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Foraging behavior of Indian honeybee *Apis cerana indica* Fabricius under Semi urban area in Goa, India

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Abstract

Understanding how short-term weather variability modulates honeybee foraging is essential for sustaining pollination services in tropical agroecosystems. We quantified the temporal dynamics and climatic drivers of pollen and nectar foraging by *Apis cerana indica* in a semi-urban coastal landscape of Goa, India, during the honey-flow season (January–May 2024). Foraging intensity was recorded at hive entrances from three colonies as returning bees with pollen loads (pollen foragers) and without pollen loads (nectar foragers), counted for 5 min at 2-h intervals (08:00–18:00 h) at eight-day intervals. Daily gridded meteorological variables (temperature, relative humidity, rainfall, wind speed, and solar radiation; $0.25^\circ \times 0.25^\circ$) were obtained from the India Meteorological Department and standardized prior to analysis. Both pollen and nectar exhibited strong diurnal structuring, with consistent maxima at 10:00 h across months; peaks were highest in March (pollen: 76.49; nectar: 80.91 bees 5 min^{-1}). Time-of-day effects were highly significant for both resources (Kruskal–Wallis: pollen $\chi^2 = 70.42$, $p < 0.001$; nectar $\chi^2 = 68.05$, $p < 0.001$), whereas month-wise effects were non-significant, indicating substantial intra-month variability and/or floral buffering. Spearman correlations suggested negative associations of foraging with temperature and wind speed. Generalized Additive Models (mgcv) captured nonlinear multivariate climatic controls with moderate explanatory power (pollen: 38.3% deviance explained; nectar: 49.7%). Wind speed exerted strong negative effects on both pollen and nectar, while solar radiation showed strong positive nonlinear effects; rainfall was not influential during the study window. Collectively, the results identify mid-morning as the most productive foraging window and demonstrate that wind and radiation are dominant climatic regulators of *A. cerana indica* foraging in coastal semi-urban environments, with implications for pollinator-friendly management and climate-resilient pollination services.

Keywords: *Apis cerana indica*; Foraging behaviour; Diurnal activity pattern; Climatic drivers; Generalized Additive Models

Introduction

Pollination by insects is a cornerstone of both natural ecosystem functioning and global agricultural productivity, underpinning the reproduction of approximately 75% of leading food crops worldwide. Among insect pollinators, honeybees play a disproportionately important role due to their social organisation, high foraging efficiency, and ability to exploit a wide range of floral resources across spatial and temporal scales (Abrol, 2012; Klein *et al.*, 2007) [5, 24]. In tropical and subtropical agroecosystems, native honeybee species such as *Apis cerana indica* Fabricius are particularly vital, as they are well adapted to local climatic conditions and contribute substantially to the pollination of horticultural, plantation, and field crops (Chauhan *et al.*, 2024; Indhu *et al.*, 2023; Nuriyah *et al.*, 2021) [8, 21, 28].

Foraging behaviour in honeybees represents a finely tuned balance between energetic gain and environmental constraints. The intensity and timing of pollen and nectar collection are shaped by multiple interacting factors, including floral phenology, colony nutritional demands, and short-term abiotic conditions such as temperature, humidity, wind speed, and solar radiation (Kamaraj and Rasappan, 2024) [22]. Among these, climatic variables exert immediate physiological and behavioural control over flight performance, sensory orientation, and resource handling efficiency, thereby regulating daily and seasonal foraging rhythms (Stabentheiner and Kovac, 2014) [33]. Consequently, understanding how weather

variability influences honeybee foraging is essential for predicting pollination services under changing environmental conditions (Mattos *et al.*, 2018) ^[26]. Previous studies have documented pronounced diurnal patterns in honeybee foraging activity, typically characterised by early to mid-morning peaks followed by afternoon declines, a trend attributed to synchronisation with anthesis, pollen dehiscence, and nectar secretion cycles of flowering plants (Gigauri, 2019) ^[15]. Seasonal variation in foraging intensity has likewise been linked to flowering phenology and resource abundance, particularly during honey-flow periods when floral rewards are abundant (Abdel-Galel *et al.*, 2021; Abrol, 2012) ^[1, 5]. However, the magnitude and consistency of these temporal patterns often vary with local climatic regimes and landscape composition, especially in semi-urban environments where natural and cultivated flora coexist (Kamaraj and Rasappan, 2024) ^[22].

Climatic drivers such as temperature and wind speed have been repeatedly identified as key regulators of honeybee activity. Elevated temperatures can impose thermal stress, increase metabolic costs of flight, and alter nectar availability through enhanced evaporation, collectively suppressing foraging intensity beyond optimal thermal thresholds (Hennessy *et al.*, 2020) ^[18]. Wind speed represents a critical physical constraint on bee flight, as increased turbulence impairs take-off, stability, and landing efficiency, thereby reducing visitation rates and successful foraging trips even at relatively low velocities (Balfour and Ratnieks, 2025; Hennessy *et al.*, 2020) ^[18, 19]. Relative humidity may further influence pollen hydration and handling efficiency, while solar radiation affects visual orientation and thoracic warming, indirectly shaping diurnal activity patterns (Abou-Shaara *et al.*, 2017; Karbassioon *et al.*, 2023) ^[3, 23].

Despite substantial research on honeybee foraging ecology, several important gaps remain. First, much of the existing literature relies on linear or univariate statistical approaches, which may inadequately capture the nonlinear and interacting effects of climatic variables on foraging behaviour. Second, studies focusing on *Apis cerana indica* in coastal and semi-urban tropical ecosystems remain limited, even though such landscapes are increasingly dominant across South Asia and are expected to experience heightened climatic variability under climate change. Third, few studies integrate fine-scale behavioural observations with high-resolution gridded meteorological data to disentangle short-term weather effects from broader seasonal trends.

In this context, the present study aims to investigate the temporal dynamics and climatic drivers of pollen and nectar foraging behaviour of *Apis cerana indica* in a semi-urban coastal ecosystem of Goa, India. Specifically, we (i) quantify diurnal and seasonal variation in pollen and nectar foraging intensity during the honey-flow season, (ii) examine pairwise associations between foraging activity and key climatic variables using non-parametric correlation analyses, and (iii) employ Generalized Additive Models (GAMs) to identify nonlinear and multivariate climatic controls on foraging behaviour. By integrating behavioural ecology with advanced statistical modelling and high-resolution climate data, this study provides mechanistic insights into how short-term weather variability structures honeybee foraging activity, with implications for pollination services and climate resilience in tropical agroecosystems.

