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To cite this article: Juan P. Torretta, Sandra S. Aliscioni, Adelia González-Arzac \& Adan A. Avalos (2017) Is the variation of floral elaiophore size in two species of Stigmaphyllon (Malpighiaceae) dependent on interaction with pollinators?, Plant Ecology \& Diversity, 10:5-6, 403-418, DOI: 10.1080/17550874.2018.1434567

To link to this article: https://doi.org/10.1080/17550874.2018.1434567


Published online: 09 Feb 2018.


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# Is the variation of floral elaiophore size in two species of Stigmaphyllon (Malpighiaceae) dependent on interaction with pollinators? 

Juan P. Torretta* ${ }^{* a, b}$, Sandra S. Aliscioni ${ }^{\text {a,b,c }}$, Adelia González-Arzac ${ }^{\text {a,b,d }}$ and Adan A. Avalos ${ }^{\text {b,e }}$<br>${ }^{a}$ Facultad de Agronomia, Cátedra de Botánica General, Universidad de Buenos Aires, Buenos Aires, Argentina; ${ }^{b}$ Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina; ${ }^{c}$ Instituto de Botánica Darwinion (IBODA), Buenos Aires, Argentina;<br>${ }^{d}$ Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina, Universidad de Buenos Aires, Buenos Aires, Argentina; ${ }^{e}$ Instituto de Botánica de Nordeste, Consejo Nacional de Investigaciones Cientificas y Técnicas, Buenos Aires, Argentina

(Received 10 August 2016; accepted 26 January 2018)


#### Abstract

Background: Intraspecific variations in floral traits of species over its geographic range can be associated with differences in pollinator assemblages and/or with environmental conditions. Aims: We evaluated the area of elaiophores in different populations of Stigmaphyllon bonariense $(n=9)$ and $S$. jatrophifolium $(n=6)$, and we hypothesised a marked reduction in their size towards their southern limits of distribution, associated with different oil-collecting bee assemblages. Methods: Area of elaiophores was calculated and we carried out linear correlations with floral size, pollinators, visitation rate and pollinator size along the latitudinal gradient of the plants' distributions. Moreover, we examined the relative size relationships using allometric analyses, to verify this reduction. Results: Floral elaiophore area decreased with latitude. However, for $S$. bonariense we observed an allometric reduction in elaiophore area with respect to floral size, while for S. jatrophifolium an isometric reduction was found. In both species, pollinator richness and visitation rate did not diminish with latitude, but pollinator size for $S$. bonariense varied. Conclusions: Our results show a reduction in the size of elaiophores in both species along their distribution range, with dissimilar tendencies, suggesting that these species may have different selection pressures that cause variation of their phenotypic traits.


Keywords: elaiophore; flower-bee interaction; Malpighiaceae; oil-collecting bees; oil-rewarding flowers

## Introduction

Intraspecific variation in floral traits is important for identifying the role of adaptive evolution in floral diversification (Hodgins and Barrett 2008), and pollinators have played a crucial role as partners in the diversification of angiosperm flowers (Herrera et al. 2006). Most animal-pollinated flowers have attractive organs (e.g., petals) and rewarding structures (e.g., elaiophores: structures that produce floral oils). Petals (or perianth) may have evolved to increase the number of pollinator visits (Ushimaru and Nakata 2001) and to determine the type of pollinator which visits them; moreover, flowers with higher quantities of reward may satisfy larger pollinators (Cohen and Shmida 1993). In plants with a wide distribution, floral traits related to adaptation to local pollinator fauna may vary in a mosaic fashion (Olsson and Ågren 2002; Thompson 2005). The geographic mosaic theory states that species interactions vary within space, exhibiting geographic selection mosaics (Giannini et al. 2013) and that interactions made by a species in great part depend on local conditions, for instance partner availability and local fitness (Mello et al. 2013). However, these changes can also be explained by abiotic gradients (Barrett et al. 2004). For example, in

Calceolaria polyrhiza Cav. (Calceolariaceae), an oilrewarding species, some studies have shown that mainly changes in pollinators, and lesser so climatic and edaphic conditions, were related to the variation of the floral reward composition at the geographic scale (Cosacov et al. 2012; 2014).

In the Neotropical region, most species of Malpighiaceae have elaiophores, and floral oil is collected by females (and some males) of numerous species of bees for nest construction and protection and/or mixed with pollen mass for larval food (Vinson et al. 1996). This pollination system is highly specialised and species of this family are effectively pollinated by a low diversity of bees, principally species of the oil-collecting genera Centris (Figure 1(a)), Epicharis (Apidae: Centridini, following the nomenclature of Michener 2007) and Monoeca (Apidae: Tapinotaspidini). However, some species lack elaiophores, or these glands can be reduced or absent in different populations of a particular species (Anderson 1979; Cappellari et al. 2011) or even show intra-individual variations (Sazima and Sazima 1989). Carvalho et al. (2005) have commented that the size of the elaiophores and the quantity of oil produced were positively correlated. On the other

[^0]

