Article

REPRODUCTIVE SYSTEM, FLORAL BIOLOGY AND POLLINATORS OF *ABUTILON GRANDIFOLIUM* IN TWO URBAN GREEN SPACES OF CIUDAD AUTÓNOMA DE BUENOS AIRES

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Abstract—Urban green spaces have gained importance in view of growing urbanization; however, limited research exists on the interactions of native plants with the local fauna, particularly comparing protected natural areas vs. recreated ones. To help fill this gap, the floral biology and pollination of *Abutilon grandifolium* (Malvaceae) were studied in an Ecological Reserve and in a square where the local environment had been recreated with native plants, both located in Ciudad Autónoma de Buenos Aires, Argentina. *A. grandifolium* was self-compatible. The flowers presented typical traits associated with biotic pollination (ornamented pollen, conspicuous perianth and rewards), particularly melittophily (diurnal anthesis, nectar, yellow-orange coloration and pleasant odour). At both sites, the most frequent visitors were *Apis mellifera* and halictid bees, collecting nectar and/or pollen. While visits from the former were predominantly illegitimate, halictids mostly performed legitimate visits. Occasional visitors included the bees *Xylocopa* sp. and *Bombus pauloensis*, syrphid flies and, more rarely, beetles. Large quantities of *A. grandifolium* pollen were found on all bee species, in positions compatible with an effective transfer to the stigmas, indicating that they likely pollinate when accessing flowers legitimately. In contrast, flies and beetles would be mainly pollen and nectar thieves. In general, the identity, frequency and activity of the floral visitors were similar at both sites, with species richness even higher in the square; suggesting that restored native plantings can support functional pollination processes in urban green spaces.

Keywords— *Abutilon grandifolium*, Apoidea, floral traits, floral visitors, native insect-plant interactions, urban green spaces

INTRODUCTION

Urban green spaces have gained prominence amid accelerating urbanisation. Even when small and fragmented, reserves, parks, squares and gardens can function as biodiversity refuges and as nodes in ecological corridor networks, supporting high species richness and abundance under appropriate management (Goddard et al. 2010; Hall et al. 2017; Haene 2020; Baldock 2020). Within this context, understanding the floral biology and mating system of a species is essential for explaining its reproductive success, population dynamics and responses to heterogeneous environments (Knight et al. 2005; Barrett et al. 2014). Consistent with the growing emphasis on native species in conservation and restoration, many urban planting schemes increasingly incorporate regional flora. Importantly, native plants in urban green spaces often attract a greater diversity and frequency of floral visitors than exotic species, provided that planting schemes ensure a continuous temporal availability of floral resources for different visitor guilds (Faggi & Ignatieva 2009; Burgueño & Nardini 2019; Zaninotto & Dajoz 2022; Araújo et al. 2022), which would otherwise be supplied by exotic species (Harrison & Winfree 2015).

In the Ciudad Autónoma de Buenos Aires, Argentina, the cultivation of native vegetation in urban green spaces has recently been prioritised. Between 2018 and 2019 the region showed the largest increase in the planting of native species in public and private areas, along with a rise in the richness of species used (Haene 2020). However, there remains a paucity of studies on the pollination biology and mating systems of native plants in these spaces—unlike in botanical gardens and reserves, where floral resources are diverse and prolonged over time (Suyama 1998; Mazzeo & Torretta 2015; Mosconi & Amela García 2019; Gualdoni Becerra 2022). Where native flora has been incorporated into parks and squares, studies have reported associations with higher occurrence and abundance of floral visitors, especially bees; concordantly, some cities, including the city of Buenos Aires, show greater bee abundance—overall and for native bees—in urban gardens containing native plants compared with gardens lacking them (Pardee & Philpott 2014; Haene 2018; Mesía Blanco 2019). In this context, Malvaceae shrubs are frequently used in local plantings.

Members of Malvaceae are mostly pollinated by insects (Knuth 1906), some being self-compatible (Parra-Tabla & Alonso 2021; Yescas-Romo & Molina-Freaner 2024). Within this family, *Abutilon* comprises more than 150 tropical and subtropical species (Fryxell 2002). *Abutilon grandifolium* (Willd.) Sweet is native to South America; it occurs between 0 and 2000 m a.s.l. It grows in modified environments and disturbed soils. This species has medicinal (Martínez Crovetto 2012), ornamental and textile uses, being cultivated for such purposes in some regions of Africa and China (Jaca et al. 2015). Although considered naturalised in certain regions of Australia, New Zealand and Pacific Islands (Global Compendium of Weeds 2007), it has been characterized as invasive or potentially invasive in Hawaii and Portugal (Staples et al. 2000; Domingues de Almeida & Freitas 2012). It is a sparsely branched shrub, generally with a single main stem. Each individual can reach 2.5 m in height. The leaves are broad and cordate. The stem bears abundant simple trichomes. The flowers are solitary, axillary, complete, actinomorphic, pentamerous, with monadelphous androecium, multilocular ovary and axillary placentation. In the southern hemisphere, it blooms from spring to summer (Parodi & Dimitri 1972), from summer to mid-autumn (Sérsic et al. 2006) or to late autumn (Jaca et al. 2015; Burgueño & Nardini 2019), depending on the region. Its floral biology is almost unknown; only the conical epidermal cells of the petals have been described, suggesting a relation with pollinators and classifying the species as melittophilous (Costa et al. 2017). Its pollen has been characterised (Abdel Khalik et al. 2021) but not exhaustively. Furthermore, its mating system has not been studied yet.

In this study, we investigate the reproductive system, floral biology and pollination ecology of *Abutilon grandifolium* in two urban green spaces in Buenos Aires city: a protected natural reserve and a public square with a sector with planted native species recreating local habitats. Specifically, we (i) describe key floral traits and phenology, (ii) assess self-compatibility and dependence on pollinators, and (iii) characterize the assemblage of floral visitors, identifying effective pollinators and comparing their composition, richness and visitation frequency between the reserve and the recreated native-plant site. By linking floral traits, pollinator visitation and reproductive output, we provide a detailed account of the reproductive and pollination system of this species in an urban context.

MATERIALS AND METHODS

STUDY SITES

The study was carried out in two populations of *A. grandifolium* in Ciudad Autónoma de Buenos Aires (C.A.B.A.), Argentina (Fig. 1). The first is a natural population located in the Ciudad Universitaria-Costanera Norte Ecological Reserve (RECU-CN) (34°32'23.5"S, 58°26'30.9"W). This protected area (Fig. 1A) covers a surface of 18 ha, bordering the Río de la Plata. The reserve originated in the 1960s as a result of land reclamation with rubble. Since then, native and exotic plant species (144 recorded/238 estimated) have spontaneously established, forming three vegetation units: wetland, forest and grassland with groves (Melzi Fiorenza et al. 2020). Within this reserve, 10 specimens of *A. grandifolium* were selected. The second population is located in Plaza Clemente, in the Colegiales neighbourhood of Commune 13 (34°34' 54.7'' S, 58°26' 39.9'' W), approximately 7 km from the reserve. It is a 0.73 ha

Figure 1. Study sites of *Abutilon grandifolium* in green spaces of the Ciudad Autónoma de Buenos Aires. A) Ciudad Universitaria-Costanera Norte Ecological Reserve. B) Clemente Square. Map base: Official map of the Subsecretary of Registries, Interpretation and Cadastre, Ministry of Urban Development and Transport, GCBA.

public square (Fig. 1, B) where native species were planted to recreate three natural habitats of the region: grasslands, riparian forests and talares (native forests dominated by *Celtis tala*). Within this population, five individuals of *A. grandifolium* were selected. Observations were made during spring, from 23 September to 6 October 2019 at the first site and from 28 September to 6 November 2020 at the second.