Study Area and Environmental Conditions

The study was conducted at the Experimental Farm of the Department of Entomology, Goa College of Agriculture, Ela Farm, Old Goa, India (15°29'36.7" N; 73°55'03.8" E), during the honey flow season from January to May 2024. The site represents a semi-urban coastal ecosystem characterised by mixed horticultural and field-crop vegetation, and patches of natural forest that collectively provide diverse pollen and nectar sources for *Apis cerana indica*. The apiary was located within a coconut (*Cocos nucifera* L.) plantation, interspersed with mango (*Mangifera indica*), banana (*Musa spp.*), arecanut (*Areca catechu*), maize (*Zea mays*), and assorted wild flora. These were monitored qualitatively to confirm continuous floral availability across months.

Goa's coastal region is marked by warm, humid tropical conditions, with daytime temperatures typically ranging from 25–34°C during the study period. To characterise environmental drivers of bee foraging, daily gridded weather data (temperature, relative humidity, rainfall, wind speed, and solar radiation) were sourced from the India Meteorological Department (IMD) high-resolution gridded dataset (0.25° × 0.25°). These data correspond to the grid cell encompassing the study location.

To align climatic variables with honeybee foraging observations, daily IMD gridded weather data corresponding to each observation date were extracted using the IMDlib Python package, which enables automated retrieval and parsing of high-resolution meteorological fields. For modelling purposes, the daily temperature, relative humidity, rainfall, wind speed, and solar radiation values were subsequently averaged or temporally interpolated to represent the environmental conditions prevailing within the foraging observation window (08:00–18:00 h). Prior to correlation analyses and the development of Generalized Additive Models (GAMs), all climatic variables were standardised (mean-centred and scaled) to ensure comparability of predictors and improve model stability and convergence.

Honeybee Colonies and Foraging Observation Protocol

Three healthy colonies of *Apis cerana indica* with uniform strength each comprising approximately seven brood frames with adequate sealed brood, pollen reserves, and honey stores—were selected and maintained under standardised conditions at the Experimental Farm. All colonies were placed on elevated metal stands fitted with ant-proof barriers and positioned under partial shade to avoid thermal stress. Foraging behaviour was quantified by recording the number of bees returning to the hive with pollen loads (pollen foragers) and without pollen loads (nectar foragers), identified visually by the presence or absence of corbicular pollen on the hind legs. Observations were conducted directly at the hive entrance at two-hour intervals (08:00, 10:00, 12:00, 14:00, 16:00, and 18:00 h) using a hand tally counter while timing each count over a fixed five-minute window with a stopwatch. Data were collected at eight-day intervals from January to May 2024, encompassing the entire honey-flow season in Goa. For each time point within each month, weekly measurements were averaged prior to statistical analysis to reduce intra-week variability and ensure consistency across colonies. This generated a structured dataset reflecting mean pollen and nectar foraging intensity across time-of-day and seasonal gradients.

Floral Resource Assessment

Materials and Methods:

To characterise the availability of pollen and nectar sources influencing *Apis cerana indica* foraging dynamics, a qualitative floral resource survey was conducted within a 500-m radius of the apiary throughout the study period. All flowering plant species visibly visited by the bees were recorded during each observation day, with emphasis on dominant horticultural crops such as coconut (*Cocos nucifera*), mango (*Mangifera indica*), banana (*Musa* spp.), arecanut (*Areca catechu*), and maize (*Zea mays*), as well as naturally occurring forest vegetation. Although detailed phenological quantification was not undertaken, presence-absence checks and visual assessments of flowering intensity were used to confirm continuous nectar and pollen availability across months. This contextual evaluation ensured that observed variations in foraging activity were interpreted against a stable background of accessible floral resources, thus enabling robust ecological inference regarding temporal shifts in pollen and nectar collection.

Data Processing and Statistical Analysis

Foraging observations from the three colonies were first organised by time of day, week, and month, after which all weekly values for each time point were averaged to obtain a representative measure of mean pollen and nectar forager return rates. Prior to inferential analysis, datasets were examined for distributional properties using the Shapiro-Wilk test to assess normality (Table; Figure 1); because both pollen and nectar counts exhibited significant departures from normal distributions, non-parametric statistical methods were employed (Razali and Wah, 2011) [31]. Temporal variation in foraging activity across the six daily observation periods was evaluated using the Kruskal-Wallis rank-sum test, while month-wise effects were assessed independently for pollen and nectar datasets (Table 4) (Okoye and Hosseini, 2024) [24].

To examine pairwise monotonic relationships between foraging intensity and individual climatic variables, Spearman rank correlation coefficients were computed. To capture potentially complex, nonlinear, and multivariate environmental drivers of foraging behaviour, Generalized Additive Models (GAMs) were constructed using the mgcv package in R (Wood, 2001), with separate models fitted for pollen and nectar counts. Each GAM incorporated smooth terms for temperature, relative humidity, wind speed, rainfall, and solar radiation, following the model structure:

$$Pollen_i = \beta_0 + S_1(Temp_i) + S_2(RH_i) + S_3(WS_i) + S_4(RF_i) + S_5(SR_i) + \varepsilon_i$$

Where,

Temp= Temperature,

RH= Relative humidity

WS= Wind Speed

RF= Rainfall

SR= Solar radiation

The same model was applied in nectar. Thin-plate regression splines were used as the smoothing basis, and variable standardization ensured numerical stability and comparability of effects. Model adequacy was evaluated using residual diagnostics, QQ-plots, histograms of residuals, observed vs fitted plots, and summary statistics including adjusted R^2 , deviance explained, F-statistics, and

generalized cross-validation (GCV) scores. All analyses were performed in R, while climatic data was downloaded using IMDlib package in python to download India Meteorological Departments daily climatic data (Nandi et al., 2024).