Figure 1. Stigmaphyllon bonariense. (a) Centris trigonoides female gathering oils with its fore- and mid-legs from the elaiophores (note the female grasping the base of flag petal with its mandibles and scraping the elaiophores). (b) Floral diameter (in frontal view) as proxy of size floral. (c) Schematic diagram of a flower showing flag petal (f.p.) and elaiophores in right sepal 1 (s.1) and sepal 2 (s.2). And (d) polygon drawing on perimeter of one elaiophore to calculate its area.
hand, shifts in the pollination system in which floral oil is being lost and pollen is becoming the main reward were corroborated in Pterandra pyroidea A. Juss. or presumed in Old World species of Malpighiaceae (Cappellari et al. 2011)

In Argentina, plant species diversity decreases markedly southwards with few species reaching $35^{\circ}-40^{\circ} \mathrm{S}$ and there is a large turnover associated with latitude. Similar patterns of distribution are observed in oil-collecting bees associated to Malpighiaceae (Roig Alsina 2000; Moure et al. 2007; Torretta and Roig Alsina 2016). It is conceivable that elaiophore size in plants would diminish towards higher latitudes and that there would be a difference in pollinator assemblages from north to south.

We evaluated this hypothesis in Stigmaphyllon bonariense (Hook. \& Arn.) C.E. Anderson and S. jatrophifolium A. Juss. along their latitudinal distribution in Argentina. We predicted that (a) the size of the rewarding structure (total elaiophore area per flower) varied more than the size of the attraction organs (floral size), being smaller in the southernmost populations (allometric hypothesis), and (b) oil-collecting bee assemblages would be less rich, have lower visitation rate, and/or the body size of bees would be smaller in populations closer to the southern limits of the distribution of the two plant species, compared to their northern populations.

## Materials and methods

## Species and populations studied

S. bonariense and S. jatrophifolium are woody perennial vines with yellow flowers, arranged in pseudo-umbels (2030 flowers per inflorescence, but only 2-3 synchronously opened), solitary or borne in dichasia (Múlgura de Romero 2005, see line 473). Natural populations ( $n=9$ for $S$. bonariense and $n=6$ for $S$. jatrophifolium) were selected in different sites of north-eastern Argentina (Figure 2) along a latitudinal gradient that extends across different types of vegetation belonging to diverse phytogeographic provinces, based on the classification of Cabrera (1971) for Argentina. These areas include tropical rain forests, riverine forests, lowland forests, palm groves, floodplains, public parks and other modified environments, with different richness of coflowering species of Malpighiaceae (Table 1). Sampling was carried out during four consecutive years, but not all sites were visited on each occasion (December/February 2013/2014, 2014/2015, December 2015 and December/ April 2016/2017 Table 1). Each visit consisted of $1-3$ days of floral collection and censuses of pollinators.

Fresh flowers were obtained from plants from natural populations. We collected between 10 and 50 flowers in anthesis of each studied individual $(n=2-5)$ and the fresh material was fixed in formalin-acetic acid-alcohol mixture


Figure 2. Distribution area in Argentina of the two species and the distribution of the studied populations of Stigmaphyllon bonariense (area with vertical lines and triangles) and S. jatrophifolium (grey area and circles); both species in same locality (squares). Population numbers correspond to those in Table 1.
for 48 h and stored in $70 \%$ alcohol. The reference vouchers were deposited in the herbaria of the Agronomy Faculty, Buenos Aires University and Darwinion Institute, Buenos Aires (SI).

Climate data (annual mean temperature and precipitation) were provided by the National Meteorological Service of Argentina for the period 1981-2010, except for Martín García Island (period 1961-1991). When climatic data for a particular locality were unavailable, we used information from the nearest weather station (Table 1).

## Floral size and total area of elaiophore per flower

For each population, flowers $(n=10)$ in complete anthesis were selected and observed using a stereomicroscope in the laboratory. The diameters of the flowers were measured (Figure 1(b)) to estimate floral size. Later, we counted the number of elaiophores per flower and took digital photographs with a camera incorporated in an optical microscope (in frontal view, all with same magnification to ensure that photographs were comparable) of the elaiophores from the two sepals to the
right of the flag petals of each flower (Figure 1(c)). The photographs were used to calculate the area of each elaiophore (Figure 1(d)), drawing the perimeter of each elaiophore and calculating the surface area of these polygons using the Motic Images Plus 2.0 ML software (function: Area). To estimate total area of elaiophore per flower, we summed the calculated areas and multiplied them by two to include the left-side sepals. In exceptional cases, the number of elaiophores per flower was different from eight; for these cases the total area was corrected accordingly.

## Assemblages of potential pollinators and floral visitors

We observed and captured species of oil- and pollen-collecting bees across populations on different days (2-6 days per population, except for Cerro Corá [population No. 10, in Figure 2] which was during just 1 day) and at different times of the day (between 8:00 and 19:00 h). We conducted censuses of a duration of 10 min on a known number of flowers (cumulative time $=\mathrm{ca} .30-180 \mathrm{~min}$ per population, Table 1) and we captured all floral visitors. With this data,
Table 1. Description of the study sites in Argentina.
$\left.\begin{array}{llllll}\hline & & \text { Stigmaphyllon bonariense } & \\ \hline \begin{array}{l}\text { Population: number - province - } \\ \text { locality (geoposition) }\end{array} & \text { Sampling date }\end{array} \begin{array}{c}\text { Sampling } \\ \text { effort (min) }\end{array}\right)$

[^1]we calculated the visitation rates by site for both species of Stigmaphyllon. Species that were observed to make contact with reproductive structures while foraging were recorded as legitimate pollinators (i.e., discriminating pollinators from floral visitors).

