperature	0.005	219.419	
	Humidity	0.001	1077	
	Species_dummy*flower	0.001	1409	
	Species_dummy* temperature	0.0001	1016	
	Species_dummy* humidity	0.000	2627	
	Species_dummy*flower*temperature*humidity	0.042	5778	
	Species_dummy*temperature*humidity	0.006	1115	

Note: VIF: Variance Inflation Factor

Table 4. ANOVA of the regression of flower availability, air temperature, and humidity on colony weight of both stingless bee species

Model		SS	df	MS	F	Sig.
Main	Regression	23.355	4	5.839	42.333	0.000
	Residual	0.690	5	0.138		
	Total	24.045	9			
Interaction	Regression	23.963	8	2.995	36.382	0.128
	Residual	0.082	1	0.082		
	Total	24.045	9			

Table 5. Coefficient of correlation and determination of the regression of flower availability, ambient temperature, and relative humidity, with the colony weight of the two bee species

	R	R-Square	Adjusted R-Square	Std error
Main	0.986	0.971	0.948	0.371
Interaction	0.998	0.997	0.969	0.287

Table 6. The model coefficients of flower availability, ambient temperature, and relative humidity on colony weight across both bee species, *T. sapiens* and *T. clypearis*

Model	Variable	Unstandardized coefficient		t	Sig.
		B	Standard error		
Main	Constant	24.092	5.285	4.558	0.006
	Species (dummy)	-0.736	0.638	-1.152	0.301
	Flower availability	-0.004	0.003	-0.427	0.687
	Temperature	-0.552	0.121	-4.559	0.006
	Humidity	0.022	0.018	1.229	0.274
Interaction	Constant	-5.787	32.038	-0.181	0.886
	Species_dummy	-3.613	3.208	-1.126	0.462
	Flower availability	-0.001	0.002	-0.749	0.591
	Temperature	0.037	0.569	0.065	0.959
	Humidity	0.330	0.206	1.598	0.356
	Species_dummy*flower	0.004	0.003	1.349	0.406
	Species_dummy*temperature	-1.365	-	-1.291	0.266
	Species_dummy*humidity	0.087	0.116	0.753	0.589
	Species_dummy*flower*temperature*humidity	-0.000002	0.000	-1.032	0.490
	Species_dummy*temperature*humidity	-0.003	0.003	-0.959	0.513

Separate simple linear regressions were conducted for each species to evaluate the sensitivity of colony weight to variation in each environmental factor individually (Table 7). For *T. sapiens*, colony weight showed a strong negative association with ambient temperature (R = 0.978, R^2 = 0.956, B = –0.589 g °C^{-1}) with a p-value of 0.004. For *T. clypearis*, the negative association with temperature was even steeper (R = 0.997, R^2 = 0.995, B = –0.994 g °C^{-1}), with a very low p-value (<0.001). Thus, within the observed range, increases in ambient temperature were associated with larger declines in colony weight for *T. clypearis* than for *T. sapiens*.

Across both *Tetragonula* species, ambient temperature exhibited a consistently stronger statistical association with colony weight development than relative humidity (although part of this pattern may be influenced by early observation dynamics following acclimatization), as reflected by higher coefficients of determination for temperature-related models ($R^2 = 0.956\text{-}0.995$) compared with humidity-related models ($R^2 = 0.496\text{-}0.819$) (Figure 5). Within the observed microclimatic range (approximately 25-33°C and 42-85% RH), this pattern indicates that variation in ambient temperature was more closely associated with changes in colony performance than variation in humidity. These relationships, however, are based on only five monthly observations per species and should therefore be interpreted as exploratory statistical associations rather than causal effects. In addition, the inclusion of early observation points may introduce additional variability related to colony adjustment rather than stable environmental responses.

Comparative analyses further indicated that *T. clypearis* exhibited a steeper negative association between colony weight change and increasing temperature and decreasing relative humidity than *T. sapiens*. Within the observed range, larger negative regression coefficients indicate that higher temperatures were associated with greater declines in ΔW for *T. clypearis*. These patterns indicate relative differences in sensitivity between species rather than precise estimates of physiological tolerance limits.

Both species showed positive associations between colony weight and flower availability and between colony weight and relative humidity. The relationship with flower abundance was stronger for *T. sapiens* ($R = 0.905$, $R^2 = 0.819$) than for *T. clypearis* ($R = 0.705$, $R^2 = 0.496$), and the slope for *T. sapiens* was statistically significant ($p = 0.035$) despite the small effective sample size. Relative humidity also exhibited strong positive associations with colony weight ($R^2 = 0.797$ for *T. sapiens* and $R^2 = 0.865$ for *T. clypearis*), with both slopes statistically significant ($p = 0.042$ and $p = 0.022$, respectively). However, given that each regression is based on only five monthly observations (three residual degrees of freedom), the high R and R^2 values, as well as the nominal p-values, should be viewed as descriptive indicators of pattern rather than as robust inferential statistics.