Results and Discussion

Temporal Dynamics of Pollen Foraging Activity

Pollen foraging activity of *Apis cerana indica* exhibited a pronounced and highly consistent diurnal rhythm, with foraging initiated shortly after sunrise, increasing steadily through the morning, and reaching a clear maximum at 10:00 h across all months (January–May). The magnitude of this mid-morning peak varied seasonally, with the highest values recorded in March (76.49 bees 5 min⁻¹), followed by April and February, and lower intensities during January and May (Table 2; Figure 2). Such mid-morning maxima are widely reported in *A. cerana* and other *Apis* species and are strongly associated with the synchronization of bee foraging schedules with anthesis timing, pollen dehiscence, and optimal microclimatic conditions, particularly moderate temperature and relative humidity that enhance flight efficiency and pollen handling (Abrol, 2012; Czekońska et al., 2023; Mattos et al., 2018) [5, 10, 26]. The sharp decline in pollen foraging during afternoon hours, with minimum activity observed around 16:00 h, reflects increasing thermal stress, reduced pollen availability following morning anthesis, and higher energetic costs of foraging later in the day, a pattern consistently documented in tropical and subtropical agroecosystems.

Table 1: Shapiro-Wilk test result for the pollen and nectar

Parameter	W Value	P-value
Pollen	0.87	1.469e-09
Nectar	0.86	8.095e-10

Seasonally, mean pollen foraging activity (averaged across all observation times) was highest in March, followed by April, with a progressive decline toward May. This trend corresponds closely with the peak flowering and pollen availability of major regional forage species such as mango (*Mangifera indica*), coconut (*Cocos nucifera*), and cashew (*Anacardium occidentale*), which dominate the floral landscape of semi-urban Goa during late winter and early summer (Layek et al., 2020) [25]. The subsequent reduction in May likely reflects declining floral rewards under pre-monsoon conditions and increasing thermal constraints on sustained pollen collection. Despite these biologically meaningful seasonal patterns, the month-wise Kruskal-Wallis test did not detect a statistically significant effect, indicating that high intra-month variability, driven by week-to-week fluctuations in weather and floral resource distribution, may have reduced statistical power to separate month-level contrasts. Similar discrepancies between descriptive seasonal trends and formal statistical significance have been reported in pollinator foraging studies, particularly where continuous or overlapping floral resources buffer colonies against abrupt seasonal transitions (Herrera, 1997) [20]. In contrast, time of day exerted a strong and highly significant effect on pollen foraging activity ($\chi^2 = 70.42$, $p < 0.001$), underscoring the dominance of diurnal forcing over seasonal controls during the honey-flow period.

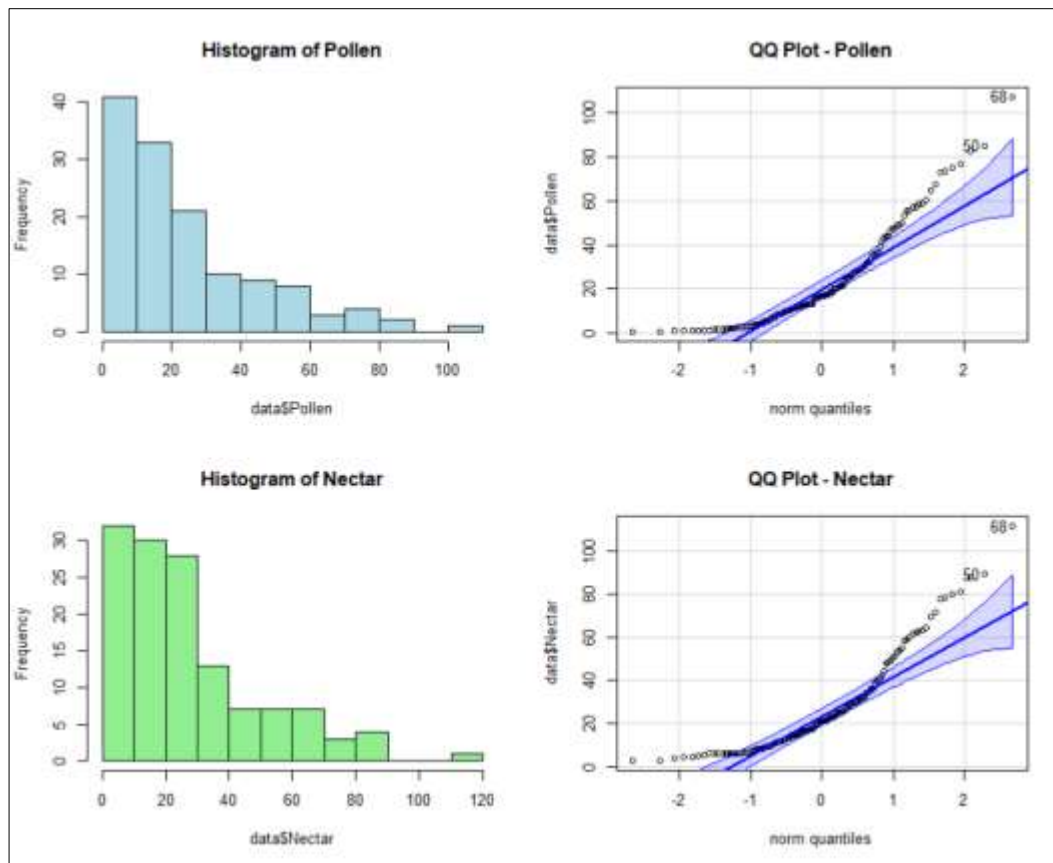


Fig 1: Distribution of pollen and nectar data

Temporal Dynamics of Nectar Foraging Activity

Nectar foraging by *Apis cerana indica* exhibited a pronounced and highly structured diurnal rhythm, closely paralleling pollen foraging but reflecting distinct physiological and ecological drivers. Across all months, nectar return rates increased rapidly after sunrise and consistently reached a sharp maximum around 10:00 h (Table 3; Figure 2), indicating strong temporal coupling between bee activity and periods of optimal nectar availability. Such mid-morning peaks are widely reported in *Apis* species and are generally attributed to the synchronization of foraging schedules with daily nectar

secretion cycles, which are typically highest during early to mid-morning when floral nectaries are most active and nectar sugar concentration is optimal (Anandhabhairavi *et al.*, 2020; Kamaraj and Rasappan, 2024) [6, 22]. The consistently higher nectar foraging intensity observed in March, followed by April, further underscores this period as the most resource-rich phase of the honey-flow season in Goa, coinciding with peak flowering of dominant forage plants such as coconut (*Cocos nucifera*), mango (*Mangifera indica*), and cashew (*Anacardium occidentale*) (Young *et al.*, 2021) [38]