Centris and Epicharis bees are medium-sized to very large and robust (Michener 2007). The bee species captured were assigned to size groups depending on their intertegular spans (Cane 1987; medium: intertegular spans $<4 \mathrm{~mm}$; large: $4-6 \mathrm{~mm}$; and very large: $>6 \mathrm{~mm}$ ). Measurements ( $n=1-5$ individuals per species) were taken using a micrometre to the nearest 0.1 mm , under a stereomicroscope in the laboratory. For each site, we calculated the average pollinator size (APS) as APS $=\left(\mathrm{IITS}_{i} \times\right.$ number of visits $\left._{i}\right) /$ total number of visits, where ITS is intertegular spans and $i$ is each pollinator species. The richness of oil-collecting bees, flower visitation rates to both Stigmaphyllon species and APS were compared among populations.

The collected bees were deposited in the Entomological Collection of the General Botany Unit, Facultad de Agronomía, Universidad de Buenos Aires, Argentina and the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia".

## Statistical analyses

To analyse the relationship between the total area of elaiophores per flower along the latitudinal gradient (nine populations across more than 1000 km for $S$. bonariense and six populations across more than 700 km for $S$. jatrophifolium), a multiple ordinary least square regression technique was applied, considering latitude, floral size and species ( $S$. bonariense and S. jatrophifolium) as predictor variables. Across the sites studied, mean annual temperature and mean annual precipitation were both strongly and inversely associated with latitude ( $r=-0.96$ and -0.93 , respectively); therefore, we used latitude as the predictor variable. Species was included in the regression model as a dummy variable ( $S$. bonariense $=0$ and $S$. jatrophifolium $=1$ ). The best explanatory model was chosen using both $R^{2}$ adj and Akaike's information criteria (Akaike 1981). Predictor variables were checked for collinearity and residuals of the chosen model for normality and homoscedasticity. The regression analysis was carried out using the average total area of flower elaiophores in each population (identical results were obtained with the individual data - not shown). All the analyses were carried out with InfoStat (Di Rienzo et al. 2010).

To explore associations between the total area of floral elaiophores and biotic variables along the latitudinal gradient, we analysed the linear correlations between floral size, pollinator richness, visitation rate and APS using Pearson's correlation.

## Allometry

We examined the relative size relationships of total elaiophore area per flower and floral size using allometric
analyses. All size data were log-transformed, and linear regressions for each species carried out; the slopes of these regressions are unaffected by the units of measurement of different structures (Smith 1980) and are commonly used in these analyses (Niklas 1994; Ushimaru and Nakata 2001). Slopes less than 1 represent an allometric relationship in which $y$ (total elaiophore area per flower) increases more slowly than $x$ (floral size), and $y / x$ declines as $x$ increases (Fairbairn 1997) among populations.

## Results

Variations in elaiophore size along the latitudinal gradient Floral elaiophore area decreased with latitude towards the south for both $S$. bonariense and $S$. jatrophifolium) (Table 3; Figure 3; Table A1). At the same time, floral elaiophore area decreased with flower size in S. jatrophifolium, but not in $S$. bonariense (Table 3; Figure 4; Table A1). In addition, floral elaiophore area increased with pollinator richness and APS in $S$. bonariense (Table 3) but not in $S$. jatrophifolium. In turn, the flower size decreased towards higher latitude in $S$. jatrophifolium (Table 3), but not in S. bonariense (Table 3).

## Allometry

The slopes of allometric regression lines were different for both species of Stigmaphyllon (Figure 5). The slope for $S$. bonariense was $0.63(P<0.0001)$ and the slope for $S$. jatrophifolium was $1.19(P<0.0001)$.

## Assemblages of potential pollinators

In total, we recorded $24 \mathrm{~h}(16 \mathrm{~h}$ in flowers of $S$. bonariense and 8 h in $S$. jatrophifolium) of pollinator observation in the populations studied. The different populations of the two species of Stigmaphyllon were visited by 10 species of Centris and 2 species of Epicharis (legitimate pollinators); additional (non-pollinating) bee species visited the flowers that foraged for floral oil and/or pollen (Table 2). Pollinator richness and APS did not diminish with latitude - except for APS of $S$. bonariense (Table 3). Both species of Stigmaphyllon showed low visitation rates and many censuses recorded no visits at all (Table 2; Table A2). Pollinator richness positively correlated with APS and visitation rate in S. bonariense (Table 3).