Table 7. R, R^2, and model coefficients for ambient temperature for each bee species (analyzed in separate MLR analyses)

Variable	**Species**	**Value**			**B**	
		R	**R^2**	**sig.**	**value**	**Sig.**
Ambient temperature	*T. sapiens*	0.995	0.999	0.127	-0.589	0.156
	T. clypaeris	0.999	0.999	0.041	-0.994	0.099
Flower availability	*T. sapiens*	0.905	0.819	0.035	0.002	0.035
	T. clypaeris	0.705	0.496	0.184	0.002	0.184
Relative humidity	*T. sapiens*	0.893	0.797	0.042	0.089	0.042
	T. clypaeris	0.930	0.865	0.022	0.107	0.022

Note: R: Coefficient of correlation, R^2: Coefficient of determination, B: Unstandardized coefficients for the variable

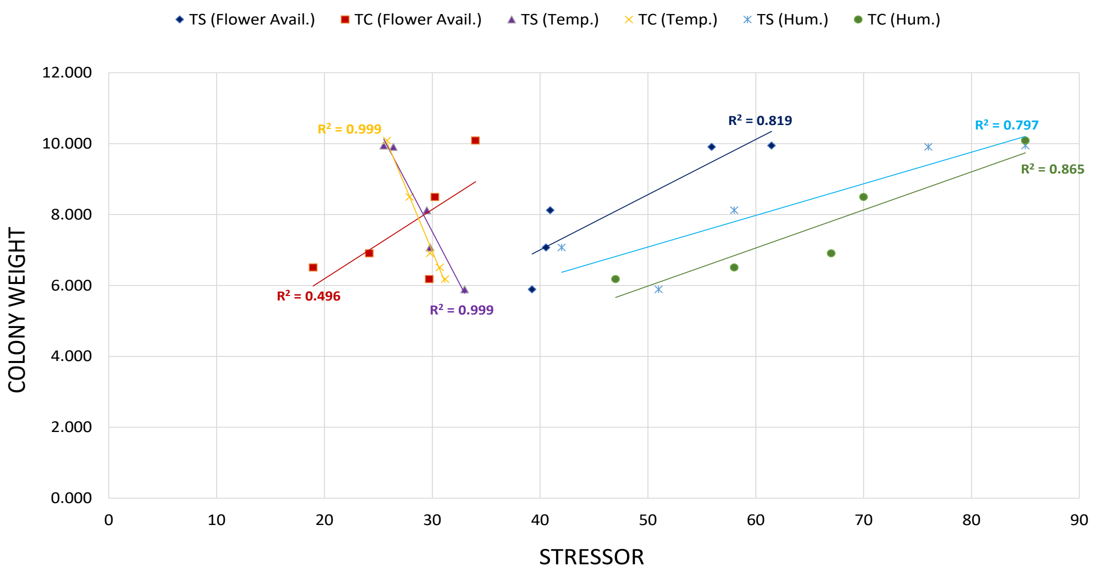

Figure 5. Relationships between the colony weight development of *T. sapiens* and *T. clypearis* with flower availability, ambient temperature, and relative humidity. Note: Y axis: Colony weight change, X axis: Stressors, TS: *T. sapiens*, TC: *T. clypearis*, Temp: Ambient temperature, Hum: Relative humidity, R^2 values are presented close to each slope of the relationship, the steeper slope indicates the greater sensitivity

Within this exploratory framework, the steeper negative temperature slope and the higher sensitivity of colony weight to humidity changes in *T. clypearis* support the interpretation that this species is more susceptible to microclimatic variation than *T. sapiens* under the observed dry-season conditions. Conversely, the stronger association between floral abundance and ΔW in *T. sapiens* suggests a comparatively greater dependence on food supply within the same period.

Pest identification and documentation

Distinctive yellow to reddish-yellow spotting was observed on the surface of propolis in affected colonies (Figure 6.A). Microscopic examination revealed the presence of insects morphologically identified as Psocoptera (*Tapinella* sp.) (Toineno et al. 2012), characterized by delicate four-wing venation, segmented antennae, and two to three tarsal segments per leg. Both adult imagines and nymphal stages were detected (Figure 7). Mite specimens were also recovered from infested propolis. Based on morphological identification, the occurrence of Psocoptera infestation represents a novel record for stingless bee colonies in Central Lombok.

Discussion

Environmental factors: Temperature and humidity as interacting stressors

Colony weight dynamics in *T. sapiens* and *T. clypearis* showed an initial decline followed by partial recovery, forming a consistent two-phase pattern across both species. This early decrease, occurring under still-favorable environmental conditions, likely reflects a transient acclimatization phase rather than a direct response to temperature, humidity, or floral availability. Behavioral disorientation and delayed foraging following relocation to enclosed or semi-enclosed systems have been reported in stingless bees and other managed bee systems (Jaffé et al. 2015). This phase may involve repeated collisions with enclosure structures, delayed initiation of foraging, and increased early worker mortality, all of which can reduce resource intake and contribute to short-term biomass decline. As foraging activity in Meliponini often stabilizes only after a period of environmental familiarization, depending on resource availability and spatial learning (Oliveira et al. 2021; Martins et al. 2023; Jacome-García et al. 2024), part of the initial reduction in colony weight observed in this study likely reflects incomplete behavioral stabilization rather than stable ecological responses. Similar patterns have been reported where colony performance is influenced by post-disturbance or environmental adjustment phases (Jaffé et al. 2015; Grüter 2020). Because this pattern was consistent across colonies and not associated with specific environmental gradients, it is best interpreted as a baseline adjustment rather than a confounding factor, although it warrants caution in early-stage data interpretation.

