

REPRODUCTIVE ECOLOGY OF THE AROMATIC PLANT *AGASTACHE MEXICANA* (LAMIACEAE): A VALUABLE SPECIES TO BE USED IN URBAN POLLINATOR GARDENS

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Abstract—The study of floral biology is essential for identifying key species to be used in urban gardens. *Agastache mexicana* (Lamiaceae) is a perennial species native to Mexico, widely studied for its medicinal properties. To evaluate its ecological potential, we characterized its floral biology and recorded the taxonomic and functional diversity of visitors (pollinators, nectar robbers and contact species) in a recently implemented pollinator garden. Over 276 hours of observation, 860 visits were recorded from 66 morpho species, distributed across 12 taxonomic orders. Of these, 57% of the records corresponded to nectar robbers, 26% to pollinators, and 17% to contact species (i.e., animals using the plants for predation, mating, nesting, etc.). A GLMM showed positive effect of ambient temperature and contrasting effects of co-flowering species depending on their location within or between patches, respectively. Visits by pollinators and nectar robbers may be related to the presence of long-lasting inflorescences composed of large tubular nectar rewarding flowers in *A. mexicana*. According to our results *A. mexicana* contributes to the attraction of high taxonomic and functional diversity, including mutualistic and antagonistic interactions, highlighting its value for implementation in the design of urban gardens focused on pollinator conservation.

Keywords—Conservation of pollinators, Contact species, Pollinators gardens, Nectar robbers, Urban gardens

INTRODUCTION

A generalized reduction in abundance of populations and even local extinction of insect pollinators has been observed worldwide (Potts et al. 2010; Pereira et al. 2021; Liang et al. 2023; Nath et al. 2023). Pollinator decline is linked to processes derived from human activities, such as deforestation, habitat fragmentation, use of pesticides, introduction of exotic species and urbanization (Tamburini et al. 2021; Hald-Mortensen 2023; Liang et al. 2023). Urban areas not only offer fewer floral resources but also create hostile environments that reduce pollinator abundance and increase population isolation (Dri et al. 2021; De Barros et al. 2022; Vaz et al. 2023).

Pollinators not only contribute to the maintenance of biodiversity in ecosystems (Ollerton 2021; Wei et al. 2021), but a significant

portion of agricultural production and the commercial success of other industries also depend on pollination (Hristov et al. 2020; Rader et al. 2020; Katumo et al. 2022). Therefore, slowing the loss of species and promoting the conservation of pollinators is essential (Cameron et al. 2011; Hung et al. 2018; Baldock 2020). Pollinator gardens enhanced by the inclusion of native plant species have been advanced as one of the most effective strategies to achieve this goal in urban areas, due to the higher positive impact on attraction of pollinators (Burghardt et al. 2009; Levé et al. 2019; Memmott & Waser 2002). A pollinator garden can be implemented in areas lacking plants or to improve spaces of secondary vegetation by creating more favorable habitats for insects, providing food and water resources, resting sites and protection from heat (Bates et al. 2011;

Salisbury et al. 2015; Berthon et al. 2021; Jacobs et al. 2023).

It should be noted that resources for pollinators provided by urban gardens may also be exploited by other non-pollinator groups. Thus, urban gardens could increase biological diversity beyond that of pollinators, allowing other and even antagonist ecological interactions, such as nectar robbing, to occur in these green spaces (Inouye 1980; Dukas & Morse 2003; Senapathi et al. 2015).

The state of Morelos, located at central Mexico, is recognized by the production of ornamental plant species. The production of native ornamental plants is mainly intended to meet local and national demands related to cultural activities and festivities. Thus, for example *Euphorbia pulcherrima* and *Tagetes erecta* are massively produced for festivities such as Christmas and Day of the Death, respectively. However, despite the high plant diversity present in Mexico, the notion of native plants to be used in pollinator gardens is currently incipient between plant growers (Mayett-Moreno et al. 2018). Several groups of native plants with ornamental potential could be successfully used for the implementation of pollinator gardens.