## Discussion

We found a marked decrease in the total area of elaiophores per flower towards the southern end of the distribution in both species of Stigmaphyllon. Even though there have been species of Malpighiaceae reported without floral elaiophores (Anderson 1979; Cappellari et al. 2011) and/or with intra-individual variations (individuals with flowers of glandular and eglandular morph; Sazima and Sazima 1989), our results confirm for the first time, a reduction in
Table 2. Pollinators and floral visitors.

| Population: number province - locality | Number of censuses ( 10 min ) | Visitation rate |  | Average pollinator size | Insect captured |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\mathrm{X} \pm \mathrm{SD}$ | Range |  | Pollinators | Floral visitors |
| Stigmaphyllon bonariense |  |  |  |  |  |  |
| 1 - Misiones - Iguazú | 18 | $0.0026 \pm 0.0027$ | 0-0.0095 | 5.50 | 7 Centris tarsata (m), 7 C. trigonoides (m), 9 Epicharis sp. 1 <br> (vl); 5 Epicharis sp. 2 (vl) | 5 Tetrapedia spp. (o) |
| $\begin{aligned} & 2-\text { Misiones - San } \\ & \text { Ignacio } \end{aligned}$ | 15 | $0.0017 \pm 0.0016$ | 0-0.0048 | 4.02 | 8 Centris tarsata (m), 4 C. trigonoides (m), 3 C. varia (1) | 3 Paratetrapedia nigrispinis (o), $2 P$. volatilis (o), 2 Tetrapedia spp. (o) |
| $\begin{aligned} & 3 \text { - Corrientes - } \\ & \text { Corrientes } \end{aligned}$ | 15 | $0.0028 \pm 0.0018$ | 0-0.0063 | 5.29 | 1 Centris burgdorfi (1), 9 C. flavifrons (vl), 1 C. fuscata (1), 3 C. pectoralis (vl), 2 C. cf. sponsa (vl), 4 C. tarsata (m), 9 C. trigonoides (m), 2 C. varia (1), 1 Epicharis sp. 1 (vl) | 2 Tetrapedia spp. (o) |
| 4 - Corrientes - Yapeyú | 8 | $0.0029 \pm 0.0024$ | 0-0.0060 | 4.25 | 1 Centris pectoralis (vl), 2 C. fuscata (1), 4 C. trigonoides (m) | 3 Ceratina sp . (p), 1 Tetrapedia sp. (o) |
| 5 - Entre Ríos Concordia | 9 | $0.0026 \pm 0.0030$ | 0-0.0087 | 4.35 | 1 Centris flavifrons (vl), 2 C. fuscata (1), 1 C. tarsata (m), 7 C. trigonoides (m) | 5 Tetrapedia sp. (o) |
| 6 - Entre Ríos - Ibicuy | 3 | $0.0013 \pm 0.0011$ | 0-0.0023 | 4.00 | 5 Centris trigonoides (m) | 1 Xylocopa frontalis (p) |
| 7 - Buenos Aires - Zárate | 6 | $0.0015 \pm 0.0021$ | 0-0.0054 | 4.00 | 1 Centris fuscata (1), 4 C. trigonoides (m) | 1 Bombus pauloensis (p) |
| $\begin{aligned} & 8 \text { - Buenos Aires - Isla } \\ & \text { Martín García } \end{aligned}$ | 12 | $0.0025 \pm 0.0022$ | 0-0.0059 | 4.25 | 3 Centris flavifrons (vl), 5 C. tarsata (m), 1 C. tricolor (m) 7 C. trigonoides (m) | 1 Megachile sp. (p?), 6 <br> Paratetrapedia <br> nigrispinis (o), 2 <br> Tetrapedia sp. (o) |
| 9 - Ciudad Autónoma de Buenos Aires | 10 | $0.0014 \pm 0.0017$ | 0-0.0040 | 3.94 | 1 Centris fuscata (1), 7 C. trigonoides (m) | 2 Tetrapedia sp. (0) |
| Stigmaphyllon jatrophifolium |  |  |  |  |  |  |
| 1 - Misiones - Iguazú | 12 | $0.0008 \pm 0.0015$ | 0-0.0045 | 3.60 | 3 Centris trigonoides (m) |  |
| 10 - Misiones - Cerro Corá | 3 | s.d. | s.d. | s.d. |  |  |
| 11 - Misiones - Apóstoles | 5 | $0.0039 \pm 0.0036$ | 0-0.0071 | 4.41 | 2 Centris bicolor (1), 2 C. tarsata (m) | 3 Tetragonisca fiebrigi (p), 5 Trigona spinipes (p/o) |
| 4 - Corrientes - Yapeyú | 11 | $0.0015 \pm 0.0025$ | 0-0.0039 | 4.62 | 1 Centris fuscata (1), 1 C. pectoralis (vl), 4 C. tarsata (m) | 2 Ceratina sp. (p), 1 <br> Tetrapedia sp. (o) |
| $\begin{aligned} & 5 \text { - Entre Ríos - } \\ & \text { Concordia } \end{aligned}$ | 8 | $0.0035 \pm 0.0039$ | 0-0.0091 | 3.97 | 3 Centris tarsata (m), 2 C. trigonoides (m) | 1 Paratetrapedia sp. (o), <br> 2 Plebeia sp. (p), 1 <br> Tetrapedia sp. (o) |
| 12 - Entre Ríos - Colón | 7 | $0.0018 \pm 0.0025$ | 0-0.0064 | 3.60 | 5 Centris trigonoides (m) |  |

[^2] indicated; o: floral oil; p: pollen.

