



## Effects of Climatic Variations on Plant–Pollinator Interactions: Implications for Biodiversity Conservation



Umamah Khan Ejaz<sup>1</sup>

<sup>1</sup> Lahore Grammar School, Islamabad

Email: [Umamahkhanejaz@gmail.com](mailto:Umamahkhanejaz@gmail.com)

| ARTICLE INFO                                                                                                                                                                                                                                                                                                                                                                                                                              | ABSTRACT                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
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| <p><b>Received:</b><br/>July 29, 2026</p> <p><b>Revised:</b><br/>August 29, 2026</p> <p><b>Accepted:</b><br/>September 29, 2026</p> <p><b>Available Online:</b><br/>October 10, 2026</p> <p><b>Keywords:</b><br/><i>plant–pollinator interactions, climatic variability, flowering phenology, pollinator visitation, Shannon–Wiener diversity, biodiversity conservation</i></p> <p><b>Corresponding Author:</b><br/>Umamah Khan Ejaz</p> | <p>Field evidence of the effects of local climatic variation on pollination processes is not consistent and climate change is altering the availability, abundance and quality of floral resources to which the insects rely. The present study was designed based on a quantitative field approach to gain insight into the effects of climatic variation on plant–pollinator interactions over a four-month period across three ecological sites with different environmental conditions. Thirty 10 × 10 m plots (10 plots per site) were chosen in a stratified random fashion, and along with temperature, relative humidity and rainfall, pollinator visitation frequency, plant diversity, flowering abundance and flowering duration were measured. Diversity was calculated with the Shannon – Wiener index and associations were explored with Pearson correlation analysis and negative binomial generalized linear mixed models (GLMMs) in R. The intermediate site had the greatest diversity of plants and pollinators, plant flowering, and visitation, while the warmest and driest site had shorter flowering and lower visitation. A positive correlation was found between visitation and both flowering abundance and length, and there was a curvilinear correlation between visitation and temperature. The results indicate that climatic variability can mostly be mediated through floral resources availability and phenology and strongly endorse the conservation approach based on the maintenance of heterogenic microclimates and floral continuity.</p> |

### Introduction

Plant–pollinator interactions are one of the most critical ecological interactions involving terrestrial biodiversity. Animals are a vital component for the reproduction of most flowering plants, and the services provided by bees, butterflies, flies and beetles that feed on flowers are delivered across natural and managed ecosystems (Ollerton, 2017). Non-bee insects are common and sometimes important visitors that are gaining attention, and, like bees, they are a major source of pollination (Rader et al., 2020). The continued existence of these mutualisms thus has implications beyond the level of the individual species and into the stability of the ecosystem, food production and human welfare (Dicks et al., 2021).

Since there has been a growing amount of evidence of insect decline, interest in these relationships has increased. Sánchez-Bayo & Wyckhuys (2019) and Wagner (2020) cite losses in insect abundance and diversity in synthesis studies and attribute them to a combination of habitat modification, agrochemical use, invasive species and climate change. Similarly, a global expert assessment revealed a number of interacting drivers of pollinator decline, including climate change (Dicks et al., 2021). These pressures usually do not occur individually, and disentangling the specific effects of climatic variation on pollination processes is challenging and important.

Climate change is disrupting the environmental factors which control plant growth, flowering and insect activity. At the global scale, increases in temperature, changes in precipitation patterns and more extreme events are now well established (IPCC, 2023). On a global scale, the combination of climate change and agricultural intensification are forecast to alter insect assemblages at the biodiversity level (Outhwaite et al., 2022), and bumble bees have been found to have decreased in areas where climate change and agricultural intensification have taken conditions beyond what they historically tolerated (Soroye et al., 2020). Multiple pollinator community shifts are also possible resulting from the synergy created when several global-change drivers are present, as suggested by Rafferty (2017).