Lamiaceae is particularly interesting as it is composed by about 600 species scattered in 32 genera, displaying nearly 60% of endemic species (Martínez-Gordillo et al. 2013). Within this family, *Agastache mexicana* (Kunth) Lint & Epling has been widely studied, particularly for its use in traditional Mexican medicine, with research focusing on its photochemical and pharmacological properties derived from the presence of secondary metabolites such as tilianin, apigenin, acacetin, quercetin, ursolic acid and oleanolic acid (Hernández-Abreu et al. 2009; Carmona-Castro et al. 2019; Nechita et al. 2023). Despite *A. mexicana* exhibits zygomorphic purple corollas arranged in abundant inflorescences, suggesting a high potential for attracting pollinators, it is traded mainly as an aromatic and a medicinal plant (Palma-Tenango et al. 2021).

Therefore, we aimed on to study the potential of *A. mexicana* to promote pollinator conservation in the context of its use in urban gardens. To do this, we identified taxonomic and functional diversity of floral visitors in a recently implemented pollinator garden composed

originally of native plants species. We also characterized the effects of seasonality (dry season and rainy season), the floral abundance of *A. mexicana*, the floral abundance of co-flowering species, and ambient temperature on visitation rate. Additionally, we also explored aspects of its reproductive biology that may be involved in pollinator attraction.

MATERIALS AND METHODS

STUDY SITE

This study was conducted in the University Pollinator Garden (UPG) at the Autonomous University of the State of Morelos, located in the city of Cuernavaca, in northern Morelos, central Mexico. The climate is classified as temperate subhumid (Cw), with mean annual temperature of 20.2 °C; annual precipitation of 1,386 mm. The most rainfall occurs between June and October being April and January the warmest and coldest months, with average temperatures of 23.3°C and 17.5°C, respectively. September is the wettest month, with an average precipitation of 275 mm.

The UPG was implemented in winter 2021 in the green areas of the Central Library, located in the northern part of the Campus (1,930 m a.s.l.). To the north, the UPG borders the area of influence of the Chichinautzin Biological Corridor, a landscape dominated by forested areas (pine-oak-fir), grasslands, and basaltic spills. This corridor allows various groups of animals to carry out part of their activities on Campus. Towards other directions, the University is surrounded by urban areas (Fig. 1). The UPG covers an area of approximately 500 m² and includes more than 400 individuals of native plant species. In addition to *A. mexicana*, the UPG includes *Duranta erecta* (white and purple varieties), *Echeveria* sp., *Justicia spicigera*, *Lantana camara*, *Salvia amarissima*, *S. buchananii*, *S. elegans*, *S. greggi*, *S. coccinea*, *S. leucantha* and *S. microphylla* (white and red varieties).

STUDY SPECIES

Agastache mexicana is a perennial herb, reaching between 1.0 and 1.2 m in height, with a typical Lamiaceae morphology, including opposite petiolate leaves, a four-angled indeterminate stem bearing 15 to 20 inflorescences per plant, exhibiting bilabiate purple flowers (Zielińska & Matkowski 2014). The flowers have four exserted, epipetalous,



Figure 1. (A) Location of the Autonomous University of the State of Morelos (yellow polygon) at north Cuernavaca City. White dots indicate the influence zone of the Natural Protected Area Chichinautzin Biological Corridor. Blue dot indicates the area corresponding to the Botanic Garden, and the red asterisks indicate the location of the University Pollinator Garden. (B) Section of a polygon with individuals of *Agastache mexicana* in the University Pollinator Garden and (C) close-up showing part of an inflorescence.

didynamous anthers and a bifid stigma. The stem can be simple or branched, erect or slightly creeping, and occasionally woody, with purple coloration in the basal and middle parts. It is cultivated in various regions, including Mexico City and the states of Hidalgo, Mexico, Morelos, Puebla and Veracruz (Verano et al. 2013). In nurseries located in northern Cuernavaca City, *A. mexicana* is cultivated and traded as an aromatic plant. To our knowledge, there are no previous studies relating its reproductive biology to its potential to attract floral visitors.

FLORAL VISITORS

All individuals of native plant species are distributed in the 18 polygons within the UPG. *A. mexicana* is present in three of these polygons. Polygons differ in size, shape and number of species (ranging from one to three species). Visitor records for *A. mexicana* were obtained from 46 censuses conducted from September 2023 to September 2024, between 08:00 to 15:00 h, using 15-minute observation periods in each polygon. The total sampling effort devoted to identifying floral visitors spanned 276 h (16,560 minutes). Of the

total censuses, 23 were conducted during the rainy season and 23 during the season. Plants within polygons were rotated for observation. Due to the high number of flowers per plant, which makes observation at the individual flower level difficult, records were made at the inflorescence level (Thompson 1988; Goulson 2003).