COMPATIBILITY SYSTEM AND REPRODUCTIVE SUCCESS

To determine if *A. grandifolium* is self-compatible and if its sexual reproduction depends on pollinators, three sets of buds close to anthesis were selected from different individuals; sets 1 and 2 were enclosed with organza bags; when the flowers opened they were subjected to one of the following treatments: 1) spontaneous self-pollination (flowers were kept in bags to exclude floral visitors during anthesis and allow spontaneous deposition of their own pollen), 2) induced self-pollination (flowers were hand-pollinated with their own pollen), 3) free pollination (flowers were tagged around the pedicel, allowing pollinators to visit); flowers of these last two treatments were bagged after hand-pollination and after anthesis, respectively, to prevent losses or damages by frugivores). The fate of each flower was monitored daily until fruit set. Immature fruits were harvested between 7 and 11 days after the abscission of the corolla, as from this time it is possible to distinguish mature from immature or abortive seeds. Relative reproductive success (RRS = [no. fruits / no. flowers] × [no. seeds / no. ovules] (Dafni 1992) was calculated for each treatment; for this, the number of ovules per ovary and per carpel was estimated as the sum of developed and abortive seeds of ten immature fruits harvested from different specimens. The degree of dependence on pollinators was assessed by the following index: 1 − (fruit set under spontaneous self-pollination / fruit set under free pollination) and assigned to the corresponding category of dependence established by Klein et al. (2007).

FLORAL BIOLOGY: ANTHESIS, ATTRACTANTS, REWARDS AND POLLEN TRAITS

To determine the floral phases, 53 buds were tagged and the following floral characters were recorded during anthesis, which were analysed together afterwards: time of opening and closing of the corolla, position and maturation of the reproductive organs, structural blossom class and colour of the different floral parts (compared with the chart of Kelly 1965). The flowers were observed every hour, between 10 a.m. and 5 p.m., for six consecutive days. Stigmatic receptivity was tested by placing hydrogen peroxide on stigmas (Osborn et al. 1988), considering the presence of bubbles as positive reaction; to avoid false positives (due to pollen deposited on the stigmas), flowers with non-dehiscent anthers were bagged at the bud phase and then tested. Floral odour was qualitatively assessed via a human olfactory test: each floral part was placed in an airtight container for 15 minutes and then evaluated by observers for the presence and perceived intensity of scent; for the location of osmophores, floral parts were submerged in a neutral red solution (0.01% w/v, aqueous) and the stained areas were recorded. The presence of nectar was examined in ten flowers that had been bagged at the bud phase. To detect the main type of reserves in pollen (starch or lipids) and the presence of pollenkitt, grains from fresh anthers were stained with iodine solution and Sudan IV, respectively. After identifying the main reserve type, pollen viability was evaluated in recently opened flowers and in flowers at the end of anthesis; grains of normal size and content that stained were considered viable, whereas smaller, collapsed, empty or unstained grains were considered non-viable (Kearns & Inouye 1993; Amela García 1999). To describe pollen morphology, acetolysed grains (sensu Erdtman 1952) and grains fixed in 70% ethanol and dehydrated in an ascending ethanol series were observed and measured with optical and scanning electron (Zeiss Supra 40 FESEM) microscopes, respectively; the terminology of Punt et al. (2007) was followed.

FLORAL VISITORS: IDENTITY, VISIT FREQUENCY, ACTIVITY ON THE FLOWERS AND POLLEN LOAD

Censuses of floral visitors to individuals of *A. grandifolium* were carried out at the reserve (35 censuses) and the square (50 censuses), during 5 and 6 days, totalling 8 h 45 m and 12 h 30 m, respectively. Each census lasted 15 minutes and was conducted on each shrub every hour from 10 a.m. to 5 p.m.. For each visiting taxon, we quantified the following variables: (i) number of visitors, defined as the number of individual visitors recorded during censuses; (ii) number of visits, defined as the total number of visits to flowers performed by those visitors, noting that a given individual could visit more than one flower during a single arrival to a plant; (iii) visitation frequency (visits h^{-1}), calculated as the total number of visits recorded for each taxon divided by the total census duration (h) at each site; and (iv) relative abundance, calculated as the number of recorded individuals of each taxon × 100 / total number of recorded individuals. Simultaneously, we recorded the floral phase visited and reward collected. Visits were categorised as legitimate (if the visitor contacted the reproductive parts of the flower) or illegitimate (if the visitor collected a reward without coming into contact with the stigmas). Visitation rates were calculated as the number of visits per flower per hour. Up to three specimens per visitor taxon were captured for taxonomic identification and analysis of the pollen load. For this, permanent preparations of the pollen they carried were made by micro-acetolysis (Genise et al. 1990). For the identification of this pollen, an herbarium collection of sympatric plant species with biotic pollination syndromes and simultaneous flowering was assembled. Pollen samples from plants were processed by acetolysis (Erdtman 1952) and reference palynological slides were prepared. The pollen carried by the visitors was identified and quantified by comparison with these reference preparations using light microscopy (LM); in cases of low pollen load, it was analysed using scanning electron microscopy (SEM), mounting the parts of the insects that carried pollen as well as pollen from *A. grandifolium* and other Malvaceae (*Sphaeralcea bonariensis*) in bloom in the study area, which have very similar palynological characteristics, for accurate identification. Pollination effectiveness was inferred from visitation behaviour and pollen placement. Because nectar- and pollen-collecting visits by *Apis mellifera* involved different patterns of floral manipulation and differed in their likelihood of contacting the reproductive organs, these visit types were analysed separately.

STATISTICAL ANALYSIS

Statistical analyses were performed with R v3.6.2 (R Core Team 2019) using the glmmTMB (Brooks et al. 2017) and emmeans (Lenth 2019) packages. In general, models were simplified as follows: significance of the different terms was

Table 1. Fruit set (no. of fruits / no. of flowers) and seed set (% mature seeds per fruit relative to the number of ovules per flower) under different pollination treatments in *Abutilon grandifolium*. Relative reproductive success (RRS) was calculated as fruit set × seed set.

	Spontaneous self-pollination	Induced self-pollination	Free pollination
N° of flowers	49	44	39
N° of fruits	44	40	39
Fruit set	0.90	0.91	1
Seed set	78	79	88
RRS (relative reproductive success)	0.69	0.72	0.87

tested starting from the higher-order terms model using likelihood ratio tests (LRTs) to compare models (Chambers & Hastie 1992) and non-significant terms ($P > 0.05$) were removed. Post hoc comparisons using contrast matrices were performed with the *emmeans* function (Lenth 2019). Differences in the number of mature seeds per fruit among reproductive treatments were evaluated using the Kruskal–Wallis test. To compare the visitation rate of the most frequent flower visitors in the square, a generalised linear mixed model (GLMM) with a negative binomial distribution was used to account for overdispersion in the data. The model included the number of visits as the response variable, visitor type and their activity (honey bees exclusively collecting nectar in successive visits, honey bees collecting pollen and/or nectar in successive visits, and halictid bees) and time of day (morning, from 10 a.m. to 1 p.m.; afternoon, from 2 to 5 p.m.) as fixed factors, shrub and date as random factors, and the number of flowers recorded as an offset to correct the number of events for an estimate of population size.