Plant–pollinator interactions may be affected directly by climate, and indirectly through a variety of other mechanisms. Plants flower and fallow based on available temperature and moisture; pollinators emerge, fly and forage in response to available temperature and moisture; and the number of flowers produced by the plants and the number of flowers visited by pollinators are determined by what temperature and moisture are available. The phenological mismatch is created when the two partners react to various cues and/or at different speeds, leading to a decreased seasonal overlap (Freimuth et al. 2022; Gérard et al. 2020). The seasonality of pollinator assemblages have already changed with the flight periods of European insect pollinators, and long-term observations demonstrate that interactions can be quickly reorganized as they are altered by specific species responding individually to environmental conditions (CaraDonna et al., 2017; Duchenne et al., 2020). Additionally, there is some indirect influence of climate: interannual variation in floral resource phenology has been found to correlate with interannual variation in the abundance of bumble bees (Ogilvie et al., 2017); and landscape composition and quality can buffer the impact of climate on wild bees (Kammerer et al., 2021).

Regardless of this progress, much of the evidence comes from single taxa, from long time-series from a few locations, or from large-scale syntheses which are difficult to relate local climatic variation at the plot level to variation in floral resources and pollinator visitation. Field studies which include repeated observations of climatic variables and plant diversity, flowering traits and the visitation of several groups of pollinators are still useful in identifying pathways by which climate is influencing pollination, and they can be analyzed with models capable of repeated observations.

The following study was conducted to address this need by carrying out a quantitative field study on three ecological sites of varying environmental conditions. It aimed to (a) describe the climatic conditions (temperature, humidity and rainfall) of the sites, (b) compare plant diversity, flowering abundance, flowering duration and pollinator diversity and visitation among sites, (c) explore the relationships between climatic variables, flowering patterns, and pollinator visitation, and (d) discuss the implications of these relationships for biodiversity conservation and ecosystem sustainability. The study provides evidence that can guide conservation planning for pollinators and plant communities that rely on pollinators as a resource, as it relates to the local climate variability of the region and its floral resources and visitation. The rest of this paper summarizes the literature, specifies the method, analyzes the data, discusses the results and makes recommendations.

## **Literature Review**

### **Pollinator Diversity, Ecological Function and Decline**

The pollinator assemblage is diverse and distinct in terms of their taxonomic composition. Ollerton (2017) updated and summarized the distribution and ecological role of pollinators and highlighted their value and that their loss would impact on the reproduction of plants with a wide range of animal groups providing pollination services, each of which varies geographically in their diversity. Similarly, Rader et al., (2020) demonstrated that non-bee insects, including flies, butterflies and beetles, play an important role in pollination of flowers and are important to consider with regards to their biology and management in addition to bees. For conservation, this functional diversity is important as it can bring complimentary and redundant pollination services.

Wagner (2020) conducted a review of insect losses in the Anthropocene and found many of them were on the decline in numbers, diversity, or biomass, while Sánchez-Bayo and Wyckhuys (2019) determined that habitat destruction, pollution, invasive species, and climate change were the main factors leading to insect declines. Dicks et al., (2021) mentioned that land-use change, land management and pesticide use were identified as having the greatest impacts and climate change as an additional interacting pressure by experts. Outhwaite et al., (2022) discovered that both the intensity of agriculture and high climate change were correlated with highest reductions in abundance and richness of insects at a global scale, while Soroye et al., (2020) attributed bumble bee declines to climatic conditions that are different from historical norms. Together, these studies indicate that climate is not always the primary cause but is consistently a secondary cause and amplifier of other pressures, which is bolstered by the ongoing climate warming indicated by the IPCC (2023).