To assess the potential of *A. mexicana* to attract floral visitors, we identified each visitor and then grouped by taxonomic order. Identification was carried out through comparison with records from the citizen science platform iNaturalistMX (<https://mexico.inaturalist.org/>) and specialized guides (Arizmendi & Berlanga 2014; Glassberg, 2017). In addition, visitors were classified functionally according to their behavior during the visit: i) pollinator, when the visitor made contact with reproductive structures of the flower; ii) nectar robber, if the visitor pierced the corolla tube to access nectar; and iii) contact species, when the visitor was present on the flower performing other activities (e.g., mating, predation, herbivory). To evaluate the potential effect of floral resource availability, we estimated the number of *A.*

mexicana inflorescences (i.e., those bearing open flowers) within each polygon, as well as the number of flowers from co-flowering species both within and among polygons. Finally, we obtained the mean ambient temperature from meteorological station No. 17 of National Water Commission (CONAGUA), Mexico, located within the University Campus, approximately 300 meters from the UPG.

FLORAL MORPHOLOGY AND LONGEVITY

The floral morphology of *A. mexicana* was characterized in five flowers from 40 plants ($N = 200$). In 100 of these, using lateral view photographs, the corolla length (distance from the base of the sepals to the apex of the upper lobes), corolla width (the area where the lobes forming the flower blade begin to expand), and calyx length (distance from the base to the apex of the sepals) were measured. In the other 100 flowers, sections were made to expose the reproductive structures. From the gynoecium, the stigma size (sum of the length of both lobes), the style length, and the ovary size (length \times width) were estimated. In the androecium, the lengths of the filaments (long and short) and the anther size (average of the length \times width of both thecae of the four anthers) were estimated. All measurements were obtained in mm from photographs on graph paper (4.3-inch LCD microscope) using tpsDIG software (Version 2.31).

Floral longevity was determined by observing 20 inflorescences from ten plants. Individual flower buds were marked (day 0) and monitored to determine the time elapsed from anthesis to wilting. These observations allowed us to establish three stages during anthesis: flower bud (between days 3 and 5), anthesis (between days 6 and 8), and wilting (after the ninth day).

STIGMA RECEPTIVITY, PRODUCTION AND VIABILITY OF POLLEN GRAINS

Stigma receptivity was assessed following Osborn (1988) by applying 5 μL of 40% hydrogen peroxide (H_2O_2) to the stigma surface of 20 flowers per floral stage (flower bud, anthesis, and wilting, $N = 60$). The stigma was categorized as receptive if it showed a positive reaction manifested as bubbling.

To estimate pollen grain production, the four anthers were removed from each one of 60 flower buds. Each group of four anthers was placed

separately in Eppendorf tubes with 100 μL of 99% sulfuric acid (H_2SO_4) for 24 hours to dissolve the tissue and release the pollen grains. After this period, each tube was placed on a vortex mixer for one minute, immediately after an aliquot (2 μL) was taken and placed in a counting chamber (Neubauer, Paul Marienfeld, Germany) (Kakui et al. 2020). Finally, the number of grains obtained in the 2 μL counts was used to estimate the total number of pollen grains in the 100 μL .

Pollen grain viability was assessed independently in 20 flowers per floral stage (flower bud, anthesis, and wilting, $N = 60$). The four anthers were placed on a slide with a drop of Lugol's potassium iodide and dried for 48 hours. Samples were observed with a microscope (10 \times) to distinguish viable (heavily stained brown colored grains) from non-viable grains (colorless or with yellowish fainter tones) (Caponio et al. 2016).

NECTAR PRODUCTION

To estimate nectar production, 40 flower buds of 15 plants were bagged, and nectar was extracted using 0.3 mm diameter capillaries. Ten flowers were haphazardly assigned to each one of three stages: flower bud, anthesis, and wilting ($N = 30$). In this case, nectar was collected between 10:00 and 11:00 h. In the remaining 10 flowers, nectar volume was measured at anthesis at three different times of the day (8:00, 11:00, and 15:00 h). For descriptive purposes, the concentration of sugars in the nectar of *A. mexicana* flowers was obtained in ten mixed samples of six flowers, using a manual refractometer (Brix Refractometer).