Table 3. Relationships between latitude, plant traits, pollinator assemblages and visitation rate in Stigmaphyllon bonariense and $S$. jatrophifolium, measured with Pearson correlation coefficient.

| Latitude | Elaiophore | Floral size | Richness | Pollinator size | Visitation rate |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Stigmaphyllon bonariense |  |  |  |  |  |
| Latitude 1 | -0.75* | -0.36 | -0.55 | -0.73 | -0.53 |
| Elaiophore | 1 | 0.45 | 0.82* | 0.81* | 0.50 |
| Floral size |  | 1 | 0.50 | 0.07 | 0.24 |
| Richness |  |  | 1 | 0.74* | 0.66* |
| Pollinator size |  |  |  | 1 | -0.66 |
| Visitation rate |  |  |  |  | 1 |
| Stigmaphyllon jatrophifolium |  |  |  |  |  |
| Latitude | -0.82* | -0.90* | 0.29 | -0.14 | 0.31 |
| Elaiophore | 1 | 0.85* | -0.13 | -0.05 | -0.01 |
| Floral size |  | 1 | -0.38 | -0.13 | -0.50 |
| Richness |  |  | 1 | 0.86 | 0.27 |
| Pollinator size |  |  |  | 1 | 0.22 |
| Visitation rate |  |  |  |  | 1 |

Note: ${ }^{*} P \leq 0.05$.


Figure 3. The relationships between elaiophore area and latitude in Stigmaphyllon bonariense (filled circles) and in S. jatrophifolium (empty circles), while flower size kept constant, are shown with the distribution of the partial residuals of the regression model.


Figure 4. The relationships between elaiophore area and flower size in Stigmaphyllon bonariense (filled circles) and in S. jatrophifolium (empty circles), while latitude kept constant, are shown with the distribution of the partial residuals of the regression model.


Figure 5. Allometric relationships between log-transformed elaiophore area and log-transformed floral size in Stigmaphyllon bonariense (filled circles; $y=1.15+0.63 x ; r^{2}=0.07 ; P=0.01 ; n=90$ ) and $S$. jatrophifolium (empty circles; $y=0.85+1.19 x ; r^{2}=0.37 ; P<0.0001$; $n=60$ ).
the size of these specialised glands in two co-generic species of Malpighiaceae along a wide range of their geographical distributions.

Our results partially support the allometric hypothesis (Prediction a). For $S$. bonariense (a species with a wider distributional range and with more populations included in this study than $S$. jatrophifolium), we observed an allometric reduction (slope of allometric line $<1$; Figure 5) in elaiophore area with respect to floral size, which did not vary across the studied populations. We also observed that for $S$. bonariense neither the pollinator richness nor the visitation rate decreases; however, we found at the same time a significant decline in the APS with latitude, where flowers have lesser elaiophores. In this species, pollinator size may principally affect the total area of floral elaiophores, due to smaller pollinators needing lower quantities of reward. Regarding the size of pollinators, Cosacov et al. (2014) have reported an inverse pattern by oil-collecting bees of C. polyrhiza. This plant species is pollinated by two pollinators: Centris cineraria (large-sized bee) in its southernmost localities and Chalepogenus caeruleus (small-sized bee) in the northernmost localities, but these oil-collecting bees occur in localities with different climatic and edaphic conditions (Cosacov et al. 2014).

We did, however, observe an isometric reduction in the total area of floral elaiophores in S. jatrophifolium (slope of allometric line $>1$; Figure 5). In this species, it appears that floral size is related to climatic conditions, as has been reported for other species (Olsson and Ågren 2002; Herrera 2005; Cosacov et al. 2012). Herrera (2005) has shown that the flowers of Rosmarinus officinalis L. decreased in mass (and corolla size) as the habitat became drier and hotter from mountain to coast. A similar pattern of intraspecific variability was exhibited by Polemonium viscosum Nutt. along a gradient of increasing aridity (Galen et al. 1987). Some floral traits involved in plantpollinator interactions, particularly those related to attraction and floral reward, in general demand large amounts of
water and nutrients (Galen 1999). Possibly, this climatic influence could also explain why this species does not reach higher latitudes. Our studied southernmost sites (numbers 6-9 in Figure 2) showed lesser annual mean temperature and precipitation (see Table 1) than other studied sites; moreover, the winter conditions of these sites are colder and with more days with frost (data not shown; National Meteorological Service of Argentina).

The richness of oil-collecting bee species associated with Malpighiaceae decreases markedly from north to south in Argentina (Roig Alsina 2000; Moure et al. 2007; Torretta and Roig Alsina 2016); however, contrary to our expectations (Prediction b), the richness, visitation rates and APS (except for $S$. bonariense) of the captured species of Centris and/or Epicharis did not exhibit differences across the distribution range studied, in either species of Stigmaphyllon.

This fact could be explained by two non-mutually exclusive interpretations: differences in the probability of observing/capturing pollinators and differences in the dependence of oil-collecting bees in Malpighiaceae species among populations. Vegetation types in the northern sites were more complex (e.g., complex structure of vegetation, high species diversity of plants), therefore observing flowering plants in the canopy and capturing bees foraging on these flowers was more difficult and this might have influenced observation/ capture rates. It is known that some species of Centris show preferences for certain strata in multilayered vegetation (Frankie and Coville 1979) while other bee species do not (Roubik et al. 1982; Roubik 1993). On the other hand, as the species richness of Malpighiaceae decreases from north to south in Argentina, the dependence of oil-collecting bees on Malpighiaceae species among the sampled sites was different. In the northern sites, species of oil-collecting bees can visit a higher number of Malpighiaceae species. Different Centris and Epicharis species were observed interacting with flowers of the same Malpighiaceae species and the same species of bees were seen collecting floral oil on
different species of Malpighiaceae (authors' pers. obs., data not reported, Vogel 1974; Giannini et al. 2013). Thus, the oil-collecting bees exhibit a high dependence on Malpighiaceae species at the populations closer to the southern limits compared to the northern populations, due to the lesser number of oil-rewarding species available for these bees.