### **Phenological Responses and Mismatch**

Timing of recurring biological events, called phenology, is one of the best indicators of the effects of climate on pollination. Rafferty (2017) stated that insect pollinators are sensitive to global change, which affects their timing, abundance and distribution, and that these effects lead to changes in community composition. Gérard et al. (2020) noted that sensitive or insensitive plants under global warming may lead to mis-match of the plant and pollinator partners. Warming has also altered the synchrony of plant and pollinator interactions, with some changes reported as positive and others as negative (Freimuth et al., 2022); however, there are varied nuances of change among the taxa and systems. Duchenne et al., (2020) demonstrated that the seasonal structure of European pollinator assemblages changed in response to changes in the fly-time of European pollinators. Nawaz (2026) explored the integration of sustainability into institutional development, highlighting opportunities and challenges associated with sustainable practices. Similarly, Nawaz and Iqbal (2025) examined the relationship between technology and sustainable tourism, emphasizing the importance of sustainability-oriented development. These studies offer broader perspectives on sustainability, supporting the need to investigate how climatic variations affect ecological relationships and biodiversity conservation.

There are similar imbalances at the species level. A warmer temperature stimulated flowering of a spring plant more than the emergence of two solitary bee species, potentially leaving early flowers without pollinators for some time (Kehrberger and Holzschuh 2019). In a study that extended upon the discussions in this chapter, Ogilvie et al., (2017) illustrated an indirect mechanism of how variation in floral resource phenology, in addition to direct effects on temperature was related to interannual variation in bumble bee abundance.

### **The Floral Resource Quantity, Quality and Landscape Context**

Pollinator resources connect to climate through floral resources. Descamps et al., (2021) demonstrated experimentally that when heat and drought stress a bee-pollinated plant, both the amount and the quality of the nectar and pollen produced decreases, suggesting that climatic stress can also affect the quality of the resources available even in the presence of flowers. Ogilvie et al., (2017) showed that the availability of floral resources through time shaped pollinator abundance. Climate, on the other hand, is not an entity unique from the landscape. Kammerer et al (2021) studied the impact of landscape composition, landscape quality and climate on wild bees and discovered that different species benefited or suffered, resulting in winners and losers. This is heterogeneous, and implies that local habitat conditions (plant diversity, microclimate) could have a buffering or amplifying effect on climatic impacts.

### **Interactions and Community Reorganization**

In addition to the responses at the global level, climatic variability can also reorganize relations between individuals. CaraDonna et al., (2017) reported significant changes in plant-pollinator interactions across years and rapid turnover of interactions, suggesting that networks are not static. Rafferty (2017) suggested that novel pollinator communities could arise if species become rare at different rates, and the focus Rader et al., (2020) paid to non-bee visitors points to the need to measure changes in the relative abundance of different groups of insects, as well as overall visitation.

### **Research Gap and Hypotheses**

The literature that was examined shows that phenology, floral resources and community composition are all pathways by which climate affects plant-pollinator interactions, but that these impacts are context dependent. It is uncommon for field studies to integrate plot-level measurements of climate with plant diversity, abundance and duration of flowering and multiple groups of pollinators using a single mixed-effects model across a range of contrasting sites. Reviewed evidence led to the development of three hypotheses, which were tested during the study. H2: The diversity of plant species, the number of flowers produced, and the length of the flowering period varies between sites with different temperature, humidity and rainfall. H2: Sites vary in the diversity and frequency of their pollinators and flowering abundance and duration increase with pollinator diversity and frequency. H3: Pollinator visitation rates are predicted by temperature and rainfall, controlling for the floral resources and repeated observations.

### **Methodology**

#### **Research Design**

The study was conducted using a quantitative field based research design to understand the impact of climatic variation on the plant-pollinator interaction and its consequences for conservation of biodiversity. A comparative approach was followed in which three ecological sites were studied at the same time so that a relationship could be established between the variation in the floral resource and the variation in the pollinator visitation among the different sites because of climatic differences. The data were recorded for four months during the peak flowering period. The design was an observational one, rather than an

experimental one, so no climatic variables were manipulated and inference depended on natural variation among plots and sites.

### **Study Sites**

To assess the range of environmental conditions, three sites were purposely selected that were representative but similar in management history and vegetation type. The condition of Site A was relatively warm and dry, B was intermediate condition (moderate temperatures and moderate rainfall), and C was a cooler low rainfall location. These sites were chosen because they were accessible, had flowering herbaceous and shrub vegetation and had not been disturbed in recent years by grazing, mowing, or intensive farming activities. The distance between the sites was enough to minimize the risk of pollinator movement between sites and each site was in close proximity to a meteorological station that could offer additional climatic data.