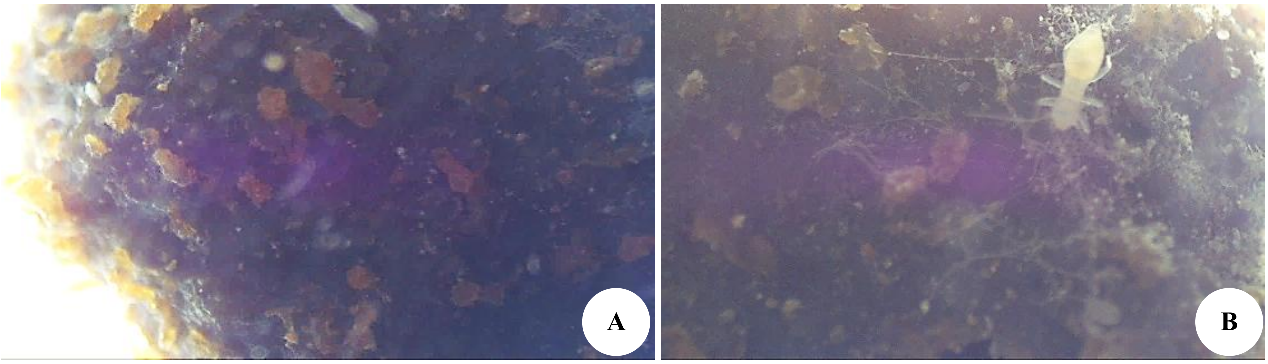

Figure 6. Psocoptera (*Tapinella* sp.) infesting *Tetragonula* colony propolis. A. Magnified view (5×) showing yellow spotting on the propolis surface, indicating fungal colonization and Psocoptera presence. B. Mite specimens recovered from infested propolis. Yellow spotting typically appears where organic decomposition has created ecological conditions favorable for Psocoptera colonization

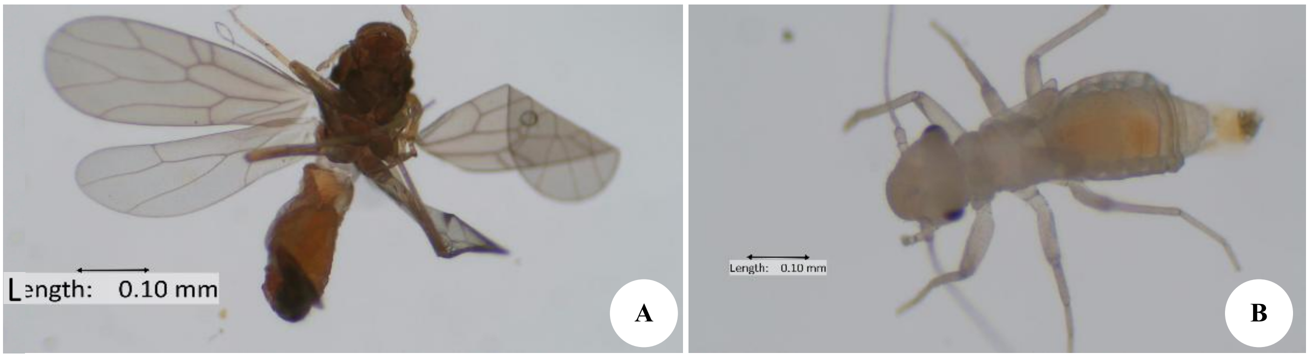

Figure 7. A. Imago and B. Nymphs mites of Psocoptera (*Tapinella* sp.) that invade the stingless bee colony

Following this acclimatization phase, colony weight became more responsive to environmental variation. Temperature showed the strongest association with colony weight across both species, suggesting that microclimatic variation plays a central role in shaping colony performance under dry tropical conditions. This finding is consistent with previous studies demonstrating that temperature regulates foraging activity, brood development, and colony energy balance in stingless bees (Becker et al. 2018; De Moura et al. 2022). In contrast, relative humidity showed weaker associations within the observed range (42-85%), indicating that its limiting effects may become more pronounced only under more extreme drought conditions (Salatnaya et al. 2020). The predominance of temperature over humidity observed here is consistent with previous physiological and behavioral studies of Meliponini. Becker et al. (2018) demonstrated that brood development in *Melipona interrupta* is highly temperature-sensitive, with sublethal effects emerging at 28-30°C and severe larval mortality above 35°C. Similarly, De Moura et al. (2022) reported that temperature plays a primary role in regulating foraging activity and nest dynamics. In contrast, humidity mainly influences food preservation and microbial growth within the hive. During the study period, relative humidity remained within a moderate range, which likely explains its comparatively weaker association with colony performance.