RESULTS

COMPATIBILITY SYSTEM AND REPRODUCTIVE SUCCESS

In all treatments, fruits containing seeds were produced, each fruit developing 8–10 mericarps (Table 1). Each ovary contained 58 ± 2 ovules (5–7 ovules per carpel). Relative reproductive success was high in all treatments, owing to the high fruit/flower ratio together with the high seed/ovule ratio (Table 1). Although seed set tended to be higher in fruits obtained by free pollination, differences among treatments were not statistically significant ($\chi^2 = 2.9465$, $P = 0.2292$). The degree of dependence of pollinators was 1.1.

ANTHESIS AND FLORAL PHASES

36 of the 53 monitored buds opened around 10 a.m., whereas 17 opened after noon; 11 of the latter remained open until the afternoon of the following day, with an average anthesis duration of 17 h (range: 4–25 h), while most of the flowers that opened in the morning closed in the afternoon, with an average flower longevity of 6 h (range: 4–7 h).

Four phases were recognised throughout the flower life span (Fig. 2), defined by the following characteristics:

- **Bud about to open (Fig. 2A):** intense orange corolla with non-displayed petals, visible through the slightly separated sepals. Light yellow, non-dehiscent anthers. Stigmas hidden between the anthers, receptive.
- **Phase 1 (Fig. 2B):** deep orange corolla, petals beginning to separate. Some anthers dehiscent. Stigmas visible between the anthers and receptive.
- **Phase 2 (Fig. 2C):** yellow–orange, fully opened, bell-shaped (campanulate) corolla (diameter = 2–3 cm). Petal colouration more intense at the margins, becoming lighter towards the base. All anthers dehiscent; pollen was found dropped at the base of the corolla. The stigmas were located between the anthers, rarely surpassing them.
- **Phase 3 (Fig. 2D):** yellow–orange corolla, with one or more petals recurved, sometimes giving the flower a bowl shape (diameter = 3–4 cm). All anthers dehiscent; some stigmas surpassed the height of the anthers.
- **Phase 4 (Fig. 2E):** whitish corolla, progressively dehydrating (especially from the distal edges of the petals) and closing.

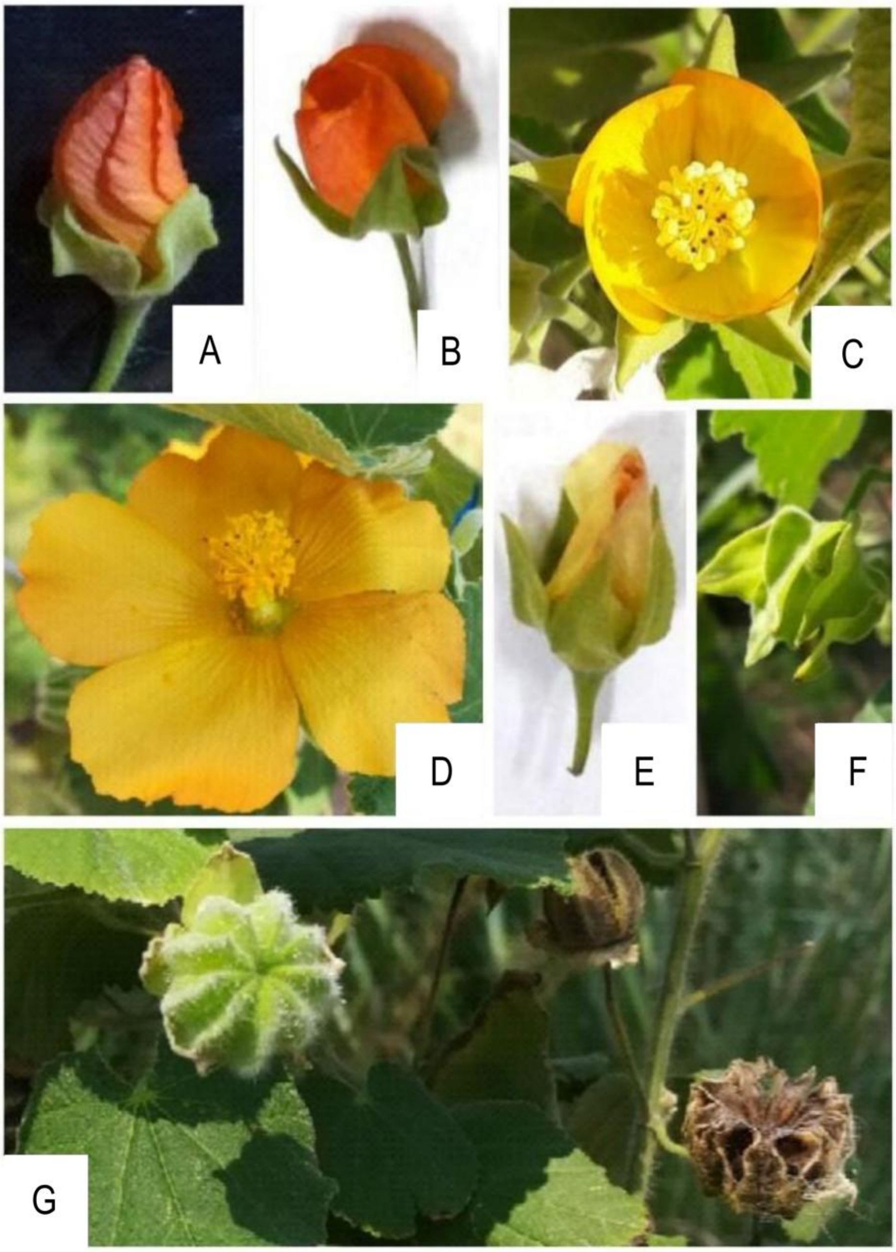

Figure 2. Phases of development of flowers and fruits of *Abutilon grandifolium*. A) bud about to open. B) flower in phase 1. C) flower in phase 2, corolla bell-shaped; the anthers (yellow) and the stigmas (purple) are observed. D) flower in phase 3, bowl-shaped corolla. E) flower in phase 4, corolla closed and dry. F) flower with recently fallen corolla. G) fruits with different degrees of development: one green immature (left) and two mature, dry and dehiscent (right).

After phase 4, the corolla abscised (Fig. 2F) and, after a few days, if fertilisation had occurred, ovary growth and fruit development became evident; fruits reached maturity after 11 days (Fig. 2G).

ATTRACTANTS AND REWARDS

According to the olfactory test, the odour was faint and emitted by the androecium; osmophores were located in the anthers as revealed by neutral red (Fig. 3A). The nectaries, formed by glandular trichomes, were grouped on both basal margins of the unguiculate petals (Fig. 3B); nectar was present in phases 2 and 3.

POLLEN: RESERVES, POLLENKITT, VIABILITY AND MORPHOLOGY

The pollen grains stained positively with both Sudan IV and iodine solution, indicating that they contained lipids and starch as reserves (Fig. 3C). Pollenkitt was present among the grains (Fig. 3C). Pollen viability was 95% in phase 1 (N = 447 grains from 3 flowers), decreasing to 89% in phase 3 (N = 872 grains from 3 flowers).