POLLEN-OVULE RATIO (P/O)

To infer the breeding system of *A. mexicana*, the pollen-to-ovule ratio (P/O) proposed by Cruden (1977) was estimated. In a sample of 60 flower buds of 15 plants, the ovaries were dissected under a light microscope (Omax) to extract the ovules. Once the number of ovules and pollen grains production were obtained (details above), the ratio between these two variables was calculated.

STATISTICAL ANALYSIS

All statistical analyses were performed in R (R Core-Team, 2020). The variation in floral morphology was analyzed using a Principal Components Analysis (PCA) based on the eight variables that describe it (corolla length and width,

calyx length, stigma size, style length, ovary size, filaments length, and anthers size). Descriptive statistics (Mean \pm 1 SD) were used to display results related to floral longevity, stigmatic receptivity, pollen grain production, and viability. To evaluate herkogamy, a Student's t-test (dependent samples) was applied, with the length of the style and the mean difference in length between shortest and longest anther filaments. Differences in nectar production each flower stage (flower bud, anthesis and wilting) and at each interval of time (08:00, 11:00 and 15:00) were obtained by comparing means using the Kruskal-Wallis test (post hoc Holm, $P < 0.05$).

Factors influencing the visitation frequency to inflorescences of *A. mexicana* were evaluated using a generalized linear mixed model (GLMM) with a negative binomial distribution (nbinom2) and a log link function, implemented with the glmmTMB package in R (Brooks et al., 2017). The response variable was the number of recorded visits, and to model visitation rate, a logarithmic offset of the number of inflorescences per plant was included; therefore, results represent visits per unit of floral display. The type of foraging behavior during the visit (pollinator or nectar robber), season (rainy and dry), and their interaction were included as fixed effects. Contact species category was not included as many of the specimens were found on stems and leaves. Floral availability (number of inflorescences with open flowers) of *A. mexicana* as well as conspecifics within and among polygons were also included as fixed effects, in addition to ambient temperature. Polygon was included as a random effect. All continuous variables were standardized (mean = 0, standard deviation = 1). Model fit was evaluated through residual simulations using the DHARMA package (Hartig, 2024). Regarding the visitation rate, we reported the predicted estimates of the GLMM for the log transformed data. Finally, we estimated marginal means using the emmeans package (Lenth & Piaskowski, 2026), with predictions on the response scale (type = "response") and holding continuous covariates at their mean values.

RESULTS

A. MEXICANA VISITORS AND FLORAL VISITATION RATE

A total of 2,748 inflorescences of *A. mexicana* were visited by 860 animals. The number of visits recorded in each census is shown in Fig. 2. Floral visitors comprised 66 morphospecies. Of these, 42 were identified to species level, 23 to genus level, and one to family level. Visitors were distributed among 12 orders (number of species): Hymenoptera (17), Lepidoptera (13), Diptera (10), Hemiptera (9), Orthoptera (5), Apodiformes (4), Araneae (3), Coleoptera (1), Mantodea (1), Passeriformes (1), Phasmatodea (1), and Squamata (1) (complete list with taxonomic identity of visitors in Table S1).

Regarding behavioral categories, 57% of records corresponded to nectar robbers, 26% to pollinators, and 17% to contact species. The most frequent species in the pollinator category were *Lasioglossum sp.*, *Archilochus colubris* and *Apis mellifera*, for nectar robber category were *Xylocopa sp.*, *Apis mellifera* and *Pseudaugochlora graminea*, while in the contact species category was *Simulium sp.*, *Oxysarcodexia sp.* and *Misumessus oblongus* (Fig. 3).

The GLMM whole model (fixed and random effects) explained variation in visitation rate with a conditional variance of 0.21. The variance explained only by fixed effects (marginal variance) was 0.14. Regarding model evaluation, no significant deviations from residual uniformity were detected (Kolmogorov–Smirnov test, $P = 0.40$), nor was there evidence of overdispersion ($P = 0.15$) or zero inflation ($P = 1.0$), indicating an adequate fit of the model to the data. Neither the type of foraging behavior during the visit (pollinator vs. nectar robber) nor season (rainy vs. dry) showed significant effects ($P > 0.18$). However, the interaction between season and behavior category was highly significant ($\beta = 1.34$, $P < 0.001$). Estimated marginal means indicated that pollinators exhibited similar visitation rates between the dry season (4.36 ± 0.79 visits per inflorescence) and the rainy season (4.04 ± 0.64 visits per inflorescence). In contrast, the visitation rate of nectar robbers increased nearly fourfold during the rainy season (11.99 ± 1.70 visits per inflorescence) compared to the dry season (3.40 ± 0.64 visits per inflorescence).