Species-specific patterns further support these interpretations. Floral availability was more strongly associated with colony weight in *T. sapiens*, whereas *T. clypearis* exhibited greater sensitivity to temperature, indicating distinct ecological response strategies between species. These differences may reflect variation in ecological niches and thermal tolerance ranges, as *T. sapiens* has been reported to operate within a relatively constrained but stable microclimatic range compared with more thermotolerant Meliponini species (Erwan et al. 2023). Elevated temperatures are known to reduce foraging efficiency and worker flight activity, thereby limiting energy acquisition at the colony level (Salatnaya et al. 2020; Erwan et al. 2023), which is consistent with the observed declines in colony weight.

Given the small sample size and block-based design, the high R and R^2 values obtained in some models should be interpreted with caution, as they may partly reflect overfitting and small-sample bias. These metrics are therefore better viewed as indicators of association strength within the present dataset rather than as evidence of strong predictive capacity under broader environmental conditions. Overall, the results indicate that environmental effects on colony performance become more interpretable only after stabilization, highlighting the importance of distinguishing early adaptation processes from ecologically meaningful responses.

Food availability as a co-limiting driver of colony development

Food availability showed a consistent statistical association with monthly colony weight change (ΔW) in both *Tetragonula* species during the July–November observation period. The strength of this association varied across species, with a higher coefficient of determination for *T. sapiens* ($R^2 = 0.819$) than for *T. clypearis* ($R^2 = 0.496$). This pattern indicates that, within the observed range of conditions, variation in floral resource availability was more closely associated with changes in colony weight in *T. sapiens* than in *T. clypearis*. As with the microclimate variables, these results represent statistical associations based on a small dataset and should not be interpreted as evidence of strict causal dependency.

This species-specific difference may reflect divergent ecological strategies: *T. sapiens* may be better adapted to environments with relatively predictable floral phenologies, whereas *T. clypearis* may originate from habitats characterized by greater seasonal variability in resource availability, potentially conferring greater flexibility under food-limited conditions. Empirical documentation of these differences remains limited; for example, Erwan et al. (2023) compared the productivity of the same two species in Lombok but did not quantitatively assess stress responses. Despite the stronger association observed for *T. sapiens,* both species exhibited similar regression coefficients for flower abundance (approximately 0.0020 g per additional flower), suggesting comparable marginal responses to changes in floral availability within the observed range.

Although temperature had a significant influence on colony weight, food availability emerged as the most consistent factor associated with colony weight variation (ΔW) across both species. This finding aligns with broader patterns reported in stingless bee research. A meta-analysis by De Lima et al. (2019) synthesizing 47 studies on *Trigona* (*Tetragonula*) spp., identified food scarcity as the most frequently reported cause of colony abandonment (34% of documented cases), surpassing pests (18%), disease (12%), and microclimate stress (8%). Our findings in Central Lombok empirically support this pattern within a specific regional context.

Seasonal declines in floral abundance from July to November coincided with the transition from the wetter early dry season to the drier late dry season. Periods of reduced colony performance were observed during months with lower flower counts, suggesting that declining floral availability may constrain colony development during this seasonal transition. While colony weight reduction appeared more pronounced when flower abundance dropped below roughly 1,500 flowers per block, this value was not statistically tested as a threshold. It should be interpreted only as a contextual reference point derived from this specific dataset.

From a management perspective, maintaining continuous and diverse floral resources throughout seasonal transitions is essential. A balanced, multifloral diet supports larval development, adult worker physiology — including hemocyte production, protein synthesis, and lipid metabolism— and maintains the histological integrity of the digestive system (Bryś et al. 2021). In contrast, monofloral resources may compromise immune function and reduce colony resilience. Accordingly, meliponiculture management in Central Lombok should prioritize floral diversity and staggered flowering phenologies through intentional planting strategies, supplemented by artificial feeding (e.g., sugar syrup and pollen substitutes) during periods of pronounced floral scarcity.

Pest dynamics: Psocoptera in relation to hive microenvironment

The detection of Psocoptera (*Tapinella* sp.) represents, to our knowledge, the first documented occurrence of this taxon in stingless bee hives from Central Lombok and expands the known pest spectrum in Indonesian meliponiculture. Previous studies on stingless bee pests have primarily reported mites, ants, termites, and beetles (Menezes et al. 2009; Pangestika et al. 2018; Toledo-Hernández et al. 2022) with no prior records of Psocoptera in this regional context. The present observations, therefore, contribute new descriptive evidence on hive-associated arthropods in *Tetragonula* colonies.

Psocoptera infestation was consistently observed in association with propolis surfaces exhibiting yellow discoloration and signs of fungal growth. While the present study did not experimentally test causal mechanisms or directly measure internal hive microclimate, this co-occurrence suggests a potential association between Psocoptera presence, organic residue accumulation, and localized microenvironmental conditions within the hive. Psocoptera are known generalist detritivores that feed on molds, starches, and cellulose-rich substrates (Ramel 2020). Under conditions of elevated humidity or reduced ventilation, the antifungal properties of propolis may be locally diminished, potentially creating favorable microhabitats for detritivorous insects, as suggested by previous studies (Velikova et al. 2000; Toledo-Hernández et al. 2022).