Pollen grains of *A. grandifolium* were spherical (Fig. 4A), with an echinate (Fig. 4B), papillate and perforate exine (Fig. 4C). The spines were conical, with concave sides, situated on a circular base (Fig. 4D), rarely occurring in pairs (Fig. 4B,

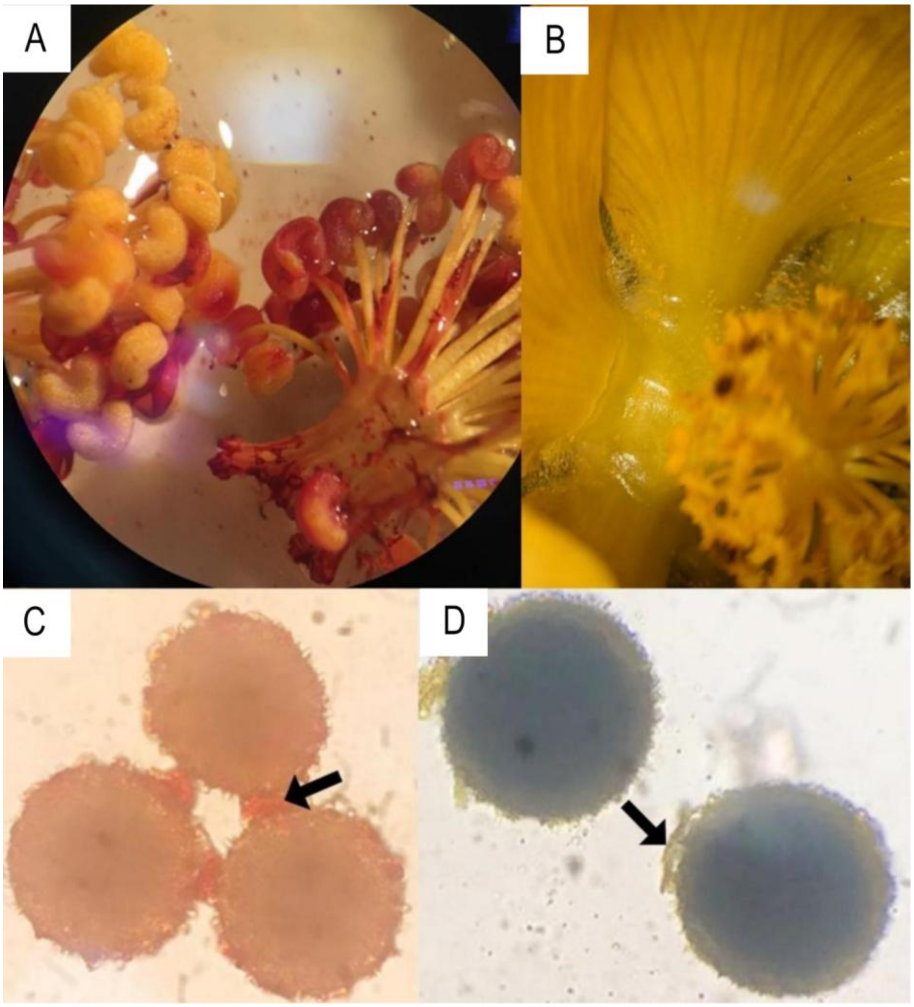

Figure 3. Attractants, reward and pollen reserves. A) Neutral red staining test positive for anthers. B) Access to the nectaries formed by glandular trichomes grouped at the base of both sides of each unguiculate petal. C-D) Pollen stained with C) sudan IV and D) iodine solution; note pollenkitt among grains (arrows).

arrow), and generally straight or slightly curved at the apex (Fig. 4E). In apical view, the ornamentation of the tectum resembled granules (Fig. 4C), whereas in lateral view it resembled papillae (Fig. 4D, white arrows). The diameter of the papillae was 0.20 µm ± 0.02 (*N* = 4), whereas that of the perforations was 0.28 µm ± 0.05 (*N* = 3). Spines had a length of 2.96 µm ± 0.41 (*N* = 10), and their diameter was 2.37 µm ± 0.45 (*N* = 2) at the base, 1.10 µm ± 0.07 (*N* = 2) in the middle and 0.31 µm ± 0.02 (*N* = 2) at the apex. The diameter of the pollen grains was 51.58 µm ± 3.12 (*N* = 6), while that of *Sphaeralcea bonariensis* was 31.65 µm ± 0.68 (*N* = 3), so they could be distinguished in the visitor pollen loads.

FLORAL VISITORS: IDENTITY, VISIT FREQUENCY AND POLLEN LOAD

In both the reserve and the square, assemblages of floral visitors were dominated by hymenopterans belonging to Apoidea (Apidae and Halictidae), whereas dipterans (Syrphidae) and coleopterans were comparatively rare (Table 2). Species richness was lower in the reserve than in the square, with six vs. nine species, respectively (Table 2). Overall visitation rate was approximately twice as high in the square as in the reserve (Table 2). In both sites, *Apis mellifera* accounted for most of the visits (> 80 %) and showed the highest relative abundance, followed by halictids. Other visitors, such as *Xylocopa* sp., *Bombus pauloensis*, syrphids and beetles, were infrequent (Table 2).

In both sites, the two most frequent visitors (honey bees and halictid bees) differed markedly in their visitation behaviour. Halictid visits were mostly legitimate, and involved the collection of nectar and pollen whereas nectar theft was rare. In contrast, honey bees performed both legitimate and illegitimate visits, although legitimate visits predominated at both sites (Table 2). The remaining visitors performed almost exclusively legitimate visits. *Xylocopa* sp. and *B. pauloensis*