Table 2: Overall mean of pollen foraging activities of *Apis cerana indica* over a five-month period (January-May)

Time	January	February	March	April	May	Mean
08.00 a.m.	10.06	15.57	50.66	51.41	34.26	32.39
10.00 a.m.	49.26	60.66	76.49	60.49	38.86	57.15
12.00 p.m.	32.26	26.74	19.24	16.99	17.19	22.48
02.00 p.m.	27.99	08.58	15.33	14.16	09.13	15.03
04.00 p.m.	16.19	06.41	10.66	09.74	05.53	09.70
06.00 p.m.	13.99	03.24	05.91	05.16	04.39	06.53
Mean	24.95	20.20	29.71	26.32	18.22	

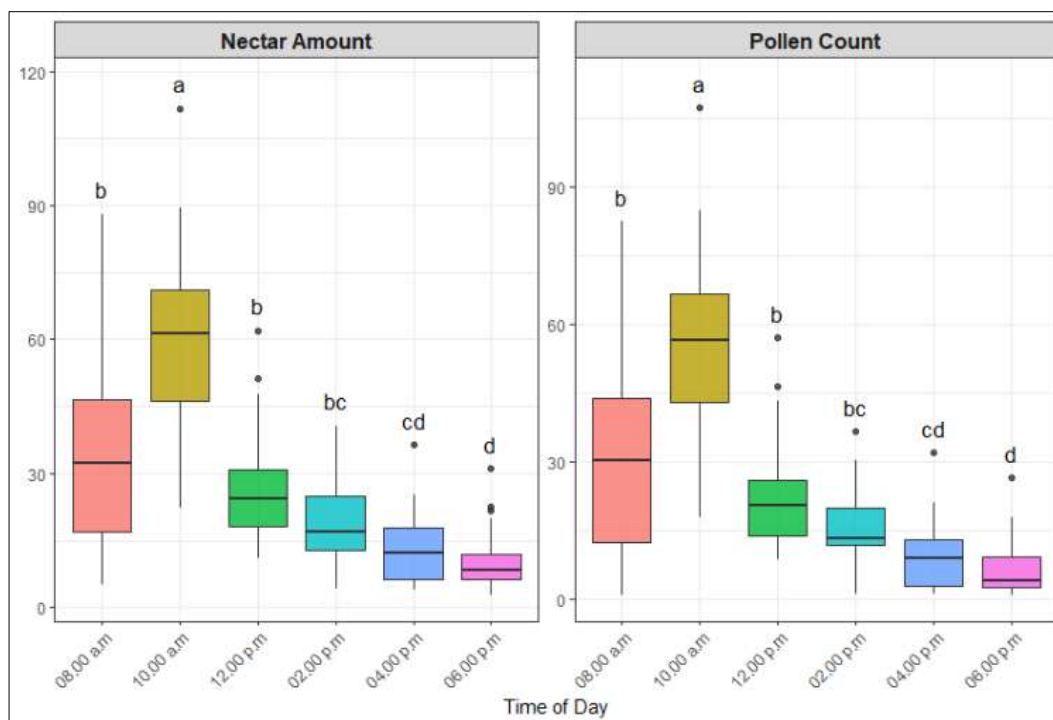


Fig 2: Dynamics of nectar amount and pollen count at different time of the day

Substantial nectar foraging during early morning hours (08:00 h), particularly in March and April, reflects not only favourable floral phenology but also microclimatic conditions that minimise physiological stress on foragers. Moderate temperatures, higher relative humidity, and lower evaporative demand during morning hours enhance nectar volume retention and reduce flight costs, thereby increasing net energetic gains per foraging trip (Heinrich, 1979; Abou-Shaara, 2014) ^[17, 2]. In contrast, nectar foraging declined sharply toward the afternoon, with the lowest activity

consistently recorded at 16:00 h across all months. This decline is ecologically consistent with rising ambient temperatures, declining nectar secretion rates, increased evaporation leading to altered nectar concentration, and reduced flight efficiency under hotter and drier conditions. Experimental studies have demonstrated that under such thermal stress, honeybees reduce foraging intensity to avoid overheating and excessive energy expenditure, even when floral resources remain available (Stabentheiner and Kovac, 2014) ^[33].

Table 3: Overall mean of nectar foraging activities of *Apis cerana indica* over a five -month period (January-May)

Time	January	February	March	April	May	Mean
08.00 a.m.	14.46	19.91	55.58	56.24	30.46	35.33
10.00 a.m.	53.92	65.16	80.91	65.16	38.19	60.66
12.00 p.m.	36.66	31.41	23.66	21.66	20.33	26.74
02.00 p.m.	32.46	12.99	19.99	18.83	10.39	18.93
04.00 p.m.	20.73	10.91	15.08	14.41	06.93	13.61
06.00 p.m.	18.53	07.83	10.58	09.74	06.06	10.54
Mean	29.46	24.70	34.30	31.00	18.72	

Seasonally averaged nectar foraging activity followed a trajectory similar to pollen collection, with the highest mean values recorded in March and April and a progressive decline toward May (Supplementary Tables S2). This seasonal pattern reflects the tight coupling between flowering phenology and pollinator activity in tropical agroecosystems, where nectar availability is governed by both plant reproductive schedules and prevailing climatic conditions (Stabentheiner and Kovac, 2016) ^[34]. Nevertheless, despite these biologically coherent trends, the month-wise Kruskal-Wallis test did not detect statistically significant differences in nectar foraging. This apparent

mismatch between descriptive patterns and statistical outcomes likely arises from high intra-month variability, driven by short-term fluctuations in weather, spatial heterogeneity in floral resources, and behavioural plasticity of foragers that allows colonies to maintain relatively stable nectar intake across months (Vijayan *et al.*, 2018) ^[35]. In landscapes with continuous or overlapping floral resources, such buffering effects are known to dampen seasonal contrasts in foraging metrics, thereby reducing the statistical power of rank-based tests to detect month-level differences (Guezzen and Forrest, 2021) ^[16].