From a management perspective, these observations suggest that Psocoptera occurrence in stingless bee hives is more likely linked to microenvironmental conditions within the hives than to direct pathogenic interactions with the bees. Consequently, control strategies should prioritize preventive environmental management rather than chemical intervention. Measures such as improving hive ventilation (e.g., increasing air circulation through enlarged entrance holes or adding mesh ventilation panels), maintaining moderate internal humidity, and conducting regular visual inspections to remove mold-contaminated propolis may reduce the risk of infestation. These practices are consistent with integrated pest management (IPM) approaches commonly recommended for stingless bee cultivation, which emphasize environmental regulation and hygiene over reactive pesticide use (Pangestika et al. 2018; Toledo-Hernández et al. 2022). Given the limited existing literature on Psocoptera in bee hives, the present findings provide preliminary, region-specific insights and highlight the need for controlled experiments to clarify causal mechanisms.

Implication for species-specific meliponiculture management

Taken together, the results indicate that meliponiculture performance in Central Lombok is associated with a combination of floral resource availability, microclimatic conditions, and hive hygiene, rather than any single dominant factor. Previous studies have similarly shown that colony dynamics in stingless bees are influenced by interactions among environmental conditions, seasonal resource availability, and internal colony regulation mechanisms (Maia-Silva et al. 2015, 2016). In tropical environments where seasonal fluctuations in floral resources are common, colonies must adjust brood production and resource allocation to maintain stability under changing ecological conditions.

First, the consistent association between floral availability and colony weight change observed in this study highlights the importance of maintaining continuous flowering resources during the July–November dry-season transition. Floral resource continuity is crucial to stingless bee colony development, as pollen provides the primary protein source for brood production. Experimental research has shown that stingless bee colonies adjust brood production in response to changes in pollen stores, increasing brood cell production when pollen availability is high and reducing brood production when pollen reserves decline (Maia-Silva et al. 2016). Seasonal variation in floral resource availability, therefore, strongly influences colony growth and worker life history in Meliponini species. In addition, studies on pollen resource diversity indicate that stingless bees exploit a wide range of floral species and often show higher pollen diversity than honey bees, highlighting their ecological flexibility in tropical ecosystems (Sayusti et al. 2026). These findings support the interpretation that establishing diverse plant assemblages with overlapping flowering periods may help stabilize colony productivity during seasonal resource shortages.

Second, species-specific differences observed in the relationships between colony weight change and microclimatic variables suggest that hive placement and microclimate management may influence relative colony performance. In the present study, *T. clypearis* exhibited stronger negative associations with elevated temperature and reduced humidity than *T. sapiens*. Environmental conditions such as temperature and humidity are known to influence foraging activity and colony functioning in stingless bees. For example, research on Meliponini species has demonstrated that successful foraging occurs only within specific environmental windows defined by suitable temperature and resource conditions (Maia-Silva et al. 2014). When environmental conditions fall outside these optimal ranges, foraging efficiency and colony productivity may decline. The comparatively weaker associations observed for *T. sapiens* in the present study may therefore indicate a broader tolerance to warmer or drier microclimates within the observed environmental range. However, these differences should be interpreted as relative ecological tendencies rather than strict physiological thresholds.

Third, the detection of Psocoptera associated with propolis degradation underscores the importance of routine hive inspection and maintenance in meliponiculture systems. Stingless bee colonies harbor diverse microbial communities and organic materials, such as propolis and pollen stores, that can support the development of secondary organisms under favorable conditions. Studies on stingless bee colony health emphasize that environmental contamination, pathogens, and opportunistic organisms may affect colony stability if hive hygiene and management practices are inadequate (Rocha et al. 2023; Requier et al. 2024). Regular hive monitoring, removal of deteriorating organic material, and maintaining adequate ventilation within the hive structure are therefore recommended practices to reduce the risk of pest establishment.

Overall, the observed differences between *T. sapiens* and *T. clypearis* indicate that species selection and management strategies should be adapted to local environmental conditions. Rather than recommending a single optimal species for all locations, the results support a context-dependent meliponiculture approach in which management practices consider local microclimate, seasonal dynamics of floral resources, and hive sanitation practices. Such adaptive management strategies are increasingly recommended for sustainable stingless bee cultivation in tropical agroecosystems.

In conclusion, this comparative study examined the responses of *T. sapiens* and *T. clypearis* to biotic (food availability and pests) and abiotic (temperature and humidity) factors within a dry tropical meliponiculture system in Central Lombok. Within the constraints of a small, block-based dataset, variation in ambient temperature showed a stronger statistical association with monthly colony weight change than relative humidity across both species. *T. clypearis* exhibited steeper negative associations with increasing temperature and decreasing humidity compared with *T. sapiens*, suggesting greater sensitivity to microclimatic variation under the observed dry-season conditions. Food availability was consistently associated with colony weight dynamics in both species, with a stronger dependence observed in *T. sapiens*.