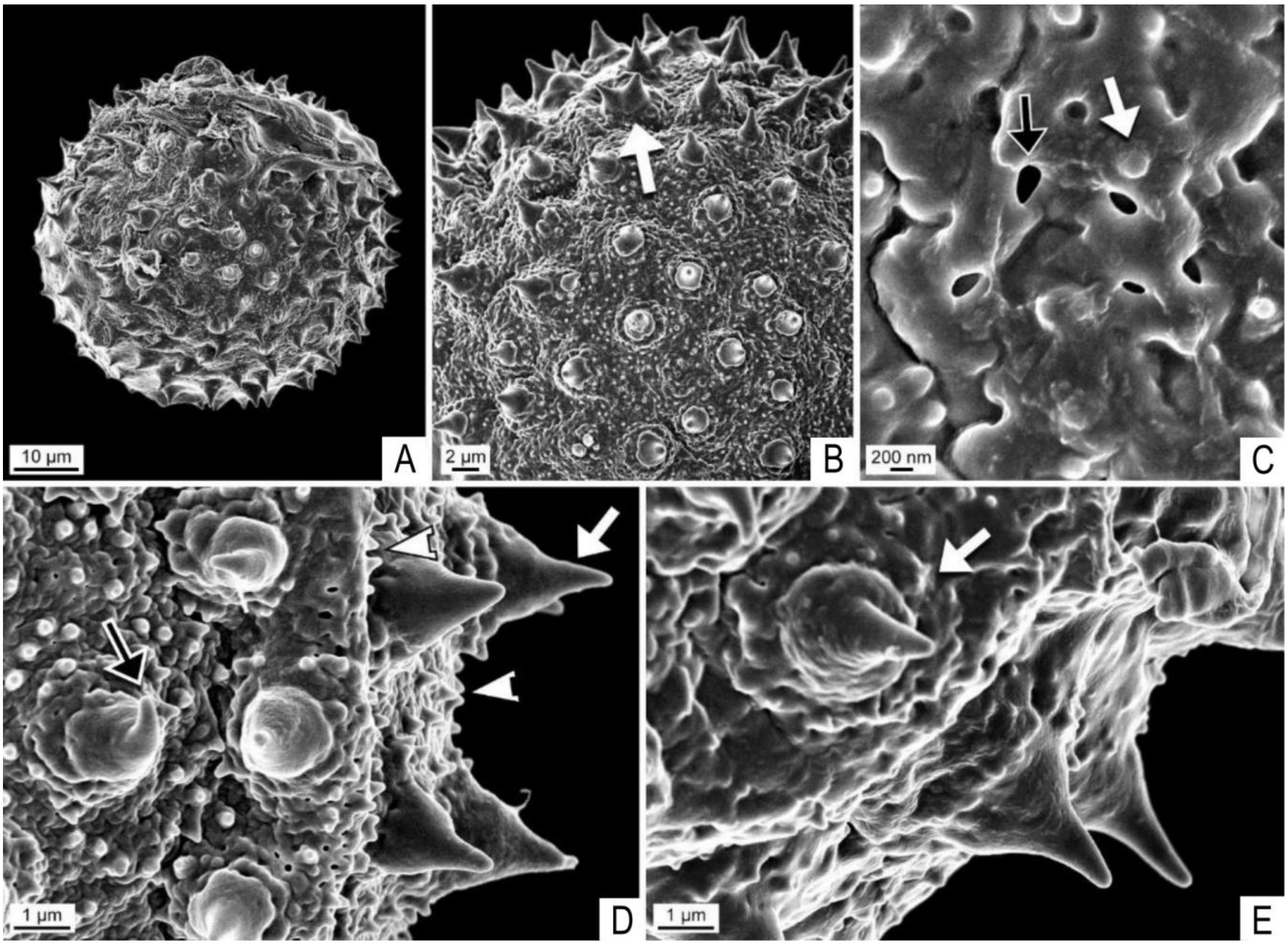

Figure 4. Pollen morphology of *Abutilon grandifolium*. A) general appearance of the grain. B) ornamentation of the exine, with (widespread) simple and (rare) double (arrow) spines. C) detail of perforations (black arrow) and papillae (white arrow). D) detail of the papillae (arrowhead) and conical spines, with apex slighted curved (black arrow) or straight (white arrow). E) detail of spine cushion.

mainly collected nectar, whereas syrphids mainly ingested pollen (Table 2); the coccinellid appeared to eat pollen and curculionids appeared to lick nectar. *Apis mellifera* also accounted for the highest absolute number of legitimate visits at both sites. In the reserve, *A. mellifera* performed more than double of the visits done by halictids, *Xylocopa* and the syrphids considered together, while in the square they far surpassed the remaining taxa.

Honey bees exhibited different movements on the flowers depending on the floral reward exploited. Individuals that illegitimately collected nectar landed on the pedicel or on the abaxial (outer) surface of the calyx and corolla and inserted their proboscis into the gap between two adjacent unguiculate petals, repeating the action on different petal pairs. Illegitimate visits were common to flowers in phases 1, 2 and 3. These visits were generally brief and the bees frequently moved on to another flower of the same plant. On several occasions, while a bee was collecting nectar, a second bee approached and contacted the first, which then flew to a nearby flower. By contrast, individual honey bees that alternated between collecting nectar and pollen in successive visits during each arrival to a plant generally accessed each of these rewards legitimately. To collect nectar, they landed on the adaxial surface of the petals, with the head oriented towards the centre of the flower, and extended the proboscis towards the petal bases, repeating this in a circular fashion. During these visits, pollen was deposited on the dorsum of the head and thorax (Fig. 5A). To collect pollen, they moved across different anthers while contacted the stigmas with the ventral region of the body; they then hovered in front of the recently visited flower, forming the corbicular pollen mass

Table 2. Floral visitor assemblage of *A. grandifolium* at (A) the ecological reserve and (B) the square: visitors number, number of visits, visitation frequency (visits h^{-1}) , relative abundance, visit types and collected rewards. L = legitimate visit, I = illegitimate visit, P = pollen, N = nectar, s = seconds, SE = standard error.

(A) Ecological Reserve

Floral visitors (order, family, species)	Visitors number	Number of visits	Visitation Frequency (visits h^{-1})	Relative abundance (%)	Visit type (%)		Reward collected
					L	I	
Hymenoptera							
Apidae							
Apis mellifera	91	553	63.2	73.39	52	48	P, N
Xylocopa sp.	5	30	3.3	4.03	100	0	N
Bombus pauloensis	3	4	0.5	2.42	100	0	N
Halictidae							
Halictidae sp. 1	20	52	5.9	16.13	98	2	P, N
Diptera							
Syrphidae							
Syrphidae sp. 1	4	42	4.8	3.23	100	0	P
Coleoptera							
Curculionidae sp. 1	1	1	0.1	0.81	1	0	N
TOTAL	124	682	77.9				

(B) Square

Floral visitors (order, family, species)	Visitors number	Number of visits	Visitation Frequency (visits h^{-1})	Relative abundance (%)	Visit type (%)		Reward collected
					L	I	
Hymenoptera							
Apidae							
Apis mellifera	328	1442	115.4	88.6	78	22	P, N
Xylocopa sp.	1	18	1.4	0.3	94	6	P, N
Bombus pauloensis	2	3	0.2	0.5	67	33	N
Hymenoptera sp. 1	4	4	0.3	1.1	100	0	P, N
Halictidae							
Augochlora sp.	17	19	1.5	4.6	nd	nd	nd
Halictidae sp. 2	14	14	1.1	3.8	91	9	P, N
Diptera							
Syrphidae							
Syrphidae sp. 2	2	2	0.2	0.5	100	0	P, N
Syrphidae sp. 3	1	2	0.08	0.3	100	0	P
Coleoptera							
Coccinellidae sp. 1	1	1	0.08	0.3	nd	nd	P
TOTAL	370	1505	120.4				

by leg movements and returned to the same flower or visited a nearby one, continuing pollen collection. On some occasions, nectar and pollen were collected in the same visit, the bee first licking nectar and then climbing onto the anthers.

In contrast, halictids showed a single visitation pattern in which they collected pollen and nectar during the same visit. They mainly visited flowers in phase 2. When collecting pollen, they moved among the anthers using their legs and jaws, contacting the stigmas with the ventral surface of the body; when collecting nectar, they usually licked between contiguous petals (Fig. 5B) and walked around the staminal column to the next bundle of nectariferous trichomes, thereby extensively contacting the reproductive organs. So after a single visit pollen was deposited on almost the entire body surface.