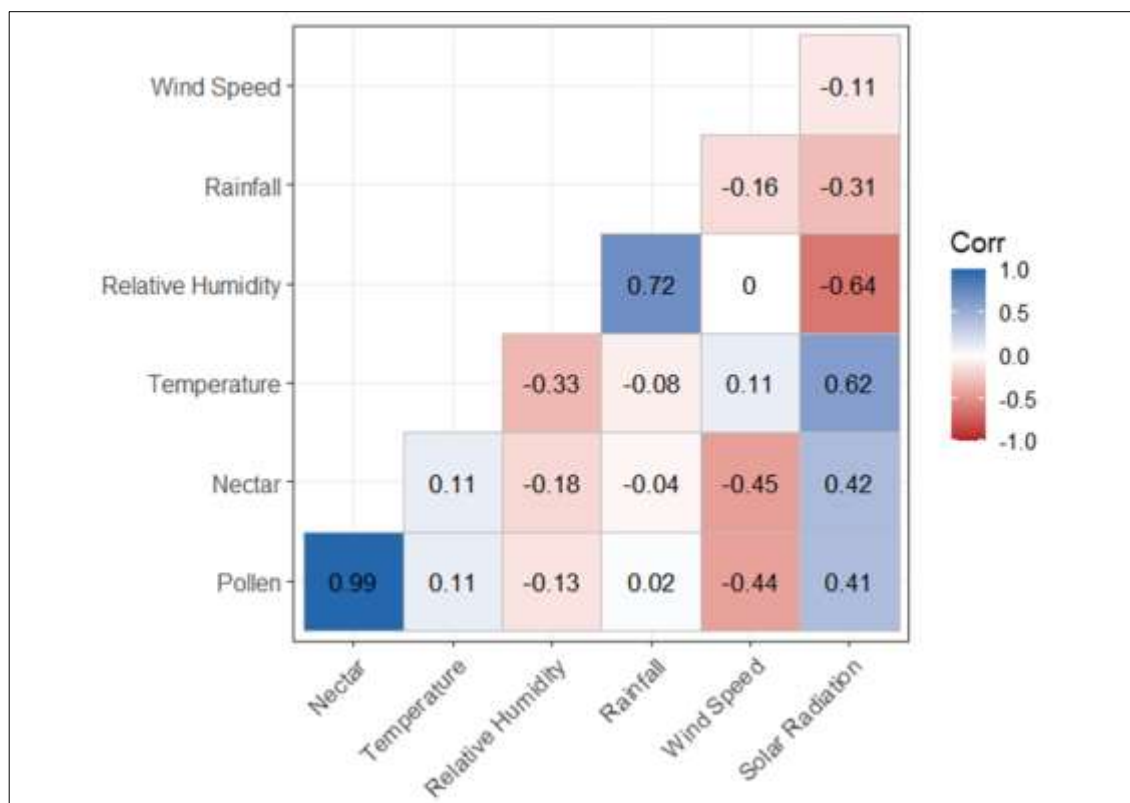


Fig 3: Spearman rank correlation of pollen and nectar with other climatic variables

In contrast to the muted seasonal signal, time of day exerted a strong and highly significant influence on nectar foraging activity ($\chi^2 = 68.05$, $p < 0.001$), confirming that diurnal environmental forcing is the primary determinant of nectar collection behaviour during the honey-flow period. Collectively, these findings demonstrate that nectar foraging by *A. cerana indica* is governed predominantly by short-term physiological optimisation in response to microclimatic and floral cues, rather than by broad seasonal shifts alone. Such fine-scale temporal optimisation enables honeybees to maximise energetic efficiency under variable tropical conditions and highlights the sensitivity of pollination services to changes in daily thermal and hydric regimes.

Climatic Drivers of Foraging Activity: Correlation Analysis

To evaluate the influence of individual climatic variables on honeybee foraging intensity, Spearman rank correlation analyses were performed using the standardized meteorological dataset (Figure 3). The analysis indicated that temperature and wind speed were the most influential abiotic factors associated with both pollen and nectar collection. Temperature exhibited a weak but consistently negative correlation with forager return rates, suggesting that higher daytime temperatures- particularly under pre-monsoon conditions-may constrain bee activity by elevating thermal stress, increasing metabolic costs of flight, and altering nectar properties such as viscosity and evaporation

rates. Higher temperature typically reduces viscosity but it also increases evaporation and may reduce nectar volume (Eswarappa *et al.*, 2025; Mattos *et al.*, 2018) [13, 26]. Similar temperature-dependent reductions in foraging intensity have been reported for *Apis cerana* and other honeybee species under tropical and subtropical conditions, where optimal activity is confined to a relatively narrow thermal window (Kamaraj and Rasappan, 2024) [22]

Table 4: Kruskal-Wallis rank sum test for pollen and Nectar

Parameter	Factor	Kruskal-Wallis chi-squared	df	p-value
Pollen	Time	70.42	5	8.4e-14*
	Month	5.08	4	0.6506
Nectar	Time	68.05	5	2.606e-13*
	Month	9.11	4	0.2451

In contrast, wind speed showed a moderate to strong negative association with both pollen and nectar foraging, highlighting its role as a key physical constraint on flight performance (Figure 3). Even modest increases in wind velocity can impair take-off, reduce flight stability, and increase energetic expenditure, thereby lowering the efficiency and success rate of foraging trips. The strength of this correlation underscores the sensitivity of honeybee foraging to wind conditions, particularly in open or semi-urban landscapes where shelter is limited (Balfour and Ratnieks, 2025; Hennessy *et al.*, 2021) [7, 19].