The detection of Psocoptera (*Tapinella* sp.) represents, to our knowledge, the first documented record of this taxon in stingless bee hives from Central Lombok and underscores the potential role of hive microenvironment and maintenance in pest occurrence. Taken together, these findings indicate that stingless bee cultivation in Central Lombok is closely associated with the integrated management of floral resources, hive microclimate, and hive hygiene, with management strategies adapted to species-specific responses and local agroecological conditions. Given the limited temporal replication and lack of replicated blocks, future studies incorporating longer-term monitoring, greater spatial replication, and higher-resolution environmental data are needed to strengthen evidence-based recommendations for resilient meliponiculture systems in Central Lombok and similar dry-season environments in West Nusa Tenggara.

ACKNOWLEDGEMENTS

The authors thank the staff of the Center for Implementation of Environmental Instrument Standards and Forestry in Mataram, Indonesia, for providing research facilities and logistical support. We acknowledge the local beekeepers in Pemepek Village, Rarung Sub-district, Central Lombok District, West Nusa Tenggara Province, Indonesia, for access to their cultivation sites.

REFERENCES

Anita D, Musyafa M, Widyastuti SM. 2022. The potency of honey bee forage on beekeeping of *Apis cerana* F. in Wanagama Education Forest, Gunung Kidul, Yogyakarta. Jurnal Ilmu Kehutanan 16 (2): 198-208. https://doi.org/10.22146/jik.v16i2.1738.

Ávila S, Beux MR, Ribani RH, Zambiazi RC. 2018. Stingless bee honey: Quality parameters, bioactive compounds, health-promotion properties, and modification detection strategies. Trends Food Sci Technol 81: 37-50. https://doi.org/10.1016/j.tifs.2018.09.002.

Becker T, Pequeno PACL, Carvalho-Zilse GA. 2018. Impact of environmental temperatures on mortality, sex, and caste ratios in *Melipona interrupta* Latreille (Hymenoptera, Apidae). Sci Nat 105: 55. https://doi.org/10.1007/s00114-018-1577-6.

Brien RMO. 2007. A caution regarding rules of thumb for variance inflation factors. Qual Quant 41: 673-690. https://doi.org/10.1007/s11135-006-9018-6.

Bryś MS, Skowronek P, Strachecka A. 2021. Pollen diet: Properties and impact on a bee colony. Insects 12 (9): 798. https://doi.org/10.3390/insects12090798.

Buchori D, Rizali A, Priawandiputra W et al. 2022. Beekeeping and managed bee diversity in Indonesia: Perspectives and preferences of beekeepers. Diversity 14 (1): 52. https://doi.org/10.3390/d14010052.

De Lima D, Lamerkabel JSA, Welerubun I. 2019. Inventarisasi jenis-jenis tanaman penghasil nektar dan polen sebagai pakan lebah madu *Apis mellifera* di Kecamatan Kairatu Kabupaten Seram Bagian Barat. Agrinimal Jurnal Ilmu Ternak dan Tanaman 7 (2): 77-82. https://doi.org/10.30598/ajitt.2019.7.2.77-82. [Indonesian]

De Moura MEK, Faita MR, Amandio DTT, Bertoldo JG, Lima VP, Poltronieri AS. 2022. Influence of some abiotic factors on the flight activity of stingless bees (Hymenoptera: Meliponini) in Southern Brazil. J Apic Res 63 (4): 603-609. https://doi.org/10.1080/00218839.2022.2028968.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1): 27-46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Erwan, Habiburrohman, Wiryawan IKG, Muhsinin M, Supeno B, Agussalim. 2023. Comparison of productivity from three stingless bees: *Tetragonula sapiens*, *T. clypearis*, and *T. biroi* managed under same feed sources for meliponiculture. Biodiversitas 24 (5): 2988-2994. https://doi.org/10.13057/biodiv/d240553.

Erwan, Purnamasari DK, Resti R, Muhsinin M. 2022. Identification of honeybee feeding plants as source of nectar and pollen. Jurnal Triton 13 (2): 206-220. https://doi.org/10.47687/jt.v13i2.254.

Faqih LFM, Mamat MII, Arshad NA, Ismail WIW, Rahman EA, Azmi WA. 2024. Foraging activity and preference of pollen sources by stingless bee, *Heterotrigona itama* in tropical lowland forest of Terengganu. Malays Appl Biol 53 (3): 171-181. https://doi.org/10.55230/mabjournal.v53i3.2740.

Grüter C. 2020. Stingless Bees: Their Behaviour, Ecology, and Evolution. Springer, Cham. https://doi.org/10.1007/978-3-030-60090-7.

Hadimani BN, Kumaranag K, Dey D. 2024. First report of nesting habits, nest architecture, and foraging behaviour of the stingless bee, *Tetragonula ruficornis* Smith (Hymenoptera: Apidae: Meliponini) from India. Sociobiology 71 (2): e10114. https://doi.org/10.13102/sociobiology.v71i2.10114.

Herwina H, Urrahmah ZS, Mairawita, Yaherwandi, Nurdin J, Janra MN. 2023. Diversity of stingless bees (Apidae: Meliponini) at vegetated habitats in Aul Tungganai Meliponiculture of Lubuk Minturun, Padang, West Sumatra. IOP Conf Ser Earth Environ Sci 1182 (1): 012023. https://doi.org/10.1088/1755-1315/1182/1/012023.