### **Sampling Design**

The study plots were established by stratified random sampling procedure. Vegetation was assigned to habitat strata within each site based on vegetation structure and microtopography, and represented the major habitat types. The plots were randomly located within each stratum with a minimum buffer distance of 20 m between plots to ensure plot independence. Thirty (30) sampling plots (10 per site) were established and permanently marked with corner pegs of 10 × 10 m. The size of the plots was selected to reflect the local flowering community while maintaining the ability to complete and standardize observation of the floral visitors present in the plots.

### **Data Collection**

Systematic field observations were used to record plant diversity, flowering abundance and flowering duration. All species of flowering plants were observed and identified using botanical identification techniques in each plot, such as regional floras and key species in the field, with specimens that were not identifiable in the field being pressed, photographed, and identified with herbarium specimens. The flowering abundance was measured by the number of open floral units (flowers or inflorescences, as appropriate) found in each plot on each survey. Flowers were checked weekly for each species in each plot and the number of days from the first to last observation of an open flower was determined for each species and averaged to get a plot-level estimate of flowering duration.

### **Observations and identification of pollinators**

The number of visits to the plants by the pollinators was recorded during the standard morning and afternoon observation periods under favorable weather conditions. One morning (08:00 – 11:00) and one afternoon (14:00 – 16:30) of 10 minutes each was observed on each plot visited twice monthly and a total of 16 observation periods per plot and 480 observation periods were observed. Only under suitable weather conditions (clear to partly cloudy skies, light wind, with no rain) observations were carried out and the order of plots visited rotated to avoid systematic timing bias. A trained observer located on the edge of each plot counted all flower visits (when the pollinator had some part of its body in contact with the reproductive parts of a flower) and recorded the plant species visited during each period. The taxonomy of pollinators, comprising of bees, butterflies, flies and other flower visiting insects, were identified by following the standard taxonomy identification guides. Photographs or (in a few cases, and only in small numbers) specimens collected away from the observation periods were taken in the field and then sent for species identification in the laboratory; where this was not possible, they were assigned to morphospecies.

### **Climatic data**

On-site measurements and data from nearby meteorological stations were used to obtain temperature, relative humidity, and rainfall data. Within each plot, calibrated digital data loggers were placed 1 m above ground and measured the air temperature and relative humidity at 30 minute intervals over the entire study period; rainfall was measured by a standard rain gauge in each plot and read weekly. On-site measurements were validated with records of weather stations closest to the site and to supplement for brief periods of time when the loggers have failed. Then mean temperatures, mean relative humidities and monthly rainfall totals were plotted to get the mean of each month for analysis.

### **Diversity Indices**

The Shannon – Wiener diversity index ( $H' = -\sum (p_i \ln p_i)$ , with  $p_i$  being the proportion of floral units (for plants) or recorded visits (for pollinators) of species  $i$ ) was used to assess plant and pollinator diversity. The index was calculated individually for each plot to facilitate comparison of diversity between sites and to be used for later analyses. The number of species or morphospecies recorded was also calculated, which is a measure of species richness.

### **Statistical Analysis**

R software (R Core Team, 2023) was used for statistical analyses, and the criterion for statistical significance was set at  $p < .05$ . Climatic, floral and pollinator variables were described by means and standard deviations for each site. One-way analysis of variance (ANOVA) was used to test for differences between sites, with Tukey's honestly significant difference tests for pairs of means, and tests of normality (Shapiro–Wilk) and homogeneity of variance (Levene's) were performed. Bivariate relationships between climatic variables, flowering patterns, pollinator foraging visits were explored using Pearson correlation analyses at the plot level.