## Conclusions

This study examined variations in the size of a specialised floral rewarding structure in two sympatric species of Stigmaphyllon, and although the total area of floral elaiophores decreased with latitude, we did not find a clear pattern that would apply to both plant species. Possibly, these species of Stigmaphyllon have different selection pressures on the variation of their phenotypic traits associated to their pollination. In $S$. bonariense, the pollinator size appears to be related in the total size of the specialised glands while in $S$. jatrophifolium climatic conditions seem to be more strongly related to total elaiophore size.

## Acknowledgements

We thank H.J. Marrero and L. Álvarez for their help with fieldwork, N. Gomiz for her work in the laboratory and for the Figure 1(c), A. Roig Alsina and L. Alvarez (Meliponini) for collaboration in the determination of bees, A. Torretta, R. Saurral and M. Zietsman for helping with the English revision and R. Saurral for providing the meteorological information. To the Administración de Parque Nacionales (Regional NEA) Ministerio de Ecología y Recursos Naturales Renovables, province of Misiones, Dirección de Áreas Naturales Protegidas, Organismo Provincial para el Desarrollo Sostenible, province of Buenos Aires, for permission to conduct part of this study in protected areas. The manuscript benefited from critical reading by M. Mendez, L. Nagy and one anonymous reviewer.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

Field work was supported by CONICET [grant number: PIP11220110100312]; ANPCyT [grant number: PICT 2013-1867] and UBA [grant number: UBACyT20020130200203BA] Argentina. JPT, SSA, AGA and AAA are affiliated with CONICET.

## Notes on contributors

Juan P. Torretta is an adjunct research scientist. His research focuses on flower-pollinator relationships with emphasis on ecology and conservation of wild native bees.
Sandra S. Alisiconi is an independent research scientist. She is interested in leaf and flower anatomy from taxonomical, phylogenetic and functional approaches.

Adelia González-Arzac is a postdoctoral student. She is interested in soil ecology, particularly in the role of soil fauna on carbon recycling.

Adan A. Avalos is a Ph.D. student, working on the reproductive biology, embryology and floral anatomy of Malpighiaceae.

## References

Akaike H. 1981. Likelihood of a model and information criteria. Journal of Econometrics 16:3-14.
Anderson WR. 1979. Floral conservatism in Neotropical Malpighiaceae. Biotropica 11:219-223.
Barrett SCH, Harder LD, Cole WW. 2004. Correlated evolution of floral morphology and mating-type frequencies in a sexually polymorphic plant. Evolution 58:964-975.
Cabrera AL. 1971. Fitogeografía de la República Argentina. Boletín De La Sociedad Argentina De Botánica 14:1-42.
Cane JH. 1987. Estimation of bee size using intertegular span (Apoidea). Journal of the Kansas Entomological Society 60:145-147.
Cappellari SC, Haleem MA, Marsaioli A, Tidon R, Simpson BB. 2011. Pterandra pyroidea: a case of pollination shift within Neotropical Malpighiaceae. Annals of Botany 107:1323-1334.
Carvalho PD, Borba EL, Lucchese AM. 2005. Variação no número de glândulas e produção de óleoemflores de Stigmaphyllon paralias A. Juss. (Malpighiaceae). Acta Botanica Brasilica 19:209-214.
Cohen D, Shmida A. 1993. The evolution of flower display and reward. Evolutionary Biology 27:197-243.
Cosacov A, Cocucci AA, Sérsic AN. 2012. Variación geográfica de la recompensa floral de Calceolaria polyrhiza (Calceolariaceae): influencia de factores bióticos y abióticos. Boletín De La Sociedad Argentina De Botánica 47:363-373.
Cosacov A, Cocucci AA, Sérsic AN. 2014. Geographical differentiation in floral traits along the distribution range of the Patagonian oil-secreting Calceolaria polyrhiza: do pollinators matter? Annals of Botany 113:251-266.
Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M. 2010. InfoStat, versión 2010. Argentina: GrupoInfoStat, FCA, Universidad Nacional de Córdoba.
Fairbairn DJ. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28:659-687.
Frankie GW, Coville R. 1979. An experimental study on the foraging behavior of selected solitary bee species in the Costa Rican dry forest (Hymenoptera: Apoidea). Journal of the Kansas Entomological Society 52:591-602.
Galen C. 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. Bioscience 49:631-640.
Galen C, Zimmer KA, Newport ME. 1987. Pollination in floral scent morphs of Polemonium viscosum: a mechanism for disruptive selection on flower size. Evolution 41:599-606.
Giannini TC, Pinto CE, Acosta AL, Taniguchi M, Saraiva AM, Alves-dos-Santos I. 2013. Interactions at large spatial scale: the case of Centris bees and floral oil producing plants in South America. Ecological Modelling 258:74-81.
Herrera CM, Castellanos MC, Medrano M. 2006. Geographical context of floral evolution: towards an improved research programme in floral diversification. In: Harder LD, Barrett SCH, editors. Ecology and evolution of flowers. Oxford: Oxford University Press. p. 278-294.
Herrera J. 2005. Flower size variation in Rosmarinus officinalis: individuals, populations and habitats. Annals of Botany 95:431-437.
Hodgins KA, Barrett SCH. 2008. Geographic variation in floral morphology and style-morph ratios in a sexually polymorphic daffodil. American Journal of Botany 95:185-195.