Jacome-García JC, Gonzalez VH, Riaño Jimenez DA, Herrera-Motta AF, Cure JR. 2024. Foraging behavior and the nest architecture of a high-Andean stingless bee (Hymenoptera: Apidae: Meliponini) revealed by X-ray computerized tomography. Apidologie 55: 33. https://doi.org/10.1007/s13592-024-01074-8.

Jaffé R, Pope N, Carvalho AT, Maia UM, Blochtein B, de Carvalho CAL, Carvalho-Zilse GA, Freitas BM, Menezes C, Ribeiro MDF, Venturieri GC, Imperatriz-Fonseca VL. 2015. Bees for development: Brazilian survey reveals how to optimize stingless beekeeping. PLoS One 10 (3): e0121157. https://doi.org/10.1371/journal.pone.0121157.

Janra MN, Herwina H, Salmah S, Rudimansyah, Jasmi. 2020. Identifikasi potensi predator dan hama pada peternakan kelulut (Hymenoptera: Apidae: Meliponini: *Tetragonula*, *Lepidotrigona*) melalui pengamatan cepat di Kabupaten Padang Pariaman, Sumatera Barat. Jurnal Sumberdaya HAYATI 6 (2): 67-74. https://doi.org/10.29244/jsdh.6.2.67-74. [Indonesian]

Maia-Silva C, Hrncir M, Imperatriz-Fonseca VL, Schorkopf DLP. 2016. Stingless bees (*Melipona subnitida*) adjust brood production rather than foraging activity in response to changes in pollen stores. J Comp Physiol A 202: 723-732. https://doi.org/10.1007/s00359-016-1095-y.

Maia-Silva C, Hrncir M, Silva CI, Imperatriz-Fonseca VL. 2015. Survival strategies of stingless bees (*Melipona subnitida*) in an unpredictable environment, the Brazilian Tropical Dry Forest. Apidologie 46: 631-643. https://doi.org/10.1007/s13592-015-0354-1.

Maia-Silva C, Imperatriz-Fonseca VL, Silva CI, Hrncir M. 2014. Environmental windows for foraging activity in stingless bees, *Melipona subnitida* Ducke and *Melipona quadrifasciata* Lepeletier (Hymenoptera: Apidae: Meliponini). Sociobiology 61 (4): 378-385. https://doi.org/10.13102/sociobiology.v61i4.378-385.

Martins AC, Proença CEB, Vasconcelos TNC, Aguiar AJC, Farinasso HC, de Lima ATF, Norrana K, Costa MBR, Carvalho MM, Dias RL, Bustamante MMC, Carvalho FA, Keller A. 2023. Contrasting patterns of foraging behavior in neotropical stingless bees using pollen and honey metabarcoding. Sci Rep 13: 14474. https://doi.org/10.1038/s41598-023-41304-0.

Meikle WG, Holst N, Colin T, Weiss M, Carroll MJ, McFrederick QS, Barron AB. 2018. Using within-day hive weight changes to measure environmental effects on honey bee colonies. PLoS One 13 (5): e0197589. https://doi.org/10.1371/journal.pone.0197589.

Menezes C, Coletto-Silva A, Gazeta GS, Kerr WE. 2009. Infestation by *Pyemotes tritici* (Acari, Pyemotidae) causes death of stingless bee colonies (Hymenoptera: Meliponina). Genet Mol Res 8 (2): 630-634. https://doi.org/10.4238/vol8-2kerr021.

Mularz ML. 2021. East Coast Dune Sunflower, *Helianthus debilis* subsp. debilis. UF/IFAS Extension, University of Florida, Florida.

Oliveira RC, Contrera FAL, Arruda H, Jaffé R, Costa L, Pessin G, Venturieri GC, de Souza P, Imperatriz-Fonseca VL. 2021. Foraging and drifting patterns of the highly eusocial neotropical stingless bee *Melipona fasciculata* assessed by radio-frequency identification tags. Front Ecol Evol 9: 708178. https://doi.org/10.3389/fevo.2021.708178.

Pangestika NW, Atmowidi T, Kahono S. 2018. Additional nest structures and natural enemies of stingless bees (Hymenoptera: Apidae: Meliponinae). Jurnal Sumberdaya HAYATI 4 (2): 42-47. https://doi.org/10.29244/jsdh.4.2.42-47.

Prasad ER, Sunojkumar S. 2013. Nectar robbery in some South Indian Lamiaceae. Ann Plant Sci 2 (10): 386-387.

Priawandiputra W, Azizi MG, Rismayanti, Djakaria KM. 2020. Daftar Spesies Lebah Tanpa Sengat (Stingless Bees) dan Tumbuhan Pakannya di Lubuk Bintialo dan Pangkalan Bulian, Sumatera Selatan. Zoological Society of London, Indonesia. [Indonesian]

Ramel G. 2020. Psocoptera: The Secret World of the Psocids (Bark Lice). https://earthlife.net.

Requier F, Leyton MS, Morales CL et al. 2024. First large-scale study reveals important losses of managed honey bee and stingless bee colonies in Latin America. Sci Rep 14: 10079. https://doi.org/10.1038/s41598-024-59513-6.

Rizqiani KD, Pujiarti R, Sunarta S. 2025. Melissopalynological investigation of *Tetragonula sapiens* honey from Lombok Island, Indonesia. J Asia Pac Biodivers 18 (3): 628-637. https://doi.org/10.1016/j.japb.2025.03.003.

Rocha VM, Portela RD, dos Anjoz JP, de Souza CO, Umsza-Guez MA. 2023. Stingless bee propolis: Composition, biological activities, and its applications in the food industry. Food Prod Process Nutr 5: 29. https://doi.org/10.1186/s43014-023-00146-z.

Rozman AS, Hashim N, Maringgal B, Abdan Kl. 2022. A comprehensive review of stingless bee products: Phytochemical composition and beneficial properties of honey, propolis, and pollen. Appl Sci 12 (13): 6370. https://doi.org/10.3390/app12136370.

Salatnaya H, Kahono S, Suhri AGMI, Ismanto A, Anggraeni I, Fara SB, Hasan PA, Hashifah FN. 2023. Diversity, distribution, nesting, and foraging behavior of stingless bees and recent meliponiculture in Indonesia. In: Aziz A (eds.). Melittology - New Advances. IntechOpen, London. https://doi.org/10.5772/intechopen.1003758.

Salatnaya H, Widodo WD, Winarno, Fuah AM. 2020. The influence of environmental factors on the activity and propolis production of *Tetragonula laeviceps*. Jurnal Ilmu Produksi dan Teknologi Hasil Peternakan 8 (2): 67-71. https://doi.org/10.29244/jipthp.8.2.67-71.

Santoso L, Indriyanto, Asmarahman C. 2022. Jenis tumbuhan sumber pakan lebah madu di Kebun Lebah Simpur Desa Kecapi Kecamatan Kalianda. Jurnal Kehutanan Indonesia Celebica 3 (1): 1-12. http://dx.doi.org/10.33772/jc.v3i1.24680. [Indonesian]

Sayusti T, Raffiudin R, Djuita NR, Perwitasari-Farajallah D, Batubara I, Priawandiputra W, Sitompul R, Jahnk SL, Behling H. 2026. Melissopalynological analysis revealed a higher pollen diversity in stingless bees than in honey bees. HAYATI J Biosci 33 (1): 196-203. https://doi.org/10.4308/hjb.33.1.196-203.

Suderajat A, Riyanto, Mulawarman M. 2021. The types of trigona bee (Apidae: Meliponinae) in three different habitats in South Sumatra. Jurnal Biologi Tropis 21 (1): 206-212. https://doi.org/10.29303/jbt.v21i1.2461.

Szigeti V, Kőrösi Á, Harnos Am Nagy J, Kis J. 2016. Comparing two methods for estimating floral resource availability for insect pollinators in semi-natural habitats. Ann Soc Entomol Fr (N.S.) 52: 289-299. https://doi.org/10.1080/00379271.2016.1261003.

Tahir H, Irundu D, Rusmidin. 2021. Jenis tumbuhan pakan lebah (*Trigona* sp.) di Desa Mirring Polewali Mandar Sulawesi Barat. Jurnal Nusa Sylva 21 (2): 39-47. https://doi.org/10.31938/jns.v21i2.339. [Indonesian]

Toineno ES, Watiniasih NL, Suartini NM. 2012. Keragaman famili Psocoptera di Nusa Penida Kabupaten Klungkung, Bali. Jurnal Biologi Udayana 16 (1): 19-22. [Indonesian]

Toledo-Hernández E, Pena-Chora G, Hernandez-Velazquez VM, Lormendez CC, Toribio-Jiménez J, Romero-Ramírez Y, León-Rodríguez R. 2022. The stingless bees (Hymenoptera: Apidae: Meliponini): A review of the current threats to their survival. Apidologie 53 (1): 8. https://doi.org/10.1007/s13592-022-00913-w.

Velikova M, Bankova V, Marcucci MC, Tsvetkova I, Kujumgiev A. 2000. Chemical composition and biological activity of propolis from Brazilian Meliponinae. Z Naturforsch C J Biosci 55 (9-10): 785-789. https://doi.org/10.1515/znc-2000-9-1018.

Vignesh BS, Anujaa B, Manickavasagam S. 2024. Pollination efficiency and foraging activity of stingless bee (*Tetragonula iridipennis* sp. group) in open field coriander cropping. J Appl Hortic 26 (1): 37-40. https://doi.org/10.37855/jah.2024.v26i01.07.

Wahyuningsih E, Syaputra M, Suparyana PK, Maya IPAT, Lestari AT. 2022. Identifikasi diversitas sumber pakan lebah berbasis lahan pekarangan pada meliponikultur. Jurnal Penelitian Hutan Tanaman 19 (1): 29-44. https://doi.org/10.20886/jpht.2022.19.1.29-44. [Indonesian]

Zacepins A, Ozols N, Kviesis A, Gailis J, Komasilovs V, Komasilova O, Zagorska V. 2022. Evaluation of the honey bee colonies' weight gain during the intensive foraging period. Agron Res 20 (2): 457-468. https://doi.org/10.15159/AR.22.017.