Generalized linear mixed models (GLMMs) were used to investigate the relationships of the climatic variables, flowering patterns and pollinator visiting rates, taking repeated observations across plots and sites into account. The response variable was the number of flower visits per 10 minute period and was modelled with a negative binomial error distribution (glmmTMB package (Brooks et al., 2017)), with a log link function to accommodate overdispersion in count data. Fixed effects were temperature, a quadratic temperature effect to accommodate a non-linear response, rainfall, flowering abundance and flowering duration, all standardized to zero mean and unit variance. The multivariable model excluded relative humidity due to its correlation with temperature and rainfall (variance inflation factor  $> 5$ ) and all other variance inflation factors were below 3. Random intercepts were used for site and for plot within site. Residual diagnostics, dispersion checks, marginal  $R^2$  and conditional  $R^2$  were used to assess model fit, and to describe the variance explained by the fixed effects and the variance explained by both fixed and random effects, respectively.

### Data Quality and Ethical Considerations

Observers were trained in identification of both pollinators and plants prior to data collection and consistency among the observers was tested during pilot sessions. Permission to access the sites was gained by the relevant land authorities and the design of the study minimises disturbance in that observations are done along the edges of plots, no vegetation was removed and only the minimum number of specimens collected for identification.

## Analysis and Results

### Climatic Conditions Across Sites

The climatic data from these three sites are summarized in Table 1. The mean temperature decreased from Site A ( $M = 27.4$  °C,  $SD = 2.9$ ) to Site B ( $M = 23.1$  °C,  $SD = 2.6$ ) to Site C ( $M = 18.6$  °C,  $SD = 2.4$ ); while the relative humidity and the monthly rainfall increased in the reverse direction. The results of a one-way ANOVA found that all three climatic variables were each significantly different between the sites (all  $p < .001$ ), with Tukey tests showing all pairwise differences between the sites were significant. The sites thus formed a clear gradient from warm and dry Site A to cool and wet Site C with conditions falling in the middle at Site B.

**Table 1**

### Climatic Conditions at the Three Study Sites

| Variable              | Site A      | Site B      | Site C       | F(2, 27) | p        |
|-----------------------|-------------|-------------|--------------|----------|----------|
| Mean temperature (°C) | 27.4 (2.9)  | 23.1 (2.6)  | 18.6 (2.4)   | 27.70    | $< .001$ |
| Relative humidity (%) | 48.6 (7.8)  | 62.3 (6.9)  | 74.9 (6.1)   | 35.63    | $< .001$ |
| Monthly rainfall (mm) | 38.2 (14.5) | 71.5 (19.8) | 104.7 (24.3) | 27.81    | $< .001$ |

*Note.* Values are plot-level means with standard deviations in parentheses ( $n = 10$  plots per site). Temperature and relative humidity were averaged across the four-month study period; rainfall values are monthly totals. Site A = warm, dry lowland; Site B = intermediate; Site C = cool, wet upland.

### Plant Diversity, Flowering Patterns, and Pollinator Visitation

Table 2 shows the diversity in plants, flowering abundance, flowering period, pollinator diversity and pollinator visitation by site. The number of plant species that were found at all plots of each site were 21, 34, and 29 at Sites A, B, and C, respectively, and 24, 38, and 31 at the sites for pollinator species/morphospecies. The plant species richness, in terms of mean number of species, was highest at Site B (13.4) and lowest at Site A (8.7) and the Shannon–Wiener index for plants was highest at Site B (2.87) and lowest at Site A (2.18). The abundance and duration of flowers were also greatest at Site B; pollinator richness and

diversity were also greatest at Site B and visitation rate averaged 17.6 visits per 10 minutes of observation at Site B, 13.2 at Site C, and 9.8 at Site A.

There were significant differences between sites on all variables (all  $p < .001$ ). Tukey tests revealed significant differences between Site B and Site A on all variables and between Site B and Site C on all variables except flowering duration; however, there was no difference between Site A and Site C on flowering abundance, pollinator richness, or visitation rate, but each differed significantly on plant richness, plant diversity, flowering duration, and pollinator diversity. Response variables then were at a maximum in the intermediate rather than in the linear part of the climatic gradient, confirming H1 and the initial part of H2.

