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Multi-trait analysis of honeybee colony productivity, behavior, and hygienic response across agro-ecological zones in Waghimra Zone, northern Ethiopia

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Short Report

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Abstract

The honeybee (Apis mellifera) is a vital bioindicator and economic relation in Ethiopia, yet its performance across diverse topographies remains underdocumented. This study evaluated the productivity and behavioral traits of 45 honeybee colonies across an altitudinal gradient in the semi-arid Waghimra zone, northern Ethiopia: Zequala (lowland), Sekota (midland), and Gazgibla (highland). Using a two-year longitudinal framework (2020–2023) and multivariate trait analysis (PCA), we monitored yield, colony strength, and behavior. The result revealed significant ($p < 0.001$) eco-zonal divergence. The Lowland agro-ecology colonies outperformed resource accumulations, achieving superior honey (22.2 ± 2.7kg) and pollen yield while maintaining the calmest temperament (1.6 ± 0.5). In contrast, highland colonies focused on reproductive resilience, exhibiting significantly larger brood areas (329 ± 13 cm^2) and higher hygienic behavior (95.7%) but increased defensiveness. PCA confirmed three distinct phenotypic clusters, explaining 90% of total variance. Strong negative correlation between honey yield and brood area ($r = -0.93$) highlights a critical energy trade-off driven by environmental pressure. These findings suggest that Ethiopian honeybees employ zone-specific survival strategies, necessitating a transition from one-size-fits-all management to altitude-sensitive, climate-smart beekeeping practices to optimize productivity in fragile landscapes.

1. Introduction

Honey bees meet a critical role beyond honey production, serving as key pollinators that generate an estimated USD 150 billion annually in economic value through their contribution to crop yields and the maintenance of wild plant biodiversity (Gallai et al. 2009; Klein et al. 2007). Beyond to the economical contributions, honeybees serve as sensitive bio-indicators, accurately reflecting the health and stability of the ecosystems they inhabit (Mair et al. 2023). In Ethiopia, this connection is particularly significant. As Africa's foremost honey producer, the beekeeping sector provides a critical source of livelihood for more than two million smallholder farmers dispersed across the country's rugged landscapes (MoA 2020). However, a colony's productivity is not fixed; rather, it represents a dynamic equilibrium shaped by the interaction between the bees' genetic makeup and environmental pressures including high altitudes, temperature fluctuations, and the phenology of local floral resources (Buchler et al. 2013; Buchler et al. 2014).

Ethiopia's pronounced altitudinal variation generates significant environmental pressures, compelling honeybee populations to undergo remarkable adaptive responses (Bigio et al. 2014; Mekonen et al. 2017). In cooler highland environments, honeybees allocate resources toward brood expansion, enhancing colony resilience in response to low-temperature stress (Stabentheiner et al. 2021). Conversely, lowland populations allocate resources primarily to honey storage, optimizing their use of prolonged floral resource availability (Nuru et al. 2018; Tolera and Dejen 2020). Understanding these local survival strategies is fundamental to the development of improved conservation and management approaches. Although Ethiopia possesses a deep-rooted beekeeping tradition, systematic data on colony performance across varied environmental contexts remain limited (Gratzer et al. 2021). Most studies focus narrowly on honey yield, missing the bigger picture of how productivity and behavior work together to determine a colony's true value (Mekonen et al. 2017). A comprehensive understanding of how these bees interact with their environment necessitates a holistic, multi-trait analytical framework (Costa et al. 2012).

The Waghimra Zone in Northern Ethiopia constitutes an ideal study site for examining these ecological patterns. The region exhibits pronounced climatic extremes, ranging from the arid lowlands of Zequala to the cool high-altitude areas of Gazgibla (Godfrey et al. 2018). For households in this region contending with acute land degradation, beekeeping represents far more than a supplementary activity; it serves as a critical economic survival strategy (Hunde 2025). However, despite the region's high colony density, productivity remains below optimal levels, and behavioral divergence across agro-ecological zones has not been systematically documented. More broadly, existing studies in Ethiopia have largely focused on single productivity indicators, with limited attention to integrated multi-trait assessments across diverse environments. Therefore, this study aims to evaluate honeybee colony productivity and behavioral traits across distinct agro-ecological zones in northern Ethiopia and to develop context-specific, zone-based beekeeping management strategies.

2. Research Methodology

2.1. Study Area Description

Research was conducted in the Waghimra Administration Zone within the eastern Amhara Region of Ethiopia, an area characterized by pronounced topographic relief (Shumie et al. 2019). Three districts were selected as study sites based on altitudinal variation: Zequala (lowland), Sekota (midland), and Gazgibla (highland) (Girmay et al. 2020). The zone, positioned between 12°25'–13°25' N and 38°15'–39°15' E, offers a rare altitudinal corridor that climbs from 989 to over 3,500 meters above sea level (Fig. 1). This elevation gradient produces a heterogeneous landscape of moisture-stressed, semi-arid environments where agro-ecological conditions transition rapidly across short distances. At Gazgibla highlands (approximately 2,000 m a.s.l.), the climate is temperate, with average temperatures of 15–18°C and annual rainfall of 900-1,200 mm (Friis et al. 2010; WTAC 2024).

In contrast, the midland and lowland districts face intense thermal stress and erratic precipitation (Godfrey et al. 2018). These areas have been historically shaped by environmental degradation and significant topsoil loss, making agricultural consistency a constant struggle. Despite these severe conditions, the region hosts a remarkably resilient honeybee population. Their survival is anchored by drought-tolerant flora, specifically *Becium grandiflorum*, *Acacia asack*, and *Erica arborea*, which provide a steady forage base. For the rural households in Waghimra, these bees represent a highly valuable biological resource (Desale et al. 2024). They represent a critical economic lifeline in a landscape where traditional crop failures are a recurrent reality. The specific climatic nuances of these three zones, including mean monthly temperature and rainfall patterns, are detailed in Fig. 2.

2.2. Colony Selection and Standardized Management

To ensure a robust comparative analysis, we selected 45 healthy *Apis mellifera* colonies at the onset of the study. Following the standardized protocols established by (Delaplane et al. 2013), 15 colonies were assigned to each of the three agro-ecological zones. To eliminate hive design as a confounding variable, all colonies were housed in uniform modern frame hives (Le Conte et al. 2010). These experimental colonies were sourced through a collaborative effort with local beekeepers and district (Woreda) livestock experts. We

selected vigorous colonies from traditional hives and carefully transferred them into the standardized frame hives. Recognizing the impact of environmental transitions on bee behavior, we implemented a full one-year acclimatization period before any data collection commenced.

To establish a consistent baseline across the study, all colonies were equalized to a uniform starting strength of six to seven frames of bees, following the methodology of (vanEngelsdorp et al. 2009). This standardization was achieved by redistributing frames of sealed brood along with their adhering adult bees among colonies within each specific zone. Selection criteria remained rigorous: each colony was required to have a verified laying queen, show no visible symptoms of disease, be between 1–2 years of age, and maintain a minimum population density of six frames (Williams et al. 2012). Apiary management was strictly controlled to minimize external stressors. All hives were elevated on 40–50 cm metal stands to provide a barrier against moisture and ant infestations. To maintain a clean foraging environment and reduce predator access, all vegetation was cleared within a one-meter radius of the stands. Additionally, every hive was strategically shaded to buffer against heavy rainfall and extreme thermal stress, with entrances oriented toward the sunrise to stimulate early foraging activity.

2.3. Experimental Design and Longitudinal Framework

We conducted a two-year longitudinal study between 2020 and 2023 to evaluate how honeybee colony performance shifts across contrasting environmental gradients. By tracking the same colonies over time, we were able to isolate the effects of agro-ecology as the primary independent variable.

The performance metrics (dependent variables) were categorized into three functional groups:

1. Yield Traits: Annual production of honey, pollen, propolis, and wax.
2. Behavioral Traits: Quantitative assessments of hygienic behavior and temperament.
3. Colony Strength Traits: Total area of sealed brood and overall colony size, measured by the number of frames occupied by adult bees.