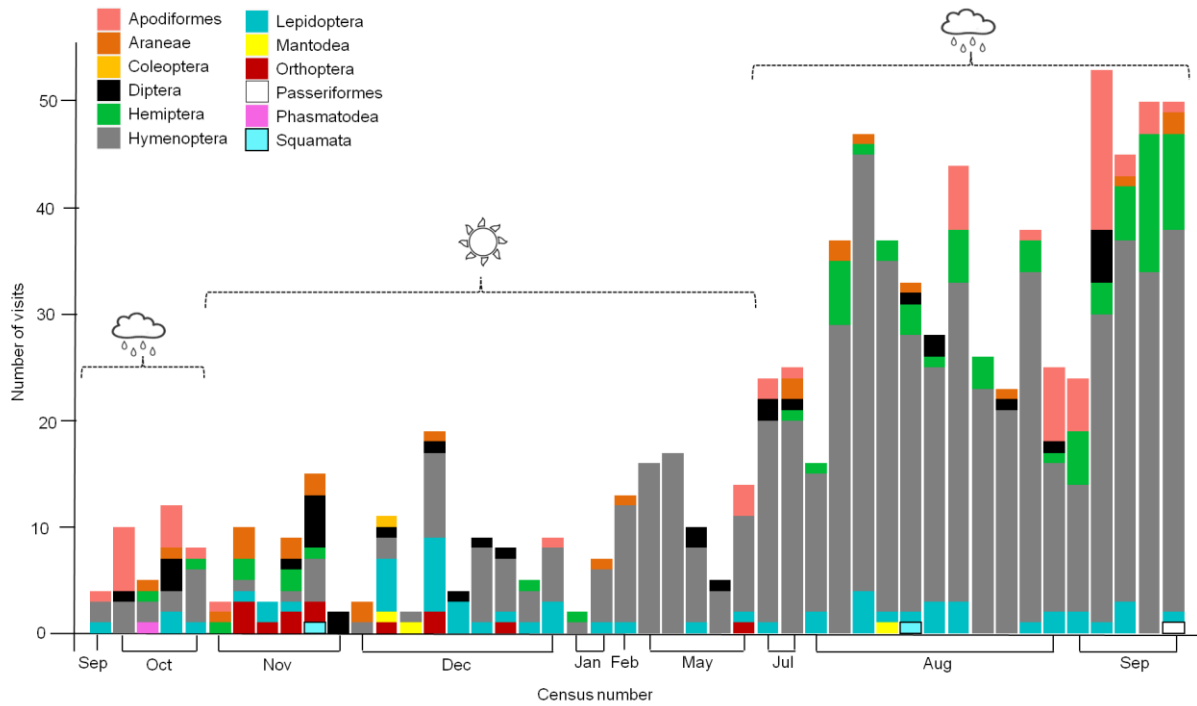


Figure 2. Number of visits recorded by taxonomic order in *Agastache mexicana* during 46 censuses at the University Pollinator Garden (UPG). Rainy and dry seasons are indicated.

Pollinators



Nectar robbers



Contact species



Figure 3. Most frequent visitors recorded of *A. mexicana* at the University Pollinator Garden (UPG) by behavioral category: pollinators (*Archilochus colubris*, *Lasioglossum* sp., *Apis mellifera*); nectar robbers (*Xylocopa* sp., *Apis mellifera*, *Pseudaugochlora graminea*); contact species (*Oxysarcodexia* sp., *Simulium* sp., *Misumessus oblongus*).

Floral availability of other species in neighboring polygons had a significant negative effect on visitation rate ($\beta = -0.42, P < 0.001$), whereas floral availability of other species within

polygons showed a significant positive effect ($\beta = 0.27, P = 0.0016$). In contrast, floral availability of *A. mexicana* within polygons did not show a significant effect ($P = 0.195$). Mean ambient

temperature also had a significant positive effect ($\beta = 0.26$, $P < 0.001$).