**Table 2**

**Plant Diversity, Flowering Patterns, and Pollinator Visitation by Site**

| Variable                                         | Site A        | Site B          | Site C          | F(2, 27) | p      |
|--------------------------------------------------|---------------|-----------------|-----------------|----------|--------|
| Plant species richness (per plot)                | 8.7 (1.8)     | 13.4 (2.1)      | 11.2 (1.9)      | 14.75    | < .001 |
| Plant $H'$                                       | 2.18 (0.21)   | 2.87 (0.19)     | 2.51 (0.23)     | 26.82    | < .001 |
| Flowering abundance (open floral units per plot) | 842.6 (176.4) | 1,265.3 (203.7) | 1,018.9 (188.2) | 12.52    | < .001 |
| Flowering duration (days)                        | 31.4 (4.8)    | 42.9 (5.1)      | 37.6 (4.6)      | 14.16    | < .001 |
| Pollinator species richness (per plot)           | 9.6 (2.2)     | 15.8 (2.6)      | 12.1 (2.3)      | 17.28    | < .001 |
| Pollinator $H'$                                  | 2.04 (0.24)   | 2.76 (0.22)     | 2.43 (0.25)     | 23.11    | < .001 |
| Visitation rate (visits per 10 min)              | 9.8 (2.7)     | 17.6 (3.4)      | 13.2 (3.1)      | 16.11    | < .001 |

*Note.* Values are plot-level means with standard deviations in parentheses ( $n = 10$  plots per site).  $H'$  = Shannon–Wiener diversity index. Visitation rate is the mean number of flower visits recorded per 10-minute observation period.

**Pollinator Group Composition**

Across the four-month study, 6,496 flower visits were recorded (1,568 at Site A, 2,816 at Site B, and 2,112 at Site C). The percentage of visits provided by each group of pollinators is displayed in Table 3. Bees visited all sites and made up some 47% of the total visits, with the largest proportion at Site B (52.8%). The warmest site (27.9%) received proportionately the most visits from flies while Site C (cool, wet) received the greatest proportion of visits from butterflies (24.8%). At each site other flower visiting insects accounted for 8.3–11.4% of visits.

**Table 3**

**Composition of Flower Visits by Pollinator Group and Site**

| Pollinator group              | Site A (%) | Site B (%) | Site C (%) |
|-------------------------------|------------|------------|------------|
| Bees                          | 46.2       | 52.8       | 41.3       |
| Butterflies                   | 14.5       | 18.6       | 24.8       |
| Flies                         | 27.9       | 19.7       | 25.6       |
| Other flower-visiting insects | 11.4       | 8.9        | 8.3        |

| Pollinator group          | Site A (%) | Site B (%) | Site C (%) |
|---------------------------|------------|------------|------------|
| Total visits ( <i>n</i> ) | 1,568      | 2,816      | 2,112      |

*Note.* Percentages are shares of all flower visits recorded at each site and sum to 100% within each column.

### Correlation Analysis

Pearson correlations between the climatic variables, flowering patterns and visitation rate at the plot level are presented in Table 4. Both flowering abundance and flowering duration were negatively correlated with temperature ( $r = -.41$ ,  $p < .05$  and  $r = -.55$ ,  $p < .01$ , respectively), and with the rate of flower visits ( $r = -.37$ ,  $p < .05$ ). Flowering duration tended to be negatively correlated with it ( $r = -.40$ ,  $p = .06$ ). Both relative humidity and rainfall were positively correlated with all three measures ( $r = .40$  to  $.53$ , all  $p < .05$ ). The greatest association was with visitation rate ( $r = .71$ ,  $p < .001$ ) and flowering duration ( $r = .58$ ,  $p < .001$ ). The temperature, relative humidity and rainfall were also moderately to strongly intercorrelated ( $r = .59$  to  $.68$ ), and this led to the collinearity checks reported in the methodology. A curvilinear term for temperature was added to the mixed model because the means for the site were shown in Table 2 to indicate that there was a peak at intermediate temperatures.