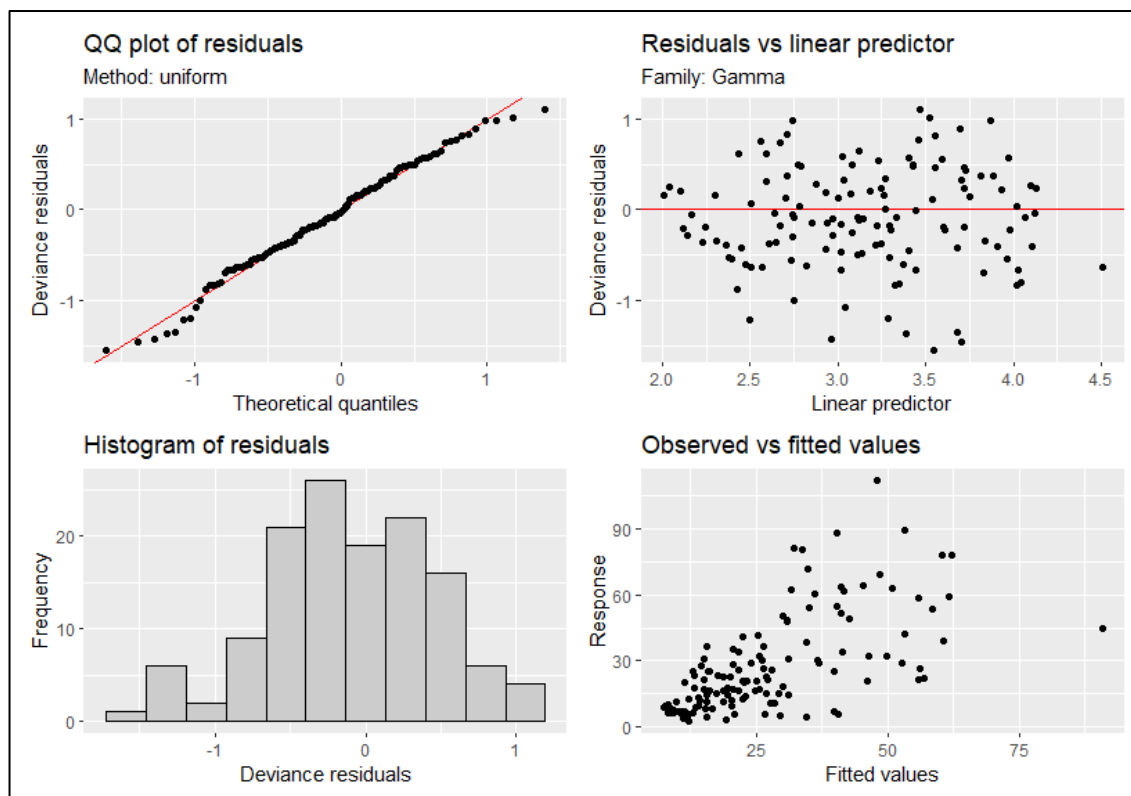


Fig 4: Diagnostic plots for the Generalized Additive Model (GAM) fitted to pollen collection data

Relative humidity displayed a positive monotonic association with pollen collection, consistent with evidence that higher humidity enhances pollen hydration, reduces desiccation, and facilitates pollen release and handling by foragers. However, its relationship with nectar foraging was weak and non-significant, suggesting that nectar intake is regulated more strongly by flower-specific traits such as nectar volume, sugar concentration, and secretion dynamics than by ambient humidity alone. Rainfall and solar radiation exhibited minimal direct pairwise correlations with foraging intensity, likely reflecting the episodic nature of rainfall and the fact that the effects of radiation on bee activity are often indirect and context-dependent, mediated through temperature, nectar secretion, and visual orientation rather than acting as independent linear drivers (Clarke and Robert, 2018) ^[9].

Multivariate and Nonlinear Climatic Effects on Foraging

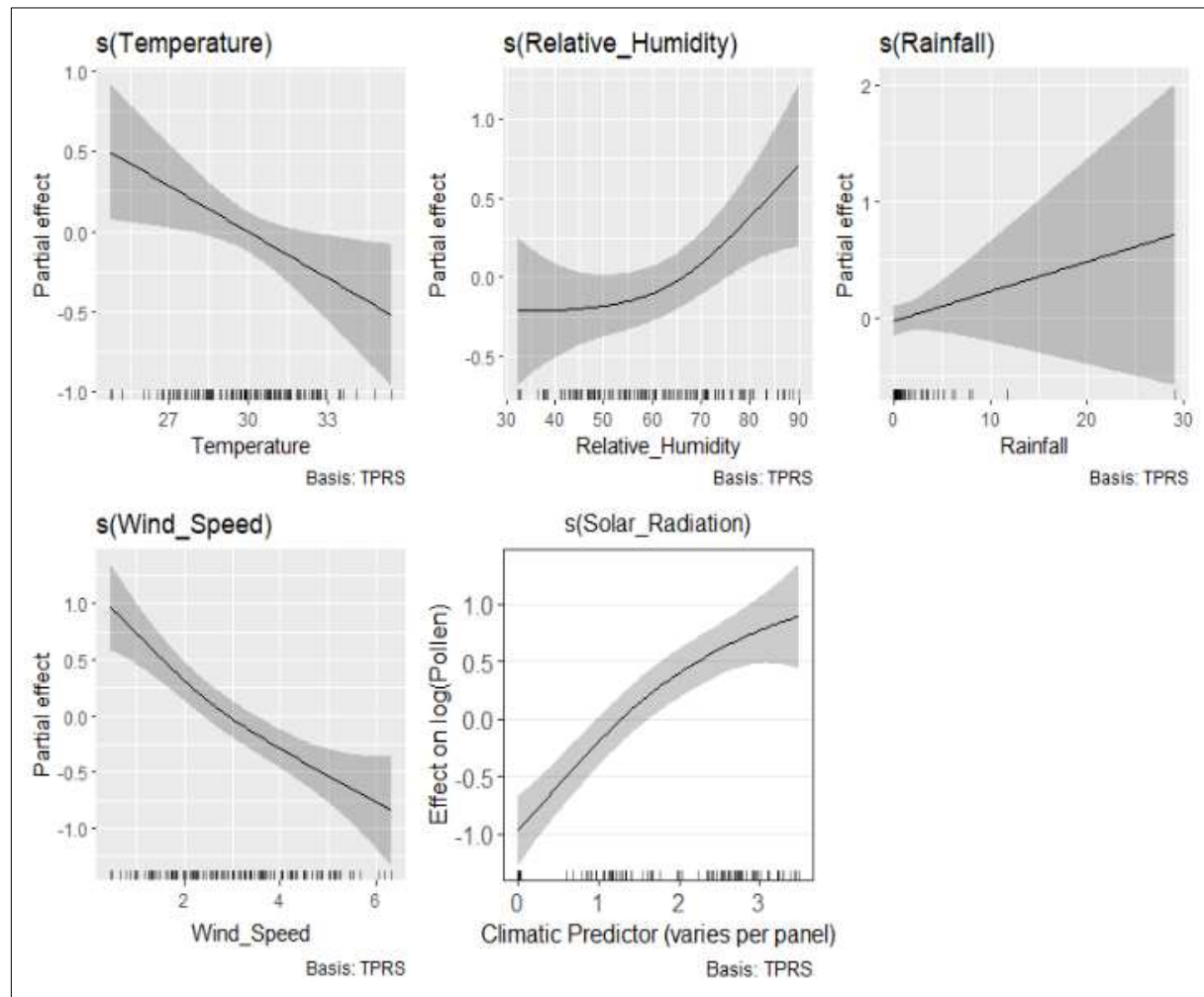
Generalized Additive Models (GAMs) demonstrated that short-term climatic variability exerted a substantial and nonlinear influence on both pollen and nectar foraging activity of *Apis cerana indica*. The fitted models showed moderate explanatory power, with the pollen GAM accounting for 38.3% of the deviance (adjusted $R^2 = 0.227$) and the nectar GAM explaining a higher 49.7% of the deviance (adjusted $R^2 = 0.352$), based on $n = 132$