FLORAL BIOLOGY

The first and second principal components, those with eigenvalues higher than unity, explained 36% and 18%, respectively, of the total variance of flower morphology of *A. mexicana* (Table S2). Variables related to flower size (corolla length, corolla width and calyx length) showed the greatest contribution to PC 1 (ranging from 0.39 to 0.53). PC 2 retained variation mainly of reproductive organs such as style length (0.42), filaments length (0.48) and anther size (-0.5). The Student's t-test indicate that *A. mexicana* flowers exhibit approach herkogamy, with the style averaging 17.04 mm longer than the filaments ($t = 44.33$, $df = 19$, $P < 0.0001$).

The anthesis was diurnal as it occurred between 08:00 and 16:00 h. The individual floral longevity was 9.3 ± 1.95 d. However, inflorescence span is variable and directly depends on the number of whorls developed. Anthesis lasts for about 3 to 4 days. Inflorescences with only two whorls last over a month while inflorescences with up to 14 whorls persisted for almost three months. Some inflorescences have been observed to exceed 20 whorls, with 25 being the maximum recorded.

Evaluation with hydrogen peroxide (H_2O_2) applied to the stigma surface showed that the stigmas were receptive from flower bud to wilting. On average (\pm SD), the two pairs of anthers

produced 5,320 (\pm 2,683) pollen grains, of which more than 70% were generally viable.

The Kruskal-Wallis test showed that nectar production volume differed between floral stages ($H_{(2)} = 13.59$, $P = 0.001$) (Fig. 4A); the median and interquartile range (IQR) was 0.07 (0.07-0.17) μ L in bud, 0.07 (0.07-0.07) μ L in anthesis, and 0.21 (0.15-0.26) μ L in wilting. Post hoc groupings (Holm) indicated significant differences between anthesis and wilting ($P < 0.0001$), while differences between bud and wilting ($P = 0.12$) and bud and anthesis ($P = 0.10$) were not. Nectar production also showed significant differences between the sampled times ($H_{(2)} = 8.82$, $P = 0.01$) (Fig. 4B), at 08:00 the med (IQR) was 0.14 (0.08-0.26) μ L, at 11:00 it was 0.14 (0.07-0.21) μ L and finally at 15:00 it was 0.07 (0.07-0.07) μ L. In this case, the lowest nectar production was at 15:00 h compared to 08:00 h ($P = 0.01$) and 11:00 h ($P = 0.03$), while the highest nectar production occurred at 8:00 h but did not differ significantly from 11:00 h ($P = 0.81$). The mean of concentration of sugars was $37.85 (\pm 8.2)$ Brix.

POLLEN-OVULE RATIO (P/O)

Ovule counting showed that each ovary can contain one single ovule per locule, resulting in a range of two to four ovules per ovary. The mean (\pm SD), each flower has 3.68 ovules (± 0.6). By relating the ovule number with pollen grain production, the estimated P/O ratio is $1,485.3 \pm 766.6$.

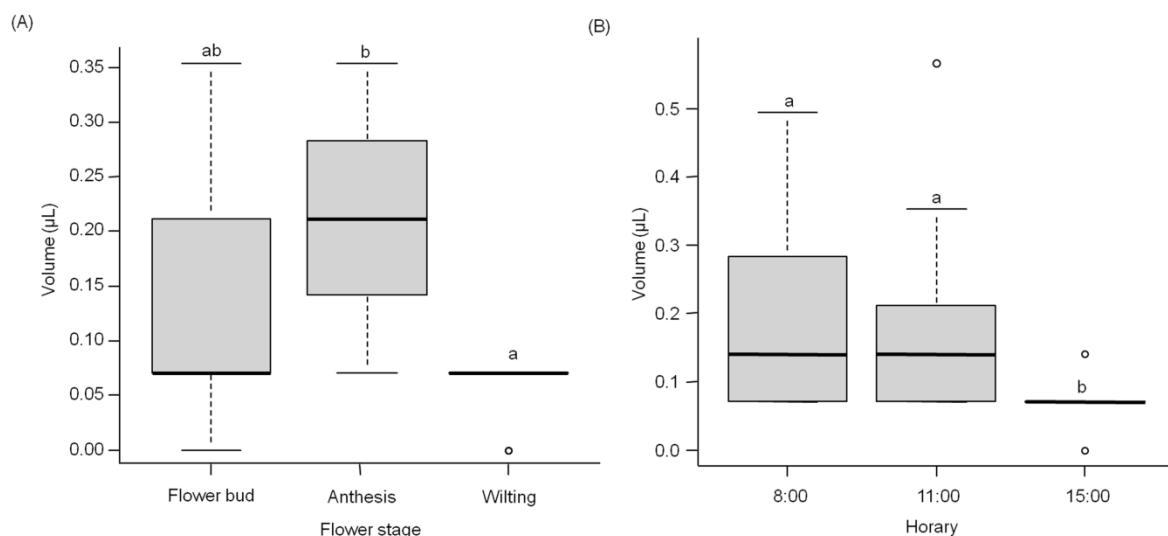


Figure 4. Variation in nectar production (μ L) of *Agastache mexicana*: (A) across flower stage during anthesis and (B) among sampling times. Different letters indicate significant differences between groups (Holm post hoc; $P < 0.05$).