**Table 4**

### Pearson Correlations Among Climatic Variables, Flowering Patterns, and Visitation Rate

| Variable                     | 1       | 2      | 3     | 4      | 5      |
|------------------------------|---------|--------|-------|--------|--------|
| 1. Temperature (°C)          | —       |        |       |        |        |
| 2. Relative humidity (%)     | -.62*** | —      |       |        |        |
| 3. Rainfall (mm)             | -.68*** | .59*** | —     |        |        |
| 4. Flowering abundance       | -.41*   | .44*   | .47** | —      |        |
| 5. Flowering duration (days) | -.55**  | .49**  | .53** | .63*** | —      |
| 6. Visitation rate           | -.37*   | .40*   | .43*  | .71*** | .58*** |

*Note.*  $N = 30$  plots. \* $p < .05$ . \*\* $p < .01$ . \*\*\* $p < .001$ .

### Generalized Linear Mixed Model

The negative binomial GLMM is reported in Table 5 and used 480 observation periods, within 30 plots and three sites. The number of flowers was the most important predictor of visitation (IRR = 1.46, 95% CI [1.27, 1.68],  $p < .001$ ): for every 1 standard deviation increase in number of flowers, the number of visits per observation period was expected to increase by 46%. Rainfall (IRR = 1.15,  $p = .020$ ) and duration of flowering (IRR = 1.21,  $p = .007$ ) were also positively correlated with visitation. There was a strong negative quadratic effect of temperature (IRR = 0.81,  $p = .003$ ) coupled with a weak negative linear effect (IRR = 0.89,  $p = .046$ ) suggesting visitation peaked at intermediate temperatures and decreased towards the warmer extremes. The random-intercept variances were 0.09 for site and 0.06 for plot within site, and these random effects accounted for 68% of the variance (conditional  $R^2 = .68$ ) and 46% of the variance was accounted for by the fixed effects (marginal  $R^2 = .46$ ). The results overall supported the test of H1 and H2 as well as the test of H3 which was that the effects of temperature and rainfall would still remain as significant factors after floral resources and the repeated structure of the observations were accounted for.

**Table 5**

### Negative Binomial GLMM Predicting Pollinator Visitation per 10-Minute Observation Period

| Predictor | $\beta$ | SE   | IRR   | 95% CI         | <i>z</i> | <i>p</i> |
|-----------|---------|------|-------|----------------|----------|----------|
| Intercept | 2.55    | 0.12 | 12.81 | [10.12, 16.20] | 21.25    | < .001   |

| Predictor                | $\beta$ | SE   | IRR  | 95% CI       | z     | p      |
|--------------------------|---------|------|------|--------------|-------|--------|
| Temperature              | -0.12   | 0.06 | 0.89 | [0.79, 1.00] | -2.00 | .046   |
| Temperature <sup>2</sup> | -0.21   | 0.07 | 0.81 | [0.71, 0.93] | -3.00 | .003   |
| Rainfall                 | 0.14    | 0.06 | 1.15 | [1.02, 1.29] | 2.33  | .020   |
| Flowering abundance      | 0.38    | 0.07 | 1.46 | [1.27, 1.68] | 5.43  | < .001 |
| Flowering duration       | 0.19    | 0.07 | 1.21 | [1.05, 1.39] | 2.71  | .007   |

Note.  $N = 480$  observation periods from 30 plots at 3 sites. Log link; continuous predictors were standardized. IRR = incidence rate ratio; CI = confidence interval. The intercept row reports the expected number of visits at mean predictor values ( $\exp[\beta]$ ). Random-intercept variances: site = 0.09; plot nested within site = 0.06. Marginal  $R^2 = .46$ ; conditional  $R^2 = .68$ .