Mello MA, Bezerra EL, Machado IC. 2013. Functional roles of Centridini oil bees and Malpighiaceae oil flowers in biomewide pollination networks. Biotropica 45:45-53.
Michener CD. 2007. The bees of the world. 2nd ed. Baltimore: Johns Hopkins.
Moure JS, Melo GAR, Vivallo F. 2007. Centridini Cockerell \& Cockerell, 1901. In: Moure JS, Urban D, Melo GAR, editors. Catalogue of bees (Hymenoptera, Apoidea) in the neotropical region. Curitiba: Sociedade Brasileira de Entomologia. p. 83-142.
Múlgura de Romero ME. 2005. Malpighiaceae. In: Burkart AE, Bacigalupo NM, editors. Flora Ilustrada de Entre Ríos (Argentina): dicotiledóneas arquiclamídeas. Geraniales a Umbeliflorales. Buenos Aires: Instituto Nacional de Tecnología Agropecuaria, Secretaría de Agricultura, Ganadería, Pesca y Alimentos. p. 71-86.
Niklas KJ. 1994. Plant allometry: the scaling of form and process. London: University of Chicago Press.
Olsson K, Ågren J. 2002. Latitudinal population differentiation in phenology, life history and flower morphology in the perennial herb Lythrum salicaria. Journal of Evolutionary Biology 15:983-996.
Roig Alsina A. 2000. Claves para las especies argentinas de Centris (Hymenoptera, Apidae), con descripción de nuevas especies y notas sobre distribución. Revista Del Museo Argentino De Ciencias Naturales, N.S 2:171193.

Roubik DW. 1993. Tropical pollinators in the canopy and understory: field data and theory for stratum "preferences". Journal of Insect Behavior 6:659-673.
Roubik DW, Ackerman JD, Copenhaver C, Smith BH. 1982. Stratum, tree, and flower selection by tropical bees: implications for the reproductive biology of outcrossing Cochlospermum vitifolium in Panama. Ecology 63:712-720.
Sazima M, Sazima I. 1989. Oil-gathering bees visit flowers of eglandular morphs of the oil-producing Malpighiaceae. Botanica Acta 102:106-111.
Smith RJ. 1980. Rethinking allometry. Journal of Theoretical Biology 87:97-111
Thompson JN. 2005. The geographic mosaic of coevolution. Chicago: University Chicago Press.
Torretta JP, Roig Alsina A. 2016. First report of Monoeca Lepeletier \& Serville in Argentina, with description of two new species (Hymenoptera: apidae). Journal of Melittology 59:1-12.
Ushimaru A, Nakata K. 2001. Evolution of flower allometry and its significance for pollination success in the deceptive orchid Pogonia japonica. International Journal of Plant Sciences 162:1307-1311.
Vinson SB, Frankie GW, Williams HJ. 1996. Chemical ecology of bees of the genus Centris (Hymenoptera: Apidae). Florida Entomologist 79:109-129.
Vogel S. 1974. Ölblumen und ölsammelndeBienen. Tropische Und Subtropische Pflanzenwelt 7:1-267.

## Appendix

Table A1. Data for floral size, total area of elaiophores for Stigmaphyllon bonariense and S. jatrophifolium in studied sites.