DISCUSSION

Agastache mexicana has been studied mainly for its medicinal properties. This study addressed it from an ecological point of view indicating that *A. mexicana* could contribute to attract floral visitors within pollinator gardens. Within a multispecies garden, our results showed the potential of *A. mexicana* to attract high taxonomic and functional diversity of floral visitors, including not only pollinators but nectar robbers, both groups represented by insect and bird species. Several contact species were also found majorly in stems and leaves performing activities such as hunting, nesting and resting.

Floral visitors were observed practically throughout the entire year, probably by the presence of flowers of other species in the garden. In specific, some traits of *A. mexicana* could facilitate visits along the year. For example, the combination of flower longevity (ca., 9 d) with the arrangement of constantly produced long-lasting inflorescences that develop up to 25 whorls promotes ample flower availability almost year-round. Thus, flowers of *A. mexicana* represent a secure resource to be used for visitors. Nearly 75% of the floral visits were performed by pollinators and nectar robbers. This high percentage and the taxonomic diversity could be related to the presence of the large tubular, brightly colored nectar rewarding flowers. The conjunct of floral traits of *A. mexicana* could favor interaction with pollinators of different sizes and food preferences, from hummingbirds to medium-size and small bees. The nectar concentration in *A. mexicana* flowers (38%) is within the range of preferences of species with active suction feeding types such as butterflies (35-40%) and capillary suction feeding types such as hummingbirds (35-45%) (Kim et al. 2011). In the case of bees, although their preference is higher (55%) (Kim et al. 2011), they have already been identified as a group that utilizes both types of resources (nectar and pollen) in *Agastache* flowers (Erickson et al. 2021; 2022). The nectar characteristics we found are like those reported for five ornamental *Agastache* cultivars which attracted mainly bees and, to a lesser extent, butterflies (Erickson et al. 2021). However, in our study, we found that a higher percentage of the total number of records corresponded not to

pollinators but to nectar robbers, a phenomenon that has not been reported in other studies with *Agastache*. In this case, individuals of *Xylocopa* sp. and *Apis mellifera* obtained nectar by piercing the corolla tube without contacting sexual organs. Overall, we observed that floral visitors such as bees, butterflies, and hummingbirds were concentrated majorly on morning, which could be associated with the fact that the highest nectar production occurred between 8:00 and 11:00 h. However, because of our limited sampling period, an extended evaluation covering most hours in the day is needed to confirm the highest production of nectar early in the morning.

Regarding the mating system of *A. mexicana*, our results suggest the coexistence of mechanisms that could favor both self-pollination and cross-pollination. On the one hand, the stigmas are receptive, and pollen viability remains high from the flower bud stage until wilting, traits that may facilitate self-pollination (Vogelmann 1983). On the other hand, the colored, large and rewarding corollas in addition to the marked approach herkogamy observed, suggest cross-pollination. This is consistent with our results of the facultative xenogamous system inferred from the pollen-to-ovule ratio, a pattern also documented in other Lamiaceae species (Rohitash 2017; Jorge et al. 2015). However, experiments that explicitly isolate floral visitors and control the source of pollen including open, cross and self-pollination trials are needed to evaluate mating system and the fitness consequences that pollinator behavior could have on *A. mexicana*. This information is needed to obtain quality seeds that could be used to obtain vigorous individuals for replanting or a source to implement more gardens.