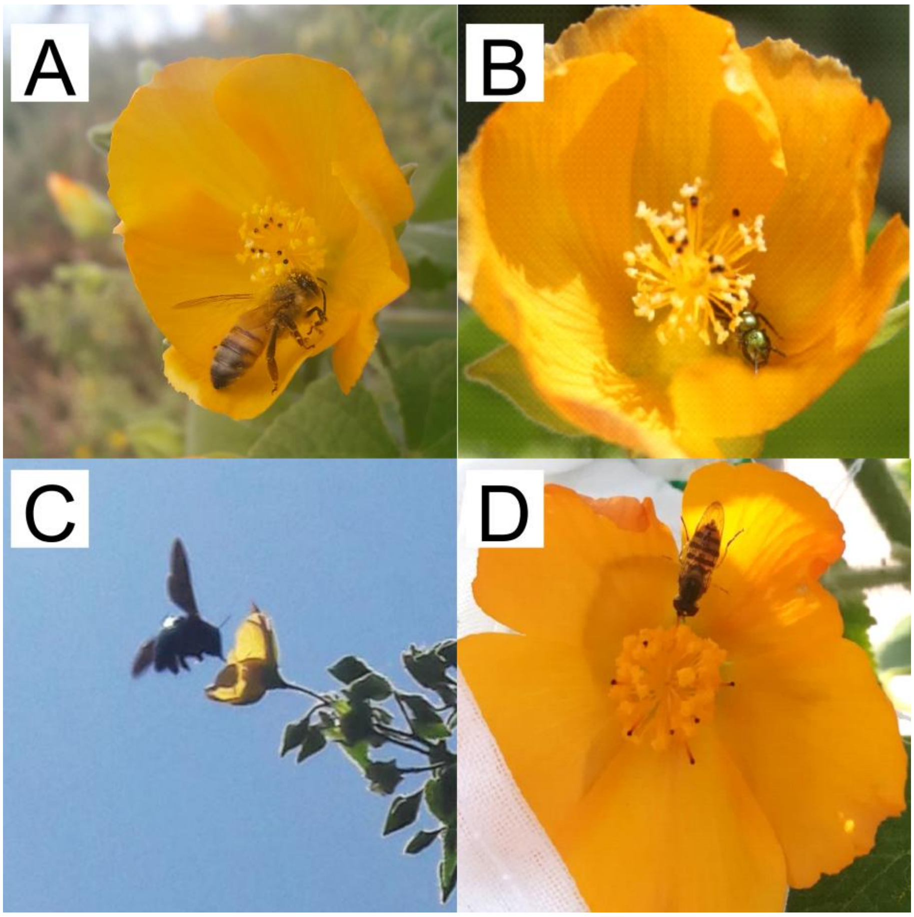

Figure 5. Floral visitors of *Abutilon grandifolium*: A) *A. mellifera* licking nectar legitimately and contacting pollen with thorax dorsum. B) halictid licking nectar. C) *Xylocopa* sp. arriving at a flower. D) syrphid hovering in front of a flower.

The remaining, occasional flower visitors also differed in their behaviour on the flowers. The large *B. pauloensis* and *Xylocopa* sp. landed on the petals (Fig. 5C), contacting the reproductive organs with the ventral surface of the abdomen while accessing nectar. Regarding hoverflies, individuals of species 2 made long visits during which they ingested pollen, landing on the anthers and moving only slightly, sometimes not covering the entire androecium; one individual of species 3 licked nectar by landing on the petals but, owing to its body size, did not contact the anthers or stigmas (Fig. 5D). Finally, a coccinellid left a phase-1 flower carrying pollen on its mouthparts, legs and probably ventral body surface, whereas curculionids were observed inside flowers with their rostrum directed towards the nectaries.

The statistical analysis of the visitation rates of the most frequent visitors surveyed in the square revealed significant differences between honey bees and halictids, and also between visit types of honey bees (Fig. 6). The rate of honey bees exclusively collecting nectar was more than three times higher than that of honey bees collecting pollen and that of halictids (post hoc comparisons: HB.nectar vs. HAL, t-ratio = 10.76, df = 73, $P < 0.0001$; HB.pollen vs. HB.nectar, t-ratio = –5.36, df = 73, $P < 0.0001$). Significant differences were also found between honey bees collecting pollen and halictids (post hoc comparison: HB.pollen vs. HAL, t-ratio = 4.56, df = 73, $P = 0.0001$). By contrast, visitation rates (Fig. 6) were similar between morning and afternoon (logit scale: β = 0.19, SE = 0.19, z = 0.99, *P* = 0.32), but flowers in phase 2 received the highest number of visits, both in the morning and in the afternoon (Fig. 7).

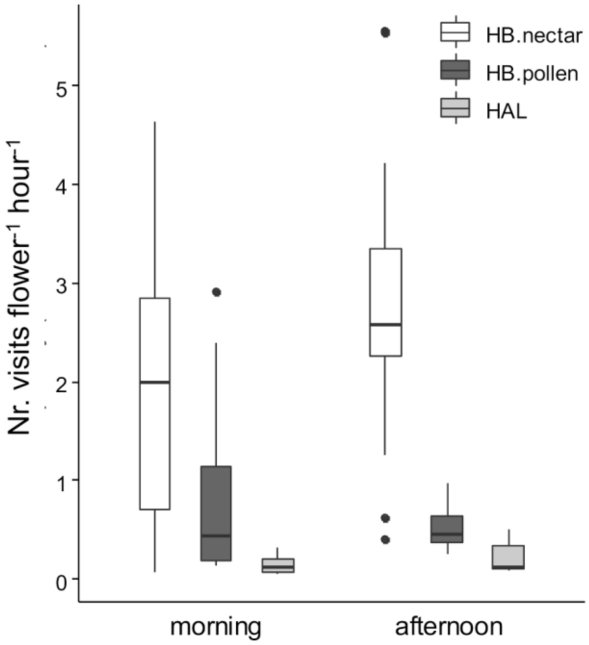

Figure 6. Visitation rate of the most frequent floral visitors of *Abutilon grandifolium* in the square. Number of visits per flower per hour performed by honey bees, exclusively collecting nectar (HB.nectar) or pollen (HB.pollen) in successive visits, and halictids (HAL) in relation to time of day (morning, 10 a.m. to 1 p.m.; afternoon, 2 to 5 p.m.). Boxplots show the median and IQR, with whiskers showing the maximum value within 1.5 IQR, and individual points mark values outside this range.

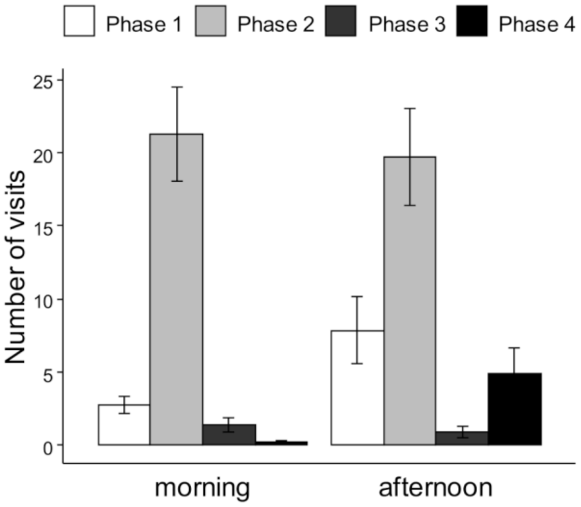

Figure 7. Number of visits (mean ± S.E.) received by *Abutilon grandifolium*, according to the floral phase (see the main text for more details) and time of day (morning, 10 a.m. to 1 p.m., n = 26 censuses; afternoon, 2 to 5 p.m., n = 22 censuses).

Most of the pollen carried by *A. mellifera* on the dorsum of the head and thorax consisted of *A. grandifolium* (Fig. 8A), whereas only a small proportion was found in the corbiculae (Fig. 8B), where *Rapistrum* sp. and *Raphanus* sp. accounted for the majority of the load, in addition to *Conium* sp., *S. bonariensis* and a non-identified species (Fig. 8B). On their side, *Xylocopa* sp., *B. pauloensis*, Halictidae and Syrphidae carried large amounts of *A. grandifolium* on the ventral body surface (Fig. 8C-E, H); the rest of the load consisted of diverse taxa, including plant species not found in bloom in the surroundings of the studied individuals. Halictids also transported grains of *S. bonariensis* on the ventral area of the body (Fig. 8C-E), as well as on the hind legs (Fig. 8F). Syrphids carried *A. grandifolium* pollen on the head dorsum and eye margins (Fig. 8G) and on the ventral area of the abdomen, together with considerable quantities of *Conium* sp (Fig. 8H).