## Discussion

### Climatic Gradients and Floral Resources

(IPCC, 2023). Climatic variation was found to be significantly correlated with the climatic resources for the pollinators, the floral resources upon which they rely. The intermediate site had the highest number of plant species, flowering plants and flowering lifespan when compared to the other sites, with the correlation results and mixed model showing warmer, drier plots to have fewer flowering plants that produced flowers for a shorter time. It reflects experimental findings that heat and drought stress also impact nectar and pollen output, as well as the composition of these floral resources in bee-pollinated plants (Descamps et al. 2021), and that the impact of climate on pollinators is not solely direct, but also mediated by floral resource phenology (Ogilvie et al. 2017). The shorter flowering period at the warmest site also increases the potential for a reduction in the temporal overlap of flowering and pollinator activity, a process that is at the core of phenological mismatch (Freimuth et al., 2022; Gérard et al., 2020), which could not be tested directly by the present design, as the timing of pollinator emergence was not recorded.

### The Composition of Pollinator Species and the Pollinator Response

The amount of flowers and how long they were present influenced the number of visits, which was greatest for moderate temperatures. A unimodal response is likely as pollinator activity is limited at both extremes by thermal limits, and there is some indication that bumble bees species decline when conditions are outside historical tolerances (Soroye et al., 2020) and that the responses of wild bees to climate vary among species and with landscape context (Kammerer et al., 2021). The variation in group composition (higher numbers of bees in the intermediate site, higher numbers of flies in the warmest site and higher numbers of butterflies in the coolest and wettest site) supports the notion that climatic variation reorganisation pollinator assemblages, and not just their numbers (Rafferty, 2017). They also highlight the importance of visitations by non-bee insects (Rader et al., 2020) and the dynamic nature of plant–pollinator interactions reported by CaraDonna et al. (2017).

### Impacts on biodiversity and ecosystem sustainability

The results have several implications for conservation. The declines in floral resource and flower visitors at the warmest site is the first instance of a negative impact of climatic stress on pollination prior to the loss of a species from the community; this is important for ecosystem sustainability because plant reproduction and food webs and habitats dependent on plants are related to visitation. Second, the close linkage between flowering abundance and visitation implies that management practices that favor or promote a diversity of continuously flowering plant communities can provide pollinators some protection from climatic stress. Third, that greater diversity at intermediate conditions suggests that landscapes with a diversity of microclimates are likely to contain more species and interactions during climate change. These implications follow the general findings that pollinator conservation cannot be tackled by a single driver or pressure, but is a result of multiple interacting drivers (Dicks et al., 2021; Outhwaite et al., 2022; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020).

## Conclusion and Recommendations

A quantitative field-based study design was used to investigate the effects of climatic variation on plant–pollinator interactions at three ecological sites. The analysis revealed that there were systematic differences in temperature, humidity and precipitation

among sites, which were linked to the plant diversity and flowering abundance, flowering duration, the diversity of pollinators and visitation frequency. The number of flowers was the most significant predictor of visitation, while flowering duration and rainfall were both positive, and temperature had a curvilinear effect with intermediate temperatures having the greatest amount of visitation. Combined, the results indicate that climatic variability has the greatest influence on pollination by decreasing and shifting the availability of floral resources, impacting pollinator diversity and community structure and consequently biodiversity conservation and ecosystem sustainability.

Based on the above findings, some recommendations are made. To ensure the long-term persistence of a diverse, continuous flowering plant community, conservation managers should preserve and rehabilitate habitats that are correlated with the most consistent measures of visitation: floral abundance and duration. Habitat heterogeneity and microclimatic refugia (whereby pollinators and plants find refuge from harsh conditions, including shaded and moist areas and sheltered locations) should be intentionally maintained by management to allow plants and pollinators to adapt to varying conditions. Pollinator monitoring needs to be combined with climate and phenological monitoring, preferably across years, to identify mismatches early and adjust management practices. Conservation planning should include all groups of pollinators, such as flies, butterflies and other non-bee insects, not just bees. Last, researchers and policymakers should consider taking a multi-scale approach to climate mitigation, as climate mitigation cannot be fully achieved through only local climate mitigation efforts (IPCC, 2023).

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