observations, indicating that nectar foraging was more strongly regulated by prevailing weather conditions than pollen collection (Table 5). The lower generalised cross-validation (GCV) score and scale estimate for the nectar model further suggest improved predictive stability for nectar returns. Diagnostic plots of the pollen GAM revealed no major departures from model assumptions, with residuals exhibiting homoscedasticity and near-normal distribution, supporting the robustness of model inference (Figure 4).

Among the climatic predictors, wind speed and solar radiation emerged as the most influential drivers of foraging behaviour, whereas rainfall exerted no detectable effect during the study period. Wind speed showed a strong negative effect on both pollen and nectar collection, with a pronounced nonlinear response for nectar ($\text{edf} = 2.37$, $p < 0.001$) and a steep negative smooth for pollen ($\text{edf} = 1.719$, $p < 0.001$) (Table 4; Figures 5–7). The smooth functions indicate a threshold-type response whereby even moderate increases in wind speed rapidly suppressed foraging activity, reflecting the aerodynamic constraints of honeybee flight and the increased energetic cost and instability associated with windy conditions. Such wind-induced compression of effective foraging windows has been widely documented and represents a critical abiotic constraint on pollinator efficiency, particularly in open and coastal landscapes (Clarke and Robert, 2018; Farooqi *et al.*, 2021) ^[9, 14].

Table 5: Summary of smooth term effects from Generalized Additive Models (GAMs) predicting pollen and nectar collection by honeybees in response to climatic variables

Predictor	edf (Pollen)	F (Pollen)	p (Pollen)	Sig. (Pollen)	Effect on Pollen	edf (Nectar)	F (Nectar)	p (Nectar)	Sig. (Nectar)	Effect on Nectar
Temperature	1.001	5.823	0.0173	*	Weak negative linear effect	1.694	2.421	0.0853	.	Slight nonlinear effect
Relative Humidity	1.889	3.677	0.0245	*	Curvilinear, positive at higher RH	1.562	1.126	0.2658	ns	No significant effect
Rainfall	1.000	1.196	0.2762	ns	No significant effect	1.000	1.755	0.1878	ns	No significant effect
Wind Speed	1.719	18.966	<0.001	***	Strong negative effect	2.370	16.103	<0.001	***	Strong negative nonlinear effect
Solar Radiation	1.981	19.678	<0.001	***	Strong positive nonlinear effect	5.762	7.871	4.00×10^{-7}	***	Highly nonlinear positive effect

**Fig 5:** Smooth effects of climatic variables on pollen collection by honeybees estimated using a Generalized Additive Model (GAM)**Table 6.** Overall performance metrics of the fitted GAMs for pollen and nectar collection

Model	Adjusted R ²	Deviance Explained	GCV	Scale Estimate	n
Pollen GAM	0.227	38.30%	0.7643	0.53225	132
Nectar GAM	0.352	49.70%	0.4002	0.31207	132

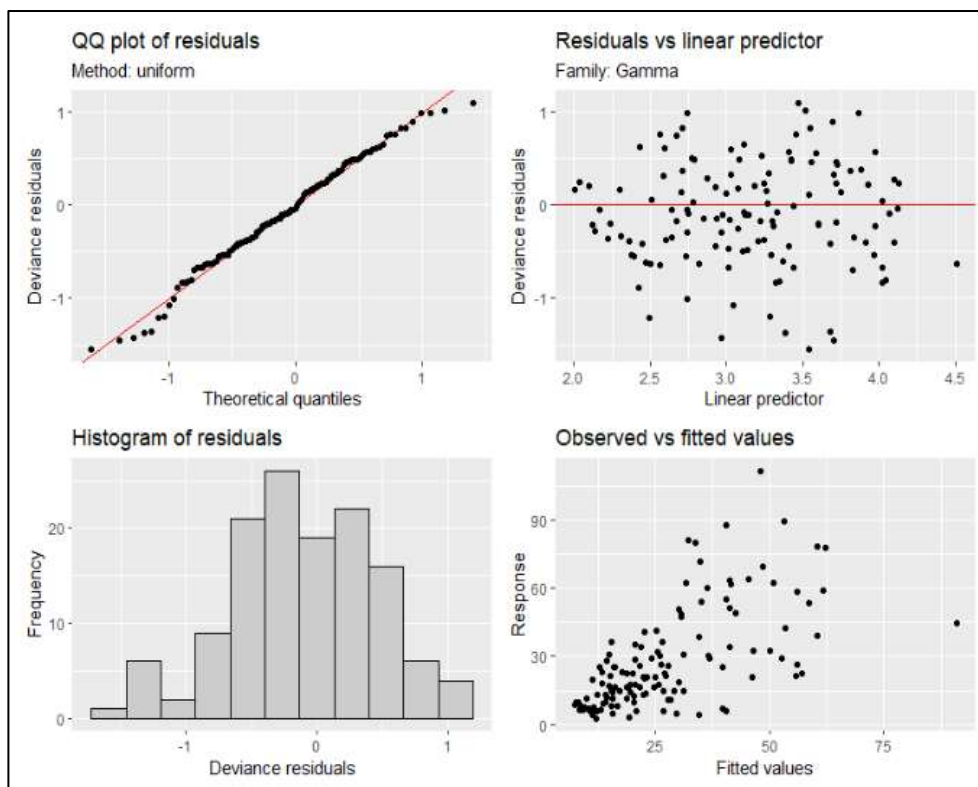


Fig 6: Smooth effects of climatic variables on nectar collection by honeybees estimated using a Generalized Additive Model (GAM).