In terms of urban biodiversity, in addition of pollinators (Hymenoptera, Lepidoptera, Apodiformes, and Diptera) and nectar robbers (Hymenoptera and Passeriformes) we also observed contact species (Araneae, Coleoptera, Hemiptera, Mantodea, Orthoptera, Phasmida and Squamata) visiting *A. mexicana*. For example, spiders were frequently observed hunting insects on inflorescences. Spiders often use flowers as hunting sites, which can sometimes deter pollinators from visiting flowers where they are present (Dukas & Morse 2003). In addition, insect eggs were frequently observed on the underside of

leaves, along with what appeared to be pupae, as well as stems showing evidence of herbivore damage. Although previous studies in ornamental varieties of *Agastache* have reported high floral visitor diversity, this diversity has generally been limited to fewer taxonomic groups (Erickson et al. 2021; 2022, Verweij et al. 2025). Our results indicate that *A. mexicana* can contribute to overall biodiversity in human-managed environments by supporting networks of both mutualistic and antagonistic interactions (Villegas & Alcalá 2025).

Besides documenting the urban floral visitors present in *A. mexicana*, we also identified abiotic and biotic factors influencing visitation rate. The GLMM showed that neither season (dry vs. rainy) nor behavior category (pollinator vs. nectar robber) affected visitation rates. However, the significant interaction between season and category indicated that visitation rate of nectar robbers was up to four times higher than those by pollinators during the rainy season. In this study, we did not assess fitness components of *A. mexicana*, and thus the effects of nectar robbers remain unclear. Nectar robbery is widely debated in literature. On the one hand, negative effects on pollinator visitation rates (Irwin et al. 2010), pollinator abundance (Zhang et al. 2007), seed weight and germination (Cuevas-García et al. 2013) have been reported. On the other hand, neutral or even positive effects on plant reproduction have also been documented (Maloof & Inouye 2000; Maloof 2001; Cuevas & Rosas-Guerrero 2015). Therefore, the evaluation of the effect of interaction with nectar robbers on components that evaluate the reproductive success of *A. mexicana* (i.e., seed production, size and germination) and its capacity to compensate for such robbery is still pending.

GLMM also indicated that visitation rate was not influenced by the availability of flowers of *A. mexicana* but neighborhood characteristics had contrasting effects depending on closeness of co-flowering species. This is to say, part of the visits received by *A. mexicana* results from a positive effect of close co-flowering species (within polygons) by attracting shared pollinators (Ghazoul 2006, Mesgaran et al. 2017). Interestingly, at a higher spatial level (between polygons), co-flowering species had a negative effect on visits. For a focal species, the mixture of flowers may

dilute the total number of visits among an increasing number of flowers (Caruso 1999). Therefore, the impact of *A. mexicana* to attract floral visitors is relative to the presence of co-flowering plants in pollinator gardens. Finally, the average ambient temperature showed a positive relationship in both groups. This means that the visit rate increased with higher temperatures, indicating that foraging activity is sensitive to thermal conditions. In the case of nectar robbers, they mostly correspond to Hymenoptera species, which tend to show higher visiting rate below 26 °C (Descamps et al. 2021), while in the group of pollinators, an increase in the activity of hummingbirds and butterflies has been documented at warmer temperatures (Franzén et al. 2022; Lucke-Lawrence & Hazlehurst 2023).

CONCLUSIONS

Even though it is sold majorly as an aromatic plant, *Agastache mexicana* could contribute to biodiversity of floral visitors in local urban gardens. Part of its potential to attract floral visitors is result of co-flowering species. However, within a multi-species urban garden, its high availability of rewarding flowers throughout the year ensures positive impacts on pollinators, which are not restricted to insect species. *A. mexicana* contributes to maintain overall urban biodiversity offering resources to a high number of species split in several taxonomic orders and behavioral categories, including nectar robbers and contact species. Furthermore, it provides refuge sites or nesting and egg-laying sites for other animals, which is considered a positive advantage of implementing pollinator gardens. Our results, taken together, demonstrate the importance of considering the characteristics of floral biology and reproductive ecology to evaluate ecological interactions of the plant species to be used in the design of pollinator gardens.

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AUTHOR CONTRIBUTION

REA conceived the study and wrote the first draft of the manuscript. ZCV conducted the study, performed all measurements, SGV contributed to experimental design, performed the statistical analyses and critically revised the manuscript.

DISCLOSURE STATEMENT

Authors declare that there are no conflicts of interest to disclose.

GENERATIVE AI DISCLOSURE STATEMENT

No generative AI was used to write this article.

DATA AVAILABILITY STATEMENT

Please contact the corresponding author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. List of visitors to *Agastache mexicana* plants in the University Pollinator Garden.

Table S2. Results from principal component analysis (PCA) based on floral morphological data of *Agastache mexicana*.

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