| Species | Population |  | Latitude | Floral size |  | No. of elaiophores | Total area elaiophore |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  | (cm) | $\log$ |  | ( $\mathrm{mm}^{2}$ ) | $\log$ |
| S. bonariense | 1 | Iguazú | 25.68 | 25 | 0.398 | 8 | 30.89 | 1.490 |
| S. bonariense | 1 | Iguazú | 25.68 | 26 | 0.415 | 8 | 29.65 | 1.472 |
| S. bonariense | 1 | Iguazú | 25.68 | 28 | 0.447 | 8 | 30.91 | 1.490 |
| S. bonariense | 1 | Iguazú | 25.68 | 25 | 0.398 | 8 | 30.84 | 1.489 |
| S. bonariense | 1 | Iguazú | 25.68 | 25 | 0.398 | 8 | 32.84 | 1.516 |
| S. bonariense | 1 | Iguazú | 25.68 | 2.6 | 0.415 | 8 | 26.10 | 1.417 |
| S. bonariense | 1 | Iguazú | 25.68 | 24 | 0.380 | 8 | 2746 | 1.439 |
| S. bonariense | 1 | Iguazú | 25.68 | 27 | 0.431 | 8 | 31.19 | 1.494 |
| S. bonariense | 1 | Iguazú | 25.68 | 24 | 0.380 | 8 | 31.76 | 1.502 |
| S. bonariense | 1 | Iguazú | 25.68 | 27 | 0.431 | 8 | 34.40 | 1.537 |
| S. bonariense | 2 | San Ignacio | 27.3 | 3 | 0.477 | 8 | 27.83 | 1.444 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.7 | 0.431 | 8 | 28.46 | 1.454 |
| S. bonariense | 2 | San Ignacio | 27.3 | 3.1 | 0.491 | 8 | 27.83 | 1.444 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.7 | 0.431 | 8 | 28.56 | 1.454 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.7 | 0.431 | 8 | 32.56 | 1.513 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.7 | 0.431 | 8 | 23.83 | 1.358 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.9 | 0.462 | 8 | 31.05 | 1.492 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.8 | 0.447 | 8 | 32.56 | 1.513 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.7 | 0.431 | 8 | 22.33 | 1.358 |
| S. bonariense | 2 | San Ignacio | 27.3 | 2.9 | 0.462 | 8 | 30.55 | 1.492 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.7 | 0.431 | 8 | 24.37 | 1.387 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.5 | 0.398 | 8 | 35.05 | 1.545 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.8 | 0.447 | 8 | 34.26 | 1.535 |
| S. bonariense | 3 | Corrientes | 27.42 | 3 | 0.477 | 8 | 34.03 | 1.532 |
| S. bonariense | 3 | Corrientes | 27.42 | 3.1 | 0.491 | 8 | 35.20 | 1.547 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.9 | 0.462 | 8 | 37.63 | 1.576 |
| S. bonariense | 3 | Corrientes | 27.42 | 3.2 | 0.505 | 8 | 35.12 | 1.546 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.9 | 0.462 | 8 | 37.03 | 1.569 |
| S. bonariense | 3 | Corrientes | 27.42 | 2.8 | 0.447 | 8 | 36.76 | 1.565 |
| S. bonariense | 3 | Corrientes | 27.42 | 3 | 0.477 | 8 | 38.23 | 1.582 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.7 | 0.431 | 8 | 27.08 | 1.433 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.8 | 0.447 | 8 | 29.08 | 1.464 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.7 | 0.431 | 8 | 24.32 | 1.386 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.9 | 0.462 | 8 | 23.60 | 1.373 |
| S. bonariense | 4 | Yapeyú | 29.47 | 3 | 0.477 | 8 | 24.98 | 1.398 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.7 | 0.431 | 8 | 22.82 | 1.358 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.8 | 0.447 | 8 | 23.18 | 1.365 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.7 | 0.431 | 8 | 24.48 | 1.389 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.9 | 0.462 | 8 | 20.35 | 1.309 |
| S. bonariense | 4 | Yapeyú | 29.47 | 2.7 | 0.431 | 8 | 24.48 | 1.389 |
| S. bonariense | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 26.02 | 1.415 |
| S. bonariense | 5 | Concordia | 31.37 | 2.6 | 0.415 | 8 | 25.65 | 1.409 |
| S. bonariense | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 27.85 | 1.445 |
| S. bonariense | 5 | Concordia | 31.37 | 2.6 | 0.415 | 8 | 28.15 | 1.449 |
| S. bonariense | 5 | Concordia | 31.37 | 2.7 | 0.431 | 8 | 28.30 | 1.452 |
| S. bonariense | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 23.48 | 1.371 |
| S. bonariense | 5 | Concordia | 31.37 | 2.6 | 0.415 | 8 | 30.41 | 1.483 |
| S. bonariense | 5 | Concordia | 31.37 | 2.8 | 0.447 | 8 | 28.33 | 1.452 |
| S. bonariense | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 29.57 | 1.471 |
| S. bonariense | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 24.46 | 1.389 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.4 | 0.380 | 8 | 29.50 | 1.470 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.9 | 0.462 | 8 | 25.88 | 1.413 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.7 | 0.431 | 8 | 23.70 | 1.375 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.5 | 0.398 | 8 | 26.51 | 1.423 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.6 | 0.415 | 8 | 25.08 | 1.399 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.6 | 0.415 | 8 | 28.83 | 1.460 |
| S. bonariense | 6 | Ibicuy | 33.85 | 3 | 0.477 | 8 | 27.54 | 1.440 |
| S. bonariense | 6 | Ibicuy | 33.85 | 3 | 0.477 | 8 | 29.58 | 1.471 |

Table A1. (Continued).

| Species | Population |  | Latitude | Floral size |  | No. of elaiophores | Total area elaiophore |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  | (cm) | $\log$ |  | ( $\mathrm{mm}^{2}$ ) | $\log$ |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.7 | 0.431 | 8 | 23.66 | 1.374 |
| S. bonariense | 6 | Ibicuy | 33.85 | 2.6 | 0.415 | 8 | 26.98 | 1.431 |
| S. bonariense | 7 | Zárate | 34.08 | 2.5 | 0.398 | 8 | 27.49 | 1.439 |
| S. bonariense | 7 | Zárate | 34.08 | 2.6 | 0.415 | 8 | 24.36 | 1.387 |
| S. bonariense | 7 | Zárate | 34.08 | 2.4 | 0.380 | 8 | 20.04 | 1.302 |
| S. bonariense | 7 | Zárate | 34.08 | 2.8 | 0.447 | 8 | 24.61 | 1.391 |
| S. bonariense | 7 | Zárate | 34.08 | 2.6 | 0.415 | 8 | 22.65 | 1.355 |
| S. bonariense | 7 | Zárate | 34.08 | 2.6 | 0.415 | 8 | 23.27 | 1.367 |
| S. bonariense | 7 | Zárate | 34.08 | 2.8 | 0.447 | 8 | 24.23 | 1.384 |