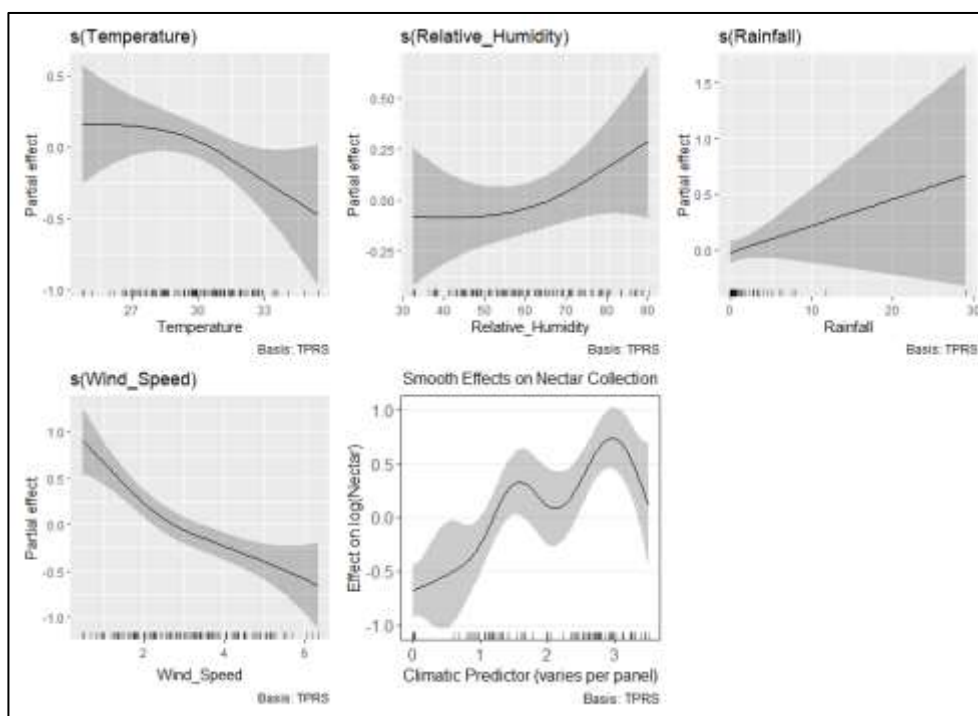


Fig 7: Smooth effects of climatic variables on pollen collection by honeybees estimated using a Generalized Additive Model (GAM)

Solar radiation exhibited a strong positive and highly nonlinear association with both pollen ($\text{edf} = 1.981$, $p < 0.001$) and nectar foraging ($\text{edf} = 5.762$, $p = 4.00 \times 10^{-7}$) (Table 4; Figures 5–6). The smooth response curves revealed a rapid increase in foraging intensity under low-to-moderate irradiance, followed by a tendency toward saturation at higher radiation levels, suggesting the existence of an optimal light regime beyond which additional irradiance yields diminishing behavioural gains. This pattern likely reflects improvements in visual orientation, floral detectability, and thoracic warming under favourable

radiation conditions, coupled with behavioural regulation to avoid overheating at extreme irradiance. The dominance of solar radiation effects in both models underscores the central role of light environment in structuring diurnal foraging rhythms of honeybees (Abrol, 2006; Schmickl and Crailsheim, 2004) [4,32].

Secondary climatic drivers exhibited resource-specific effects. Temperature showed a weak but significant negative linear effect on pollen foraging ($\text{edf} \approx 1.0$, $p = 0.0173$), whereas its influence on nectar collection was marginal and slightly nonlinear ($p = 0.0853$) (Table 4). This asymmetry

suggests that pollen foraging is more sensitive to thermal stress, potentially due to temperature-dependent constraints on flight performance, pollen handling efficiency, and the timing of anther dehiscence, while nectar foraging remains comparatively resilient through behavioural reallocation among diverse floral sources. Relative humidity exerted a significant curvilinear positive effect on pollen collection ($\text{edf} = 1.889$, $p = 0.0245$) but had no significant influence on nectar returns ($p = 0.2658$) (Table 4; Figure 7). The pollen smooth indicates enhanced activity under moderately high humidity, likely associated with improved pollen hydration and reduced desiccation, followed by stabilisation at higher humidity levels. In contrast, nectar extraction appears less directly constrained by ambient humidity in heterogeneous floral environments. Rainfall showed no significant effect on either foraging stream, most plausibly because rainfall events were infrequent or temporally decoupled from observation periods, limiting their effective influence within the analysed dataset (Table 4) (de Figueiredo-Mecca *et al.*, 2013; Descamps *et al.*, 2021).

This study elucidates the temporal structure and climatic regulation of pollen and nectar foraging behaviour of *Apis cerana indica* in a semi-urban coastal ecosystem of Goa, India. Foraging activity was governed primarily by strong diurnal rhythms, with consistently higher pollen and nectar returns during early to mid-morning hours and a pronounced decline toward the afternoon. These patterns were stable across months, indicating that short-term physiological and microclimatic constraints exerted stronger control over foraging behaviour than broader seasonal variation during the honey-flow period. Although peak foraging intensity occurred during March and April, corresponding to maximum floral availability, month-wise differences were not statistically significant, reflecting high intra-month variability and buffering effects of continuous floral resources. Correlation and nonlinear modelling approaches collectively demonstrated that wind speed and solar radiation were the dominant climatic drivers of foraging activity, while temperature and relative humidity exerted secondary, resource-specific influences. The Generalized Additive Models further revealed nonlinear threshold responses, highlighting narrow optimal environmental windows for efficient foraging.

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Author Contribution Statement

RS, SN and BSD conducted the experiment, SB analyzed the data and RS, SB, SN and BSD prepared the manuscript.

Conflict of Interest

No conflict of interest.

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