DISCUSSION

In this study, it was shown that the native shrub *Abutilon grandifolium* is self-compatible, melittophilous and that, in an urban context, both studied populations, even in different years, hosted broadly similar pollinator assemblages in terms of composition and main functional groups.

The fruits and seeds obtained by induced and spontaneous self-pollination indicate that *A. grandifolium* is self-compatible. The degree of dependence on pollinators, less than 10 %, was little, *sensu* dependence categories established by Klein et al. (2007). Since fruit production was > 30 %, it would be highly self-compatible, according to the classification proposed by Dafni (1992). But the seed set increased (though not significantly) when pollinators were allowed to intervene. In many flowers, one or more stigmas were located slightly above the level of the anthers (herkogamy), which would facilitate xenogamy (Sargent et al. 2006; Waites & Ågren 2006). In most of the buds, the stigmas were receptive before the dehiscence of the anthers (protogyny) and, once the anthesis had started, all the anthers were dehiscent; due to the proximity of stigmas and anthers in most of the flowers, self-pollination can take place. Thus, under natural conditions, fruits and seeds can be produced by autogamy or xenogamy. Facultative autogamy has been reported in other species of the genus (Abid 2006; Abid et al. 2010). It is probable that this condition favours the invasiveness of this species and even its naturalisation.

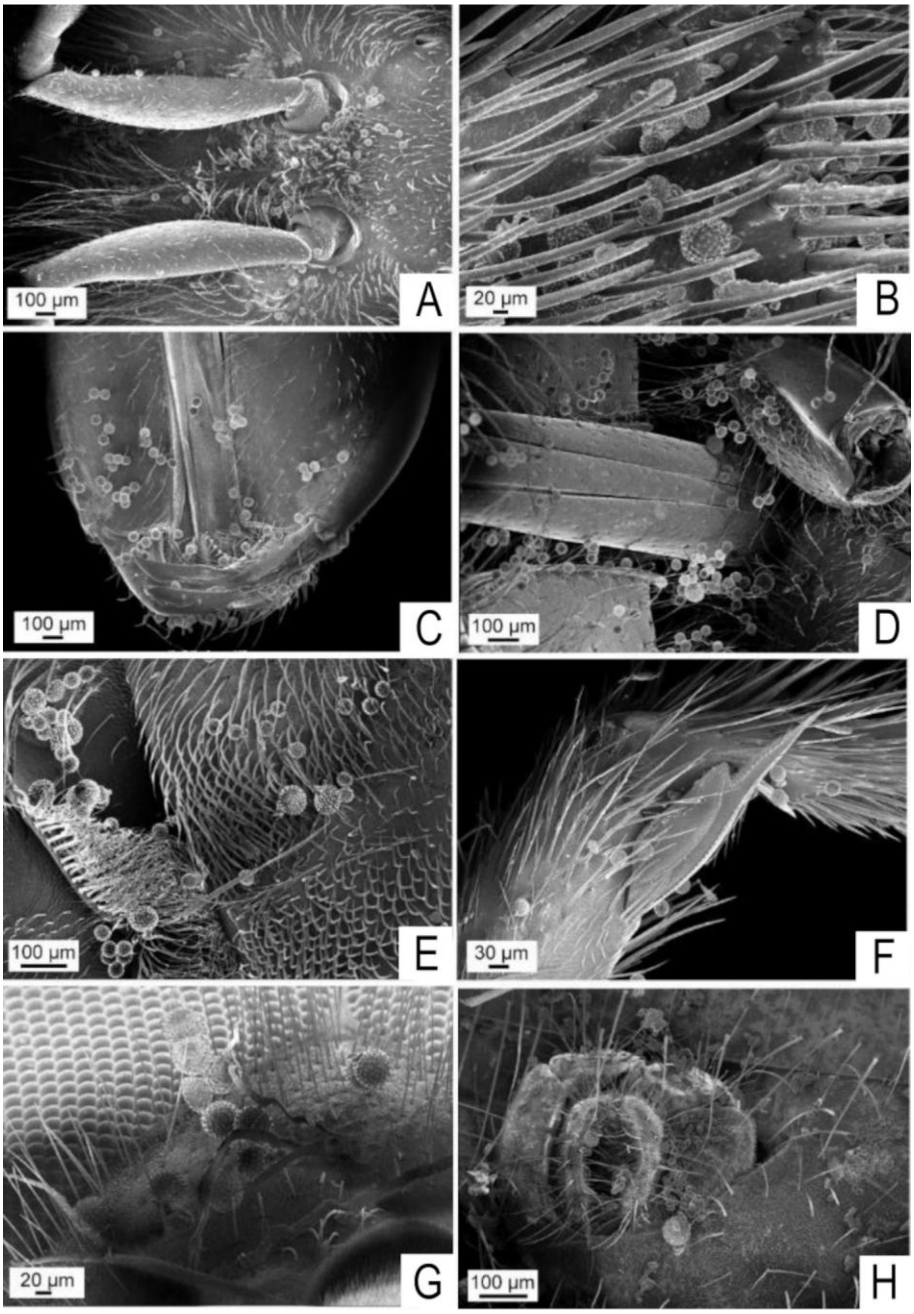

Figure 8. Pollen carried by floral visitors analysed with SEM. A-D, *Apis mellifera* (one specimen). A) *Abutilon grandifolium* pollen between the antennae. B) *A. grandifolium* and *Sphaeralcea bonariensis* pollen on the corbicula. C-F, Halictidae (sp. 1, two specimens). C) ventral area of the head with grains of *A. grandifolium.* D) surroundings of the proboscis base with *A. grandifolium* and *S. bonariensis* pollen grains. E) ventral view of the abdomen with *A. grandifolium* and *S. bonariensis* pollen grains. F) hind leg with *S. bonariensis* pollen grains. G-H, Sirphidae (two specimens from different species). G) edge of the eyes with grains of *A. grandifolium*. H) ventral view of the end of the abdomen with pollen of *A. grandifolium*, *S. bonariensis* and *Conium* sp.

The floral traits (diurnal anthesis, yellow–orange and bell- to bowl-shaped corolla, mild and pleasant aroma, nectar and pollen supply) are associated with the melittophilous pollination syndrome (Faegri & van der Pijl 1979). Nectar is available at several points arranged circularly, constituting a "round-about" flower (Endress 1996). These floral traits are consistent with attraction of bee visitors and with efficient pollen transfer.

The pollen grains, larger than 50 µm, are classified as large according to Erdtman's (1986) size categories; however, our measurements differ from the description of *Abutilon molle* (syn. *A. grandifolium*) reported by Shaheen et al. (2009). The exine exhibits perforations and spines, as in *Abutilon pictum* (Del Pino & Díez 1990). The shape of the spines and their cushion-like bases is typical of the Abutilieae tribe, in contrast with representatives of other Malvaceae tribes

(Christensen 1986; El Naggar & Sawady 2008; Abdel Khalik et al. 2021). These surface traits, together with the presence of pollenkitt, may influence how pollen adheres to the bodies of different visitors.