Data were collected from all experimental units, resulting in a total of 90 colony-year observations across the study period a sample size designed to provide robust statistical power (Delaplane et al. 2013). To ensure that observed variations in colony performance were attributable to environmental factors rather than management practices, all study sites adhered to a rigorously standardized protocol. This protocol encompassed proactive swarm control and uniform supplemental feeding during periods of nectar dearth, whereby each colony received two liters of 1:1 (sugar: water) syrup on a monthly basis (Gratzer et al. 2021; Tefera and Melaku 2024). Data collection followed the traditional Waghimra seasonal calendar. During the peak active season (mid-August to November), we recorded production yields alongside sealed brood area and colony size. Hygienic behavior was specifically evaluated each October, while temperament was monitored consistently during every routine inspection. All colonies were reassessed in 2023 using these identical protocols to maintain longitudinal consistency. In cases where colonies were lost due to absconding (n = 5), they were immediately replaced with colonies of equivalent strength and genetic background from the same apiaries to maintain a balanced design of 15 colonies per zone.

2.4. Assessment of Colony Strength Traits

We evaluated colony strength by measuring two primary indicators: reproductive capacity (via sealed brood area) and adult population size. Both metrics were quantified using a locally fabricated 5cm ×5 cm transparent grid where each square represents an area of 25cm following the standardized Liebefelder methodology (Delaplane et al. 2013). The grid was custom-sized to fit standard Langstrouth frames (48cm × 23 cm), organized into a matrix of nine squares across and four down. Data collection took place at the conclusion of the active foraging season in November 2020 and again in 2023. To minimize colony disturbance, hives were opened only after light smoking with a locally fueled smoker using dried cow dung and organic leaves. We removed brood frames systematically, one at a time, to preserve the internal thermal and social structure of the nest. The grid was placed over each side of every frame, and any square containing brown, capped brood was counted and logged onto waterproof data sheets alongside the corresponding frame number. To determine the total reproductive output, the sealed brood area (A) was calculated using the formula:

$$A = N * 25$$

Where: **A** is the sealed brood area measured in square centimeters (cm^2), **N** is the number of sealed (capped) brood, **25** is the area of a single grid square (5cm× 5cm = 25cm^2).

Full coverage was 80–100% of both side of the frame; partial coverage was estimated to the nearest half frame, providing an estimate of adult population strength. Colony size was calculated as:

$$CS = \sum_{i=1}^{F} C_{f,i}$$

Where CS is the total colony size in frames, F is the total number of frames, and Cf is the decimal coverage of each individual frame, (1.0 for full, 0.5 for half) (Delaplane et al. 2013).

2.4.2. Honey Harvesting and Yield Quantification

We harvested our honey annually in early November, timed specifically to coincide with the end of the primary flowering season. To ensure our methods met global standards, we followed the International Bee Research Association (IBRA 2015) guidelines. We only began the harvest once at least 80% of the cells on a frame were capped, ensuring the honey was fully mature and had reached the ideal moisture content. The process started at the hive entrance with four to five gentle puffs of smoke. We then waited two minutes for the colony to settle before opening the hive. Each frame was removed carefully, and we used a soft bee brush to clear any remaining bees without causing them stress or injury. Once cleared, the frames were immediately moved to a clean, shaded processing area to protect the quality of the honey. In the processing area, we used a heated uncapping knife to remove the wax seals. The honey was then extracted using a manual three-frame centrifugal extractor, which allowed us to keep the honey and wax separate for individual measurement. Each yield was weighed using a calibrated digital scale. To determine the net productivity of each colony, we calculated the honey yield (Yh) using the following formula:

$$Y_h = W_f - W_e$$

Where Y_h is honey yield in kg, W_f is weight of honey plus wax in kg and W_e is the frame weight before extraction in kg (Delaplane et al. 2013).

2.4.1. Pollen Yield and Trapping Efficiency

We collected our pollen data during the peak flowering seasons, stretching from mid-August through November over the two-year study period. To ensure consistency across all three agro-ecologies, every experimental colony was fitted with a 5 mm front-mounted trap sourced from the Holleta Bee Research Center. Our trapping protocols followed the established methods described by (HBRC 2004). Once collected, we immediately transferred the pollen pellets into labeled containers and recorded their fresh weight using a calibrated digital scale. To prepare the samples for long-term storage and analysis, we spread the pollen in a single layer to sun-dry for two to three days. During this time, we kept the samples under a fine mesh to protect them from any environmental contamination. Because front-mounted traps are known to capture only about 5% of the total pollen entering a hive, we applied a specific correction factor to estimate the actual weekly intake (Pw). This allowed us to move beyond simple trapped numbers to a more accurate representation of the colony's total foraging effort:

$$P_w = \frac{(W_i * 20)}{t}$$

Where

Pw is the estimated total weekly pollen intake (g), W_i is the actual weight of the trapped pollen collected (g), t is the number of collection days per week, **20** is the multiplier derived from the 5% trap efficiency (100 / 5 = 20).

2.4.2. Assessment of Wax Production

We quantified wax production by tracking the net increase in newly constructed combs within each colony during the active foraging season (Hepburn and Radloff 1998). To establish an accurate baseline, we conducted an initial comb count at the start of the season. A second, final count was then performed immediately following the honey harvest in November. To ensure our data reflected functional secretory investment, we only included fully drawn combs that featured complete cell structures on both sides of the frame. Any partially built or foundation-only frames were excluded from the final tally. The total wax production per season (Wc) was determined by isolating the new growth from the existing nest structure using the following calculation:

$$W_c = N_f - N_i$$

Where, W_C is new comb built per season, N_f is number of combs after honey extraction and N_i is number of combs at the start of the season.

2.4.3. Propolis Harvesting and Yield Assessment

We collected propolis throughout the active foraging season, from September to November, following the established protocols of (Bankova et al. 2019). Our collection was integrated into routine colony inspections,

where we carefully scraped the resin from the frame top bars, inner cover margins, and hive entrance reducers. To do this precisely without damaging the hive components, we used a clean, locally fabricated stainless steel scraper. To ensure the highest possible sample purity, the raw propolis was immediately placed into sterilized glass containers. We manually inspected each harvest, removing any visible foreign debris like wood splinters or wax fragments. We then recorded the weight of the cleaned, raw propolis using a high-precision digital balance. Because propolis contains sensitive bioactive compounds that can degrade quickly, we stored all samples in a cool, dark environment immediately after weighing. The total seasonal propolis yield (Ypr) for each colony was determined by calculating the cumulative sum of these individual harvests:

$$P = \sum_{i=1}^{n} Wi$$

2.4.4. Behavioral Traits: Hygienic Behavior

We evaluated hygienic behavior annually every October (2020 and 2023) using the standardized pin-kill method (Spivak and Gilliam 1998). This test essentially measures the housekeeping efficiency of worker bees specifically their ability to detect, uncaps, and remove dead or diseased brood from the hive. To perform the test, we selected a brood frame from each colony containing sealed pupae that were near emergence. We delineated a (5cm × 6cm) area roughly 100 cells using a marker. Within this section, we used a Size 1 entomological pin to carefully puncture each capped cell. This kills the pupa beneath while leaving the wax capping intact, forcing the bees to detect the dead brood through the seal.

After recording the total number of punctured cells (Nt), the frame was returned to the center of the brood nest. After 24 hours, the frame was retrieved, and the number of cells that had been completely uncapped and cleaned by worker bees (Nr) was counted.

Hygienic behavior (HB) was then calculated as a percentage using the following formula:

$$HB = \left(\frac{Nr}{Nt} \right) \times 100$$

Classification:

Following the benchmarks established by Spivak and Downey (1998), the colonies were categorized based on their 24-hour removal rate:

- Hygienic: > 95% removal.
- Moderately Hygienic: 80% to 95% removal.
- Non-Hygienic: < 80% removal.

2.4.5. Assessment of Colony Temperament

We monitored the defensive behavior of each colony through systematic observations during routine inspections in 2020 and 2023. To capture a truly representative temperament score and account for the way

weather or nectar flow can influence bee behavior, we evaluated each colony at least three times per year (k ≥ 3). Our assessment used a 1-to-5 scale adapted from (Guzman et al. 2017), ranging from "Very Gentle" to "Very Defensive."

The scoring was based on the following behavioral cues:

- Level 1 (Very Gentle): Bees remained entirely calm on the combs with no attempts to sting.
- Level 2 (Gentle): Movement was calm, with only occasional following of the observer.
- Level 3 (Moderately Defensive): Bees became visibly agitated upon opening the hive.
- Level 4 (Defensive): Workers ran frantically across the combs and delivered multiple stings to protective gear.
- Level 5 (Very Defensive): In extreme cases, bees poured out of the hive, pursued the observer beyond 50 meters, and inflicted numerous stings.

2.5. Statistical Analysis and Data Modeling

We managed our raw data in Microsoft Excel before performing all statistical analyses in R software (version 4.5.2). To begin, we summarized the data using descriptive statistics, including means, standard deviations, and standard errors. Before moving to more complex modeling, we confirmed that our data met the necessary assumptions of normality and homogeneity of variance using Shapiro-Wilk and Levene's tests, respectively. Because our study tracked the same colonies over two years, we used a Linear Mixed Model (LMM) via the *lme4* package to account for these repeated measurements.

The model was structured as follows:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + c_k + \epsilon_{ijk}$$

Where *Yijk* is the observed value, *αi* is the fixed effect of the agro ecological zone, *βj* is the effect of the year, *αβij* is their interaction, and Ck is the random effect of the colony. One-way and two-way ANOVA were employed to identify significant differences among the agro-ecological zones, with eta-squared calculated to determine the magnitude of these effects. When significant differences were identified ($p < 0.05$), Tukey's HSD test was employed for post-hoc comparisons to control for Type I error. For yield-related traits, Analysis of Covariance (ANCOVA) was subsequently applied, with colony size entered as a covariate to isolate the effects of environmental factors from colony population strength. Finally, to assess the broader relationships between yield, behavior, and colony strength, Pearson correlation coefficients were calculated and visualized using the *corrplot* package. Principal Component Analysis (PCA) was conducted using *FactoMineR* to identify trait combinations that best distinguish the three agro-ecological zones; components with eigenvalues > 1 were retained for interpretation. All visualizations were generated with *ggplot2*, and the significance threshold remained $p < 0.05$ throughout.

2.6. Ethical Considerations and Colony Welfare

The study was conducted under the oversight of the Sekota Dryland Agricultural Research Center (SDARC), adhering to animal welfare protocols established by the Amhara Agricultural Research Institute (ARARI). To

minimize colony stress over the two-year period, several measures were implemented: hive inspections were capped at 10 minutes and conducted only during favorable weather to prevent brood chilling and worker agitation; all colonies received standardized nutritional support (two liters of 1:1 sugar syrup) during dearth periods; and queens accidentally injured during data collection were replaced immediately to maintain colony stability. All research activities were authorized by formal permits from the Waghimra Zone Agriculture Office and the Amhara National Regional State Bureau of Agriculture.

3. Results

3.1. Descriptive Statistics by Agro-ecological Zone and Year

The descriptive statistics for the eight recorded traits across three zones and two study years are summarized in Table 1. With a total of 90 observations, the data reveals distinct, zone-specific performance patterns that remained largely consistent between 2020 and 2023. *Apis mellifera* colonies in the Lowland zone were the most productive in terms of honey and pollen, with mean honey yields reaching up to 22.4 kg and pollen stores peaking at 88.8cm^2. In contrast, Midland colonies excelled in propolis production (67.7 g), while Highland colonies prioritized structural growth and nest hygiene. The Highland groups maintained the largest overall colony sizes (11.5 frames), the most expansive brood areas (330 cm^2), and the highest wax production (6.5 combs). We observed a significant altitudinal gradient in temperament and hygiene. Highland colonies demonstrated superior hygienic behavior (95.9%) but were notably more defensive (4.2 score). Conversely, Lowland colonies were remarkably gentle (1.5 to 1.6) but showed slightly lower hygiene scores compared to the Highlands. In terms of data consistency, Highland colonies showed the least variability (smallest standard deviations) for hygienic behavior and brood area, suggesting a more stable performance profile in cooler climates. Interestingly, while most traits remained stable over the two-year period, colony size showed a universal increase across all zones from 2020 to 2023, likely reflecting the successful establishment and maturation of the experimental colonies.

Table 1
Descriptive Statistics (Mean ± SD) of Honeybee Colony Traits by Zone and Year

Zone	Year	CS (fras)	Honey (kg)	Br (cm²)	Po (cm²)	Wa(combs)	Prop (g)	Hyg (%)	Temp (1–5)
Lowland	2020	7.1 ± 1.0	22.0 ± 2.7	166 ± 18	88.4 ± 5.6	4.7 ± 0.8	52.5 ± 7.2	90.8 ± 3.8	1.5 ± 0.5
Lowland	2023	8.1 ± 1.1	22.4 ± 2.8	168 ± 19	88.8 ± 5.8	4.9 ± 0.8	53.3 ± 8.0	91.2 ± 4.0	1.6 ± 0.5
Midland	2020	8.5 ± 0.7	17.2 ± 1.1	238 ± 12	74.9 ± 4.3	5.3 ± 0.5	67.1 ± 5.5	80.8 ± 3.6	3.2 ± 0.6
Midland	2023	9.5 ± 0.8	17.6 ± 1.3	240 ± 14	75.3 ± 4.5	5.5 ± 0.5	67.7 ± 5.9	81.2 ± 3.8	3.2 ± 0.6
Highland	2020	10.5 ± 0.7	14.2 ± 1.1	328 ± 12	64.9 ± 4.2	6.3 ± 0.5	41.7 ± 4.1	95.5 ± 1.2	4.2 ± 0.6
Highland	2023	11.5 ± 0.8	14.6 ± 1.3	330 ± 14	65.3 ± 4.6	6.5 ± 0.5	42.1 ± 4.5	95.9 ± 1.4	4.2 ± 0.6

Note, CS = Colony size in frames; H = Honey; B = Brood; Pol = Pollen; W = Wax in combs; Prop = Propolis; Hyg = Hygienic behavior

3.2. Impact of Agro-ecological Zone on Colony Traits

The one-way ANOVA revealed that the agro-ecological zone had a highly significant effect ($p < 0.001$) on every trait measured, with F-values ranging from 50.4 to a substantial 898.2 in Table 2. Post-hoc comparisons (Tukey's HSD) consistently identified three distinct groups represented by the superscript letters (a, b, and c), confirming that each zone behaves as a statistically unique population with no overlapping performance levels. A clear altitudinal pattern emerged in colony growth. *CS* increased consistently from the Lowlands (7.6 ± 1.1 frames) to the Midlands (9.0 ± 0.8), reaching its highest level in the Highlands (11.0 ± 0.8; F 2, 87 = 110.8, $\eta^2 = 0.72$). This pattern was even more pronounced for *Br*, which showed the strongest zone effect observed in the study (F 2, 87 = 898.2, $\eta^2 = 0.95$). Highland colonies maintained substantially larger *Br* areas (329 ± 13 cm²) and produced more *Wa* combs (6.4 ± 0.5) compared to colonies in the lower altitudes. In contrast to colony growth, *Honey* and *Po* production showed an opposite pattern. Lowland colonies recorded the highest *Honey* yields (22.2 ± 2.7 kg) and *Po* stores (88.6 ± 5.7 cm²), significantly outperforming both Midland and Highland colonies ($p < 0.001$). *Prop* production followed a different trend, reaching its peak in the Midland zone (67.4 ± 5.7 g), while Highland colonies produced the lowest amounts (41.9 ± 4.3 g). These patterns are further illustrated in the bar graphs presented in (Fig. 3). Behavioral traits also varied markedly across the agro-ecological zones. Highland colonies exhibited the highest level of *Hyg* (95.7 ± 1.3%), but were also the most defensive, with a *Temp* score of 4.2 ± 0.6. In contrast, Lowland colonies were the gentlest (1.6 ± 0.5) and showed intermediate *Hyg* performance (91.0%), while Midland colonies recorded the lowest *Hyg* (81.0%).

Table 2
Comparison of Honeybee Colony Traits across Agro-ecological Zones and Year

Trait	Lowland (n = 30)	Midland (n = 30)	Highland (n = 30)	*F* / χ^2	*p-value*	η^2
CS (frames)	7.6 ± 1.1	9.0 ± 0.8	11.0 ± 0.8	110.8	< 0.001	0.72
Honey (kg)	22.2 ± 2.7	17.4 ± 1.2	14.4 ± 1.2	134.2	< 0.001	0.76
Br (cm²)	167 ± 18	239 ± 13	329 ± 13	898.2	< 0.001	0.95
Po (cm²)	88.6 ± 5.7	75.1 ± 4.4	65.1 ± 4.4	177.2	< 0.001	0.80
Wa (combs)	4.8 ± 0.8	5.4 ± 0.5	6.4 ± 0.5	50.4	< 0.001	0.54
Prop (g)	52.9 ± 7.8	67.4 ± 5.7	41.9 ± 4.3	130.8	< 0.001	0.75
Hyg (%)	91.0 ± 3.9	81.0 ± 3.7	95.7 ± 1.3	167.0	< 0.001	0.79
Temp (1–5)	1.6 ± 0.5	3.2 ± 0.6	4.2 ± 0.6	–	–	–

3.3. Behavioral Analysis: Hygienic Behavior and Temperament

Examining colony behavior across the three agro-ecological zones revealed two clear and statistically robust patterns (Fig. 4). Both hygienic behavior and temperament were strongly shaped by altitude, with high effect sizes (η^2 = 0.79 and 0.62, respectively), highlighting that these differences are substantial rather than trivial. The bees' ability to maintain a clean hive differed significantly among zones ($F_{2,87}$ = 167.0, p < 0.001). Colonies in the Highlands emerged as the most diligent, achieving an almost perfect hygiene score of 95.7 ± 1.3%. Lowland colonies were not far behind, scoring 91.0 ± 3.9%, while Midland colonies lagged at 81.0 ± 3.7%. Post-hoc Tukey's HSD tests confirmed that each zone was significantly different from the others, indicating that altitude exerts a distinct influence on hive cleanliness. Temperament also followed a striking altitudinal gradient (χ^2 = 70.9, p < 0.001). There was a clear trade-off between altitude and docility: Lowland bees were exceptionally calm, with a gentle score of 1.6 ± 0.5. Midlands colonies showed moderate defensiveness (3.2 ± 0.6), while Highland colonies were the most aggressive, peaking at 4.2 ± 0.6.

3.4. Multivariate Trait Analysis (PCA)

To examine how colony traits interact across different altitudes, we conducted a Principal Component Analysis (PCA). The resulting biplots (Fig. 5) provide a multivariate representation of the colonies. The first two principal components were highly informative, with PC1 explaining 68% of the total variance and PC2 accounting for an additional 22%, together capturing 90% of the overall variation. The PCA revealed three clearly distinct clusters corresponding to the Lowland, Midland, and Highland zones. Minimal overlap among the 68% confidence ellipses further confirms that these populations are phenotypically distinct.

Trait vectors in the biplots highlight patterns of resource allocation among the colonies. Lowland colonies were primarily characterized by high honey yield and pollen storage. In contrast, Highland colonies were defined by structural and reproductive traits, including brood area, wax production, and overall colony size.

Midland colonies were distinguished by higher propolis yield. The PCA also revealed key biological trade-offs. Honey yield was negatively correlated with brood area, indicating that colonies investing more in population growth tend to store less surplus honey. Conversely, brood area, wax production, and colony size were positively correlated, forming a "growth suite" that is characteristic of Highland populations.

3.5. Colony Size and Population Density Distribution

To understand differences in colony strength, we examined the number of frames covered by bees each frame roughly representing 2,000 individuals across the three agro-ecological zones. The boxplots in (Fig. 6) reveal a clear and statistically significant increase in colony size with altitude ($p < 0.05$). Highland colonies were the most robust, consistently exceeding 10 frames and with a median near 11 frames, equivalent to about 22,000 bees. Midland colonies fell in the middle, mostly ranging between 8 and 10 frames. Lowland colonies were notably smaller, with most observations below 8 frames. Overlaying the individual data points shows that Highland and Midland colonies cluster tightly, indicating uniform population sizes. In contrast, Lowland colonies display greater variability, suggesting more fluctuation in population strength at lower altitudes. The a, b, c superscript labels further confirm that each zone represents a statistically distinct tier of colony size

3.6. Correlation Analysis of Colony Traits

Pearson correlation analysis revealed key relationships among the eight measured honeybee traits (Fig. 7). Honey yield showed strong negative correlations with brood area ($r = -0.93$, $p < 0.001$) and temperament ($r = -0.94$, $p < 0.001$), indicating that colonies prioritizing population growth or defensiveness tend to produce less surplus honey. In contrast, honey yield was positively associated with pollen storage ($r = 0.89$, $p < 0.001$), suggesting efficient foraging benefits multiple resources simultaneously. Brood area was central to colony development, showing positive correlations with colony size ($r = 0.73$) and temperament ($r = 0.93$), but a negative association with pollen storage ($r = -0.92$). Strong positive relationships among brood area, wax production, and colony size indicate coordinated growth and hive-building capacity, particularly in highland colonies. Secondary traits such as propolis yield and hygienic behavior displayed weaker correlations with primary resources, highlighting potential trade-offs as colonies allocate energy toward growth or defense.

Table 3
Pearson Correlation Coefficients (r) Among Honeybee Traits (n = 90)

Trait	Honey	Brood	Pollen	Wax	Propolis	Hygienic	Temp	Frames
Honey	1							
Brood	-0.934***	1						
Pollen	0.887***	-0.921***	1					
Wax	-0.412***	0.588***	-0.389***	1				
Propolis	0.215*	-0.308**	0.276**	-0.184	1			
Hygienic	0.326**	-0.358**	0.289**	-0.152	0.089	1		
Temp	-0.943***	0.932***	-0.882***	0.476***	-0.267*	-0.344**	1	
Frames	0.401***	0.732***	-0.626***	0.882***	-0.198	-0.118	0.488***	1
* p < 0.05; ** p < 0.01; *** p < 0.001								

4. Discussion

This study provides a comprehensive look at how eight key honeybee traits shift across Ethiopia's diverse agro-ecological zones. Our data makes it clear: the environment is the primary driver of colony productivity and behavior. Most importantly, we've identified a distinct biological trade-off between honey production and brood development a finding that has significant implications for how we manage and breed bees sustainably in the region.

4.1. Environmental Drivers of Productivity

Honey yield exhibited a consistent altitudinal gradient, peaking in lowland zones and decreasing with elevation. This pattern corroborates existing evidence that warmer temperatures and extended dry seasons enhance nectar flow dynamics, especially from drought-resistant flora (Abrol 2012; Requier et al. 2017). Within Ethiopia, lowland regions are dominated by *Acacia-Commiphora* woodland vegetation. These species are recognized for producing abundant nectar and pollen pulses during key flowering periods (Fichtl & Adi 1994; Meixner et al. 2010; Mekonen et al. 2017). These findings underscore the tight coupling between honey production and local ecological conditions. Conversely, brood area exhibited the inverse trend, attaining maximum values in the highlands. This highland growth strategy is likely attributable to the cooler temperatures and higher precipitation characteristic of these altitudes, which may alleviate environmental stressors and allow colonies to allocate more resources to brood production. thereby enabling colonies to allocate greater resources toward brood production (Abou-Shaara et al., 2017; Nurnberger et al. 2019). This inverse relationship wherein lowland colonies allocate resources toward honey storage while highland colonies prioritize brood production constitutes a classic trait documented among East African honeybee populations (Bienefeld & Pirchner 1990; Hepburn & Radloff 1998; Nurnberger et al. 2019). Secondary product synthesis also responded to distinct environmental gradients. Propolis collection peaked in the midlands, where ecological conditions are most transitional. The mosaic of forest and agricultural land in this zone

offers a diverse resin supply, providing a likely explanation for the increased propolis harvesting activity (Bankova et al. 2019; Mair et al. 2023; Simone-Finstrom & Spivak 2010; Stabentheiner et al. 2021). Wax production exhibited a strong positive correlation with brood area, a pattern consistent with the energetic constraints of wax synthesis. Given that wax secretion is energetically demanding and directly tied to nest expansion, colonies maintaining larger brood nests necessarily produce more comb to sustain colony growth (Mekonen et al. 2017; Nurnberger et al. 2019; Nuru et al. 2018; Seeley 1985). While environmental conditions clearly shape the allocation of resources within colonies, these factors also influence behavioral traits, colony size, and the interactions among different colony characteristics, which we explore in the following sections.

4.2. Adaptive Behaviors: Hygiene and Temperament

Altitude exerted a pronounced influence on colony behavioral profiles, suggesting that colony phenotype represents a direct adaptation to local environmental conditions. Hygienic behavior was highest in the highlands and lowest in the midlands a pattern likely attributable to elevated disease pressure. The cooler, more humid conditions characteristic of highland environments typically favor the proliferation of brood pathogens such as chalk brood and ecto-parasites such as *Varroa destructor* (De la Rua et al. 2009; Fries et al. 2003; Friis et al. 2010; Porrini et al. 2003). Under such conditions, colonies lacking rigorous nest hygiene face reduced survival prospects, thereby exerting natural selection in favor of enhanced hygienic traits (Alemu, 2015, Bigio et al. 2014; Le Conte et al. 2010; Spivak & Reuter 2001). In contrast, the diminished hygienic performance observed in midland colonies may indicate lower pathogen pressure in this zone, potentially enabling a reallocation of energetic resources toward alternative fitness-related traits (Tarpy 2003).

Colony temperament followed a distinct altitudinal gradient, with lowland bees exhibiting exceptional gentleness and highland colonies showing the highest defensiveness. This elevation in aggression likely reflects adaptive responses to environmental constraints, such as limited foraging opportunities and cooler temperatures, conditions that typically favor heightened resource defense (Guerrero-Molina et al. 2016). Interestingly, honey yields decreased with increasing colony defensiveness, consistent with the prevailing view in apiculture that gentler colonies are more productive. This relationship likely reflects a trade-off, wherein colonies invest less energy in defense and more in foraging efficiency (Guerrero-Molina et al. 2016; Guzman-Novoa et al. 2002, 2017; Hepburn & Radloff 1998, Tarpy 2003). These behavioral adaptations not only reflect local environmental pressures but also influence how colonies allocate resources among growth, defense, and productivity, linking directly to the life-history trade-offs observed across zones.

4.3. Life-History Trade-offs and Trait Associations

A prominent pattern in our data is the clear trade-off between honey production and brood development. Given finite resource availability, colonies face an allocative decision: invest in current workforce capacity through brood rearing or in future survival through honey storage. Our results demonstrate that colonies generally do not excel in both strategies concurrently (Fries et al. 2003; Gebremedhin et al., 2019; Seeley 1985). The PCA results strongly support this bifurcation. Lowland colonies are defined by honey and pollen storage, while highland colonies are characterized by brood expansion, wax production, and larger colony size. The positive correlation between colony size and wax production is biologically consistent a larger, expanding population requires greater comb area for egg laying and resource storage (Hepburn & Radloff,

1998; Tubbs et al. 2025). Similarly, the strong correlation between honey and pollen storage reflects pollen's critical function as the colony's primary protein source. This protein sustains nurse bees in rearing a healthy workforce, which ultimately forms the large foraging contingent required to maximize honey yield (Brodschneider & Crailsheim 2010; Delaplane et al. 2013). This trade-offs and trait correlations highlight how environmental pressures shape colony specialization, providing a natural framework for applied management strategies.

4.4. Practical Implications for Beekeeping and Conservation

The correlations observed in this study were, in several instances, remarkably high exceeding 0.90. This indicates a profound ecological integration, wherein trait expression is tightly coupled with environmental context. Notably, shared environmental pressures likely magnify these associations; the colonies do not exhibit a suite of independent traits but rather represent a cohesive, integrated phenotypic response to the landscape.

From an applied perspective, our findings yield a clear specialization map for the region. Lowland colonies are optimally suited for intensive honey production. Midland colonies occupy a distinctive niche as the premier resource for propolis collection. Highland colonies characterized by robust brood areas and superior hygienic behavior are ideal candidates for colony expansion and queen rearing. The principal constraint in the highlands remains temperament. Although managing such defensive colonies presents challenges, selective breeding offers a viable pathway: retaining the high productivity and hygienic traits of these bees while progressively selecting for reduced defensiveness (Bienefeld & Pirchner 1990).

From a conservation perspective, these populations represent more than geographic isolates they embody locally adapted genetic lineages shaped by selective pressures unique to their environments. Preserving this adaptive diversity is critical. With ongoing habitat loss and climate change, we risk eroding the genetic combinations that confer resilience to these bees in their native landscapes (De la Rua et al. 2009; Hepburn & Radloff 1998; Nurnberger et al. 2019; Seeley1985). True sustainability in regions like Waghimra hinges on integrated landscape management that secures the floral resource base essential to these distinct populations (Abrol 2012; Potts et al. 2010, 2016, Tarpy 2003; Tolera & Dejen 2020).

Limitations of the Study

While this study provides a robust longitudinal analysis, several limitations should be acknowledged. First, data collection was interrupted during the 2021–2022 seasons due to the COVID-19 pandemic and regional conflicts, which limited field access. Nevertheless, the consistency observed between the 2020 and 2023 datasets suggests that the identified agro-ecological adaptations reflect stable, long-term colony traits rather than short-term seasonal fluctuations. Second, although distinct zonal phenotypes were characterized, a common garden experiment would be necessary to disentangle fixed genetic adaptations from environmentally induced plasticity. Finally, while the sample of 45 colonies offered high statistical power ($p < 0.001$), broader studies across additional districts would help verify whether these patterns are representative of the wider Northern Ethiopian honeybee population.

Conclusion and Recommendations

Our finding provides larger evidence that agro-ecology is the primary driver of honeybee colony performance in the semi-arid landscapes of northern Ethiopia. Our finding reveals a clear phenotypic divergence between altitudes, where colonies have developed specialized survival strategies. Lowland colonies operate as resource hoarders, prioritizing high honey (22.2kg) and pollen accumulation alongside a remarkably gentle temperament. Highland colonies, on the other hand, put more emphasis on population resilience. To deal with cooler thermal stress, they have much larger brood areas and better hygiene (95.7%), but they are also more defensive. The strong negative correlation (r=-0.93) between honey yield and brood area confirms a fundamental biological trade-off: colonies cannot simultaneously maximize both reproductive growth and surplus honey storage. These distinct zonal phenotypes suggest that Ethiopian honeybees are locally adapted to their specific environmental pressure rather than showing uniform performance. The following are the major recommendations: First, zone-specific production should prioritize honey and pollen harvesting in Lowlands, while Highlands should serve as multiplication hubs for queen rearing and colony splitting. Second, targeted breeding should focus on hygienic efficiency in the Highlands and docility combined with yield in the Lowlands to enhance local adaptation. Third, conservation of drought-resilient forage particularly *Becium grandiflorum* and *Acacia asack* is critical to sustain the nutritional baseline of these resilient populations. Finally, genomic research is required to determine whether the observed divergence reflects heritable local adaptation or environmental plasticity, a distinction essential for guiding long-term breeding and conservation strategies.

Declarations

Statements and Declarations

CRediT authorship contribution statement

Ertiban Desale: writing original draft, Data curation, formal analysis, writing review & editing, Supervision. **Ayalew Girmay**: data curation, formal analysis, software, data collection and management. **Yesuf Ibrahim**: conceptualization, data curation, formal analysis, data collection. **Meresa Lemma**: data curation, formal analysis, data management. All authors contributed to fieldwork, validation, and approved the final manuscript.

Declaration of competing interest

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

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Data availability statement

The data supporting the findings of this study are available from the corresponding author, Ertiban Desale, upon reasonable request.

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Declaration of generative AI and AI-assisted technologies

During the preparation of this work, the authors used AI-assisted digital tools to support language editing, grammar correction, and the clarification of R software syntax. These tools were used solely to improve the clarity and organization of the manuscript. The authors reviewed and edited the output and take full responsibility for the content of the article.

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Figures

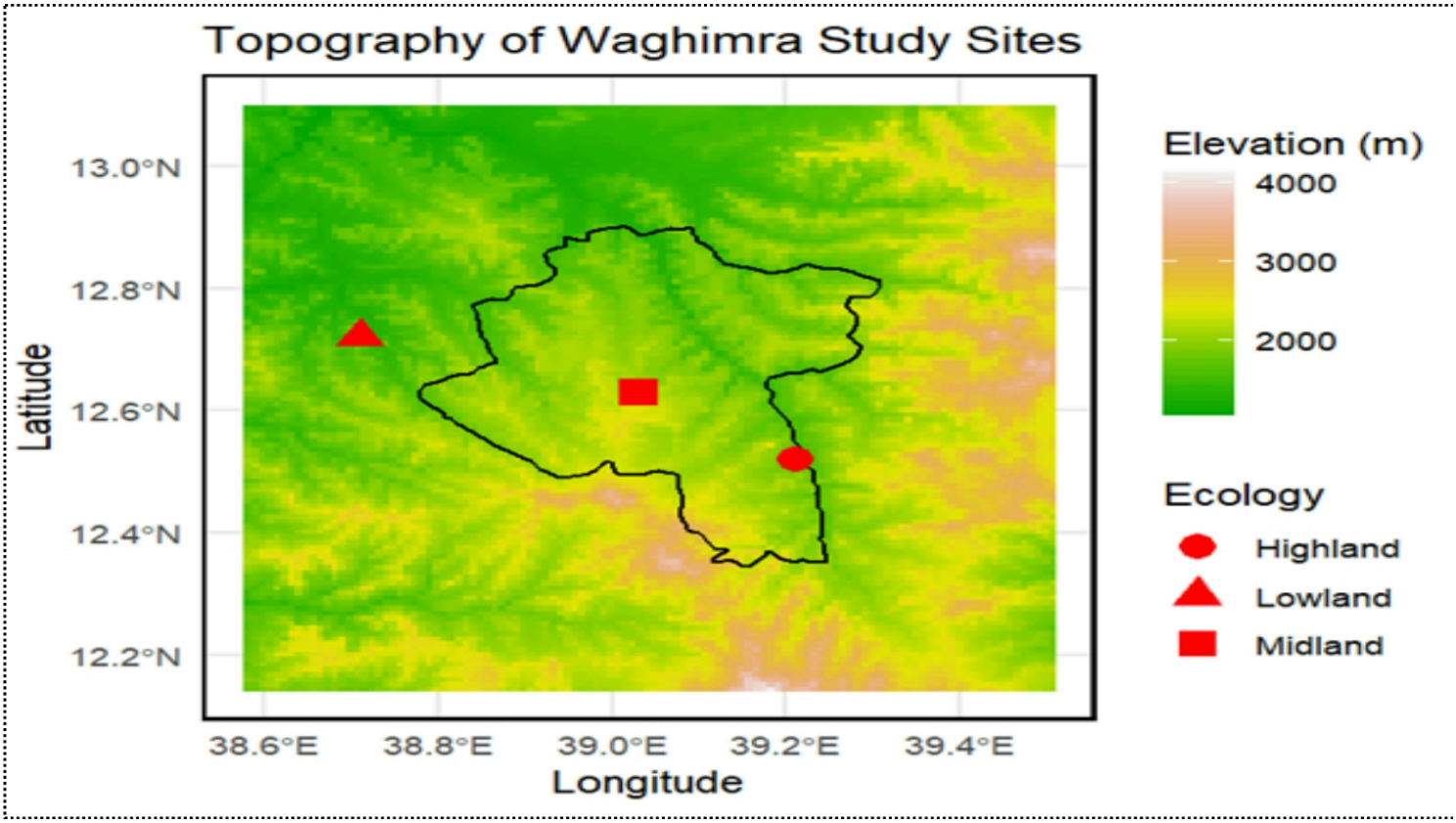


Figure 1

Topographic and administrative profile of the study districts in Waghimra Zone

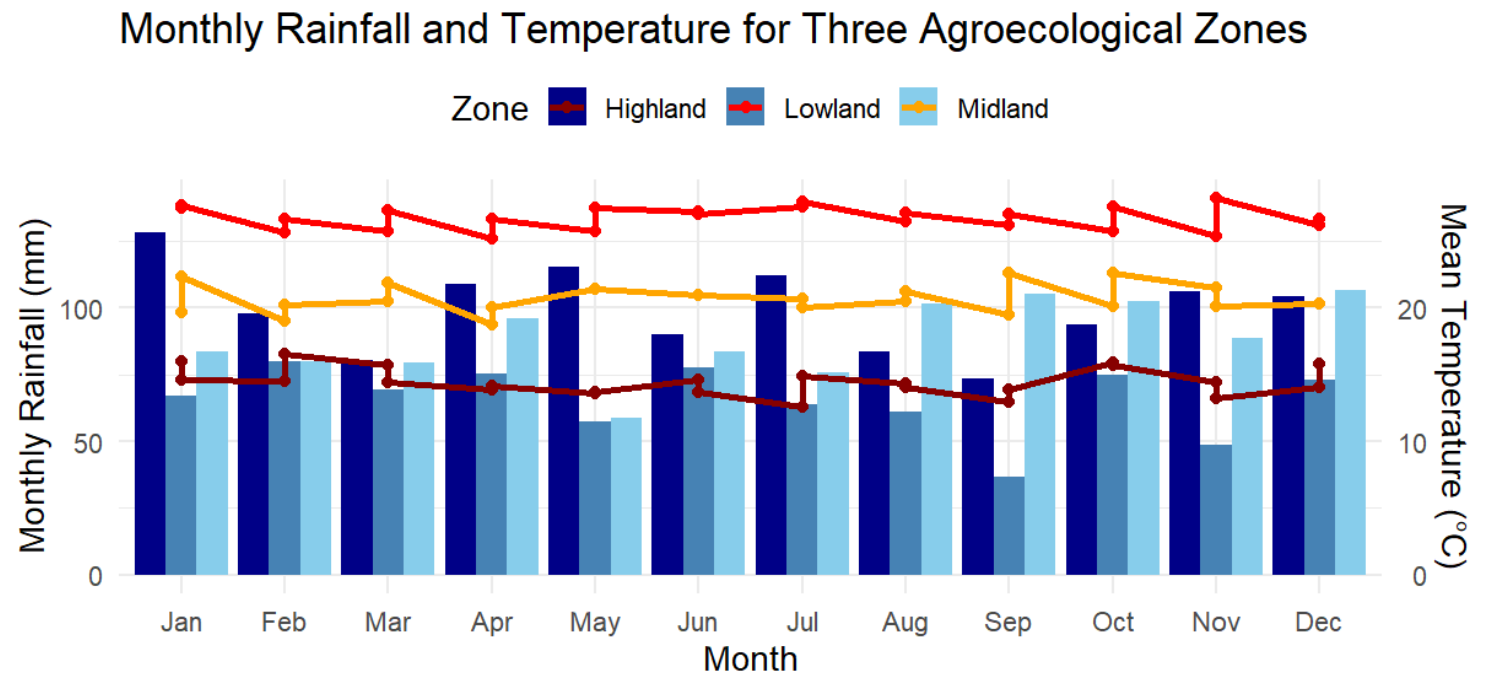


Figure 2

Monthly rainfall and mean temperature (°C) patterns across the three agro-ecological zones

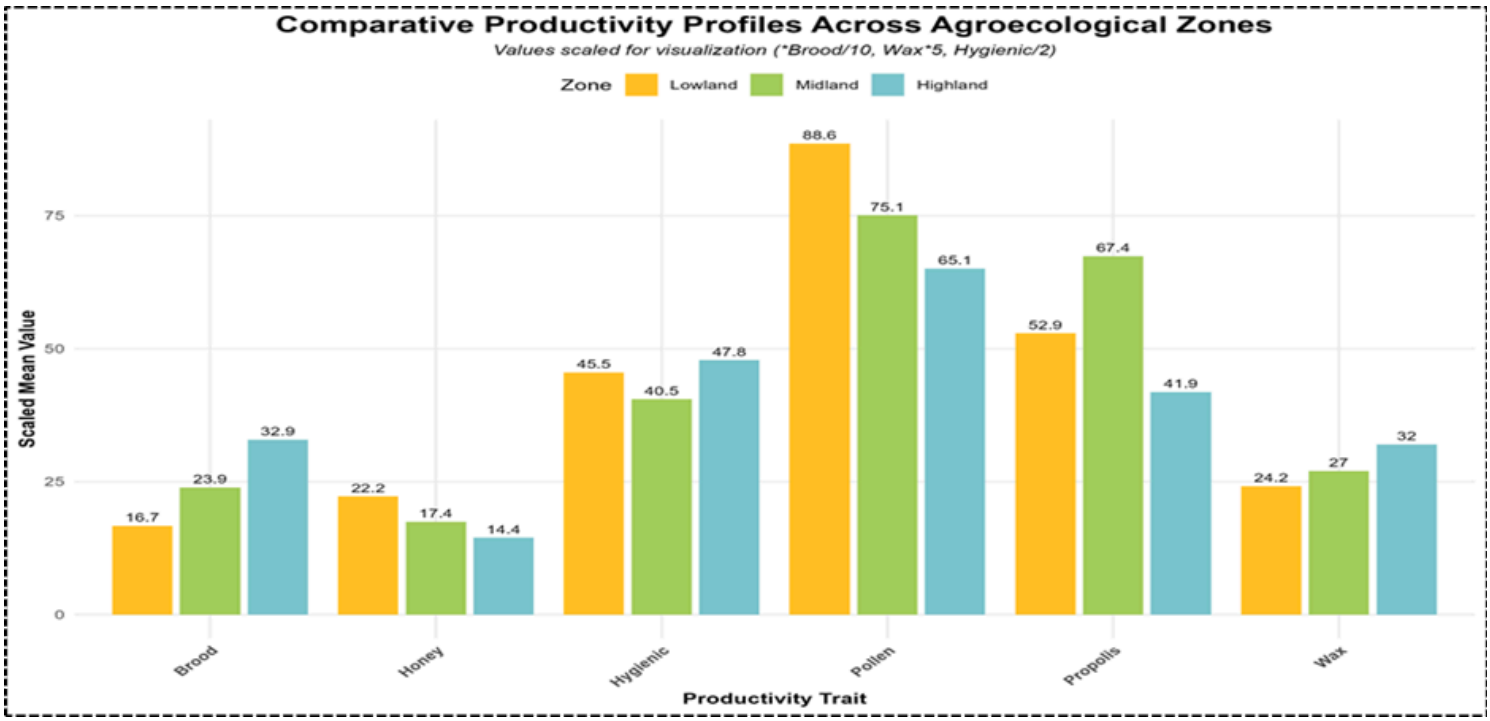


Figure 3

Production traits of honeybee colonies across three agro-ecological zones

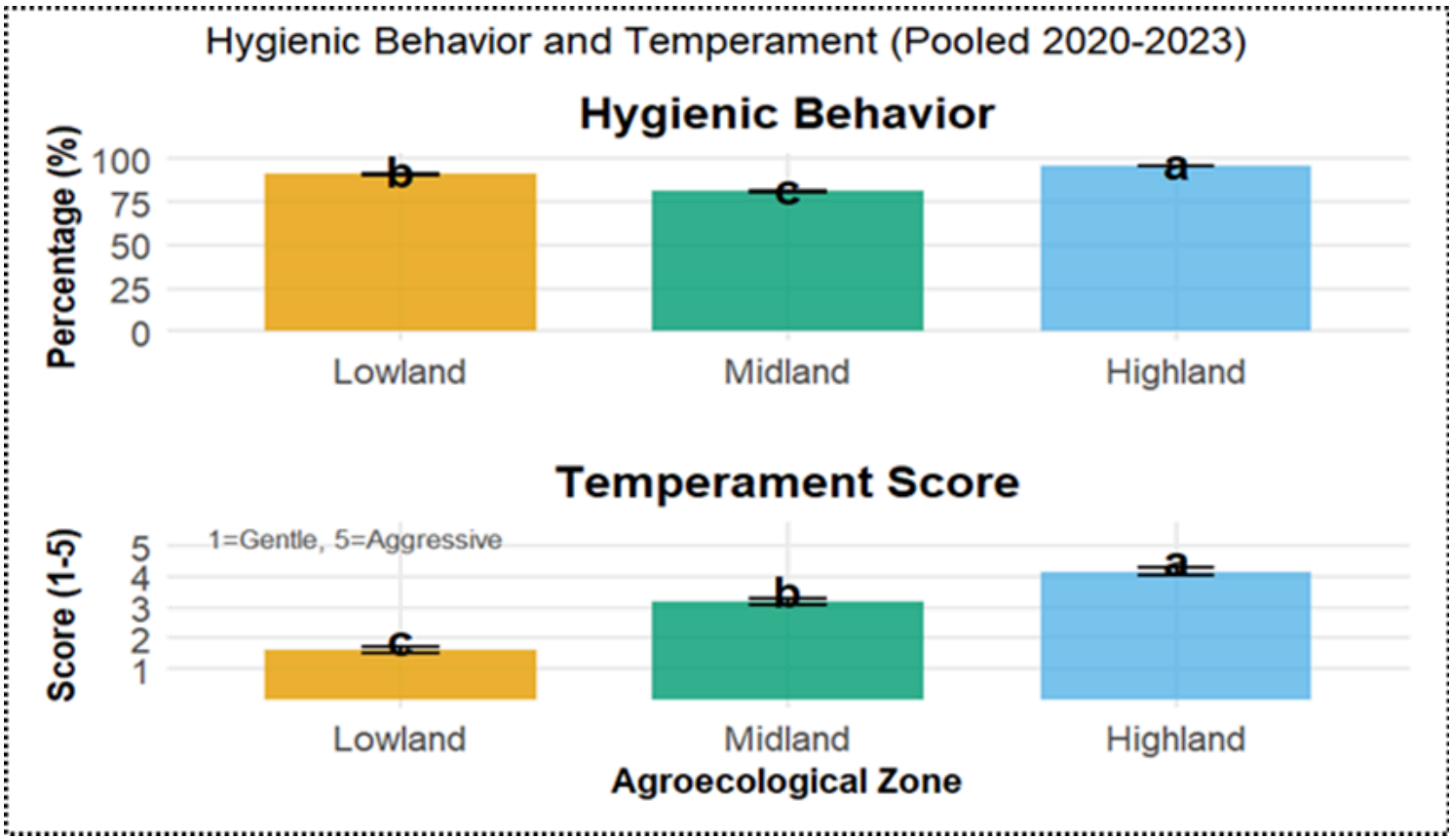


Figure 4

Hygienic behavior and temperament of honeybee colonies across three agro ecological

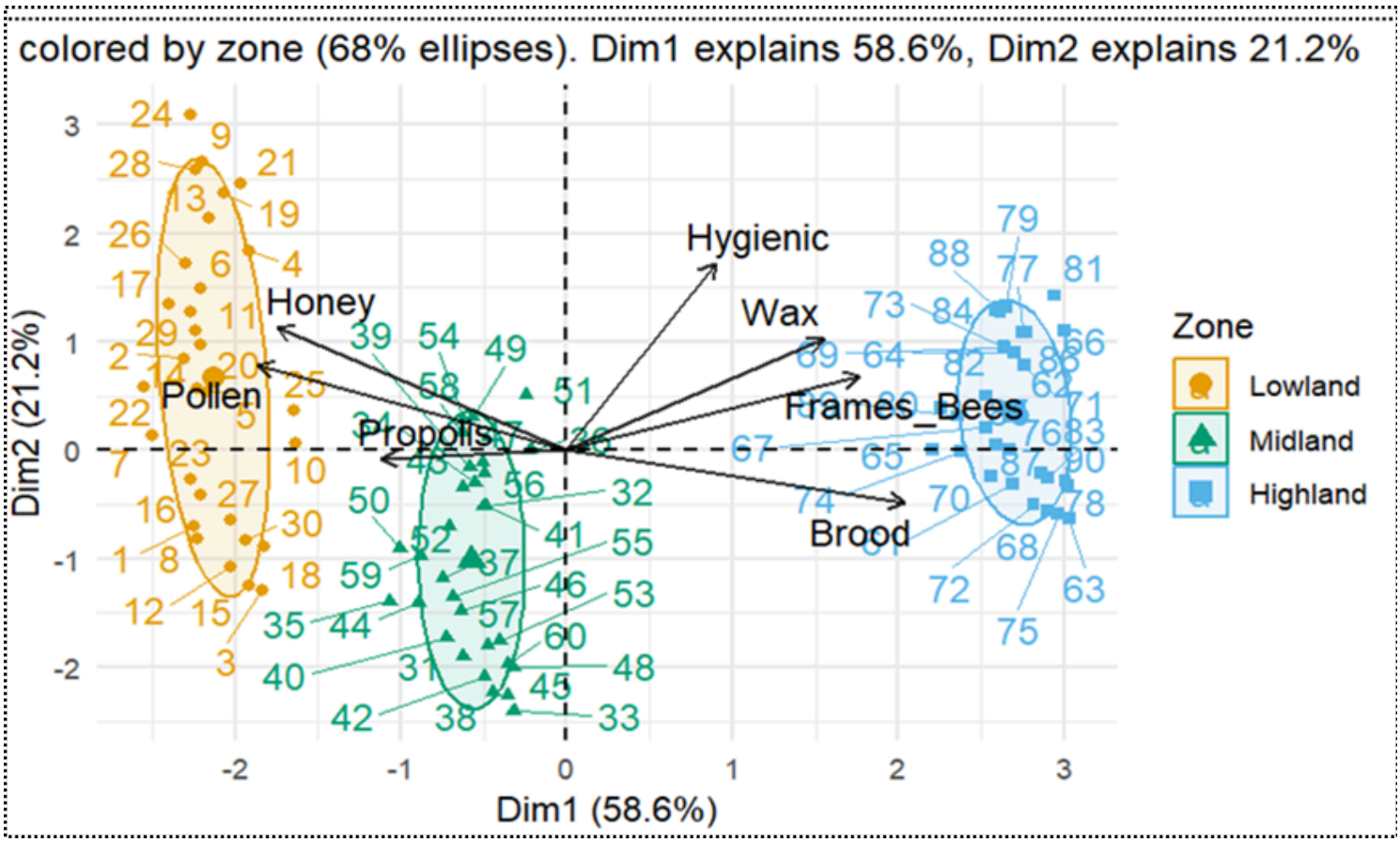


Figure 5

Principal Component Analysis biplots of honeybee colony traits across three agro ecological

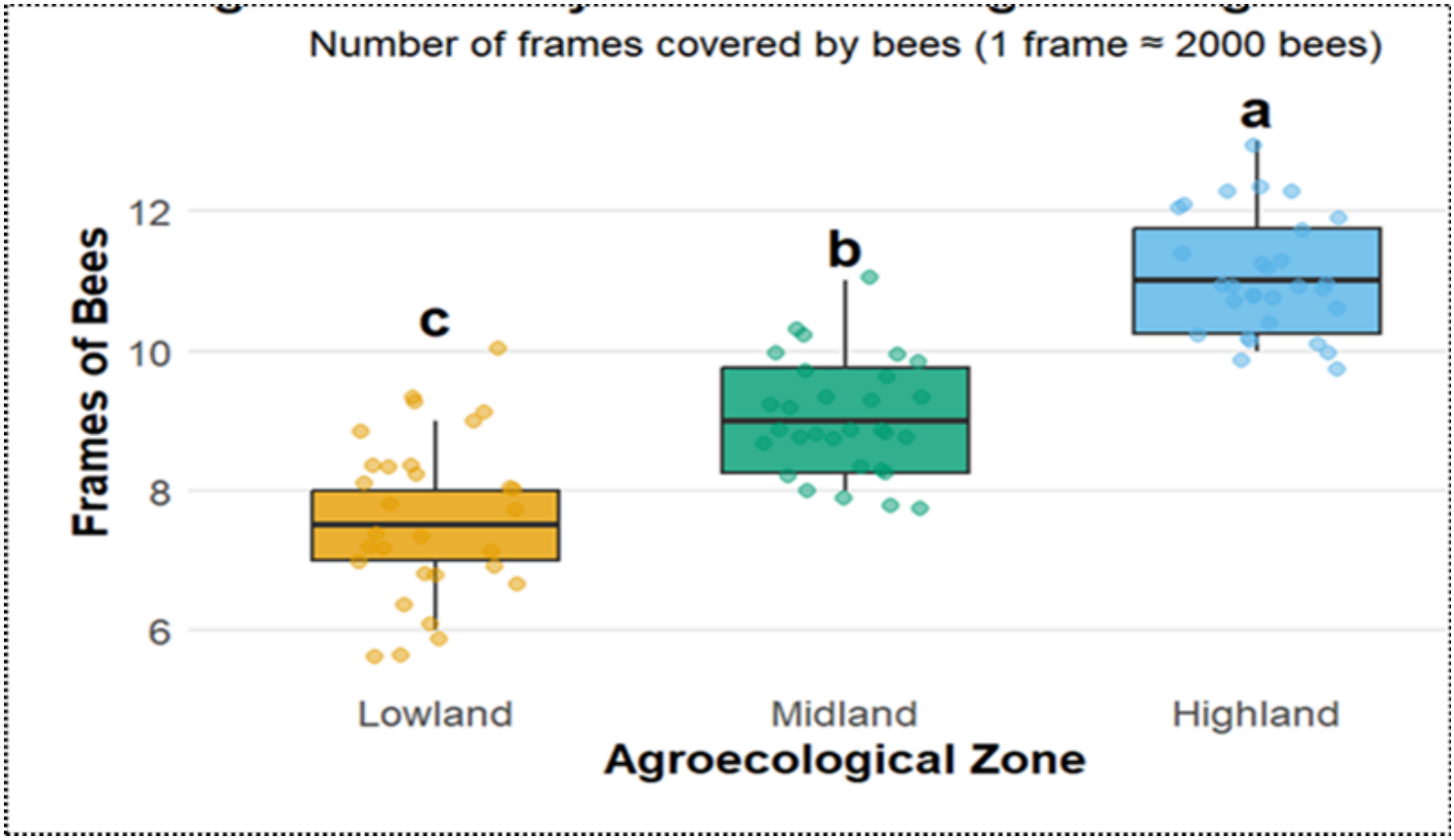


Figure 6

Colony size distribution of honeybee colonies across three agro ecological zones

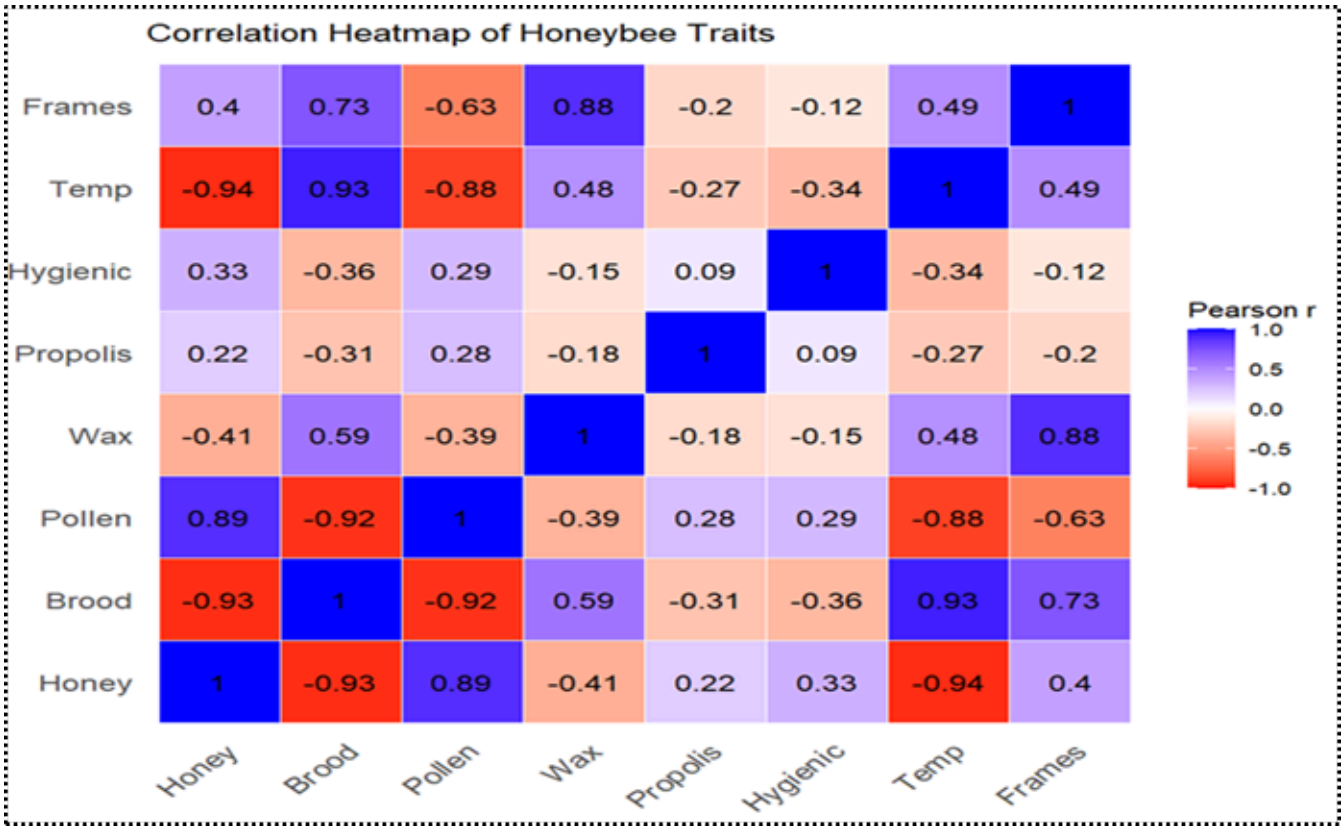


Figure 7

Heatmap of Pearson correlation coefficients among eight honeybee colony traits (n = 90)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Suplimentarytable.pdf