Visitor assemblages were similar in both sites, though the observations in each one were performed in different years, with clear numerical dominance of *Apis mellifera*, but with evidence of higher pollination effectiveness by halictid bees. Owing to the closeness of stigmas and anthers, almost all recorded visitor taxa are capable of transferring pollen (autogamous or allogamous) to the stigmas, either when they legitimately suck nectar or when they land on the anthers to collect (bees) or ingest (flies) pollen. However, due to differences in visit frequency, body size and behaviour on the flowers, their contribution to pollination is expected to differ. Pollen deposition of *A. grandifolium* was nototribic in *A. mellifera* and halictids while sternotribic in the remaining visitors. *A. mellifera*, although the most frequent visitor and clearly capable of pollinating during legitimate visits, also performed a proportion of illegitimate visits at both sites. In such visits, due to the way it accesses nectar without contacting anthers or stigmas, honey bees would act as nectar thieves (Inouye 1980). Nectar theft can negatively affect plant reproduction, since reduced nectar availability can decrease potential legitimate visits (Irwin et al. 2010). The absence of mechanisms preventing illegitimate visits by *A. mellifera* to *A. grandifolium* flowers could be related to the fact that this interaction is relatively recent in evolutionary terms (Hanna et al. 2014), as these bees were introduced to America a few hundred years ago (Whitfield et al. 2006). However, despite the high proportion of illegitimate visits, *Apis mellifera* contributed the highest absolute number of legitimate visits at both study sites. In contrast, the second most frequent visitors, halictids, rarely visited *A. grandifolium* flowers illegitimately. Furthermore, because they moved more easily within the corolla (due to their smaller bodies), and contacted a larger number of anthers and stigmas, carrying *A. grandifolium* pollen on body regions with high probability of contacting stigmas. So, they can be considered the main pollinators of *A. grandifolium* in the studied populations. Among the less frequent visitors, given the robust bodies and abundant hairiness of *Bombus pauloensis* and *Xylocopa* sp., these bees could transfer large amounts of pollen during their (exclusively legitimate) visits. Syrphids would act as pollen (and occasionally nectar) thieves. Among beetles, the coccinellid would be a pollen thief, while the curculionid, which can ingest nectar through the characteristic rostrum of this family, would be a nectar thief. Most Coccinellidae are carnivorous, but some can feed on pollen (González 2009). Curculionids visiting flowers can obtain different rewards, including nectar (Bernhardt 2000; Lehnebach 2002). No visits by Lepidoptera were recorded, although they were present in both sites and have been reported as frequent visitors to *Abutilon indicum* and *Sida ovata*, both Malveae and with similar floral morphology, attractants and rewards as *A. grandifolium* (Dawar et al. 1994; Abid et al. 2010).

The effectiveness of pollination is determined both by the efficiency of the pollinating agent in transferring pollen to the stigmas and by the intensity of visits (Freitas et al. 2014). The analysis of pollen loads (taxa, relative abundance and distribution on the body) confirmed that the most frequent visitors carried large quantities of *A. grandifolium* pollen on body areas capable of contacting stigmas. In the case of honey bees and halictids, pollen deposited on their heads or dorsal body surfaces while sucking nectar may be transferred efficiently to stigmas; by contrast, pollen actively collected and packed in the corbiculae would be transported to the nest, not contributing to pollination. The low frequency of pollen-collecting visits and the small amount of *A. grandifolium* pollen in the corbiculae of *A. mellifera* is consistent with the idea that large grain size, spines and pollenkitt (all traits present in *A. grandifolium*) hinder the packing of mallow pollen grains by corbiculate bees (Lunau et al. 2015; Konzmann et al. 2019).

The differences in the abundance of the main hymenopteran visitors may be related to their distinct foraging and nesting habits, as well as degrees of sociality (which influence food collection). Halictids, at least *Augochlora*, are solitary or semi-social, have a generalist diet and nest in the ground or in decaying wood (Dalmazzo et al. 2014). Many solitary bee species restrict their flights to a few hundred metres around their nest (Gathmann & Tschamtke 2002; Zurbuchen et al.

2010). Therefore, their visits would reflect the presence of nests in trunks or in the soil both in the reserve and in the square. In contrast, *A. mellifera* is eusocial (living in colonies of tens of thousands of individuals), can travel several kilometres on foraging flights and often concentrates activity temporarily on one resource. In addition, on the university campus adjacent to the reserve, there were honey bee colonies, which may partly explain their high visitation frequency. Regarding the less frequent hymenopterans, *Bombus* bumblebees are eusocial, but their colonies comprise a few hundred individuals and they usually nest on the ground under leaf litter (Goulson 2003). *B. pauloensis* collects nectar and pollen from numerous families, including Malvaceae (Abrahamovich & Díaz 2002). In the square, given the characteristics of the study site and the surrounding blocks, the presence of *B. pauloensis* nests in the vicinity would be rare, which would explain their low abundance, not only their low visitation to *A. grandifolium*; in the reserve, a site with greater nesting availability, visits were only slightly more frequent, probably because these bumblebees were visiting assiduously the abundant flowers of nearby *Solanum sisymbriifolium* individuals. *Xylocopa* are solitary, nest in soft wood and are usually polylectic (Lucia 2011) and polytropic (Amela García 1999). These large bees do not fit comfortably into *A. grandifolium* flowers and would prefer more rewarding nectar sources or flowers offering easier pollen collection. Besides, alternative resources, particularly richer and more abundant in the reserve, could have driven all this polytrophic floral visitor occupancy on *A. grandifolium*, especially evidenced by the heterogenic (except of *Bombus*) pollen loads.

Regarding the number of flowers visited per individual, in both sites *A. mellifera* and *Xylocopa* sp. visited more flowers per foraging bout than *B. pauloensis* and halictids. The latter two would therefore contribute more to xenogamy between plants than species that tend to visit successive flowers of the same shrub, thus performing geitonogamy to a greater degree.

The similar floral-visitor assemblage, behaviour on flowers and relative visitation frequency in the reserve and in the square suggest that the square provides conditions that allow the recruitment and activity of floral visitors, at least for *A. grandifolium*, and that the incorporation of this species into this urban green space is effective in attracting pollinators. Species richness was even higher in the square. In another comparative study between a reserve and an urban green space with cultivated native plants in Ciudad Autónoma de Buenos Aires (Mosconi 2020), species richness was also lower in the reserve. This may be because recreated urban spaces with native flora usually offer a greater or more continuous floral supply, probably even superabundant, in contrast with urban green spaces lacking such management (Andrada et al. 2024). Regardless of richness, the square would function as a stepping-stone, forming part of a biological corridor between RECU-CN and other reserves in C.A.B.A., as well as nearby reserves in the Área Metropolitana de Buenos Aires (AMBA) and other urban green spaces. The presence of pollen from plant species not in bloom at the study sites indicates that floral visitors travel further than within the sampled area and, therefore, are capable of interconnecting these areas. A home range larger than that offered by urban green spaces (urban strips planted with sunflowers) has also been documented for *A. mellifera* and *Bombus terrestris* through analysis of pollen loads, suggesting that they forage in other habitats within the urban matrix (Potter et al. 2019). In terms of pollination, biological corridors favour the presence of floral visitors foraging among nodes as well as pollen flow between plant populations, thereby possibly contributing to maintaining outcrossing.

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AUTHOR CONTRIBUTION

All authors (Cáceres, Pablo Daniel; Laino, Leandro Ezequiel; Estravis-Barcala, Cecilia; Lajad, Rocío; Amela García, María Teresa) contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Cáceres Pablo Daniel and Laino Leandro Ezequiel and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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No potential conflict of interest was reported by the author(s).

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OpenAI's ChatGPT was used to assist with English language editing and clarity in selected parts of the manuscript during revision. The authors reviewed, edited and approved all AI-assisted text, and no AI tool was used to generate data, perform analyses, or draw scientific conclusions.

DATA AVAILABILITY STATEMENT

The data used to write this article are available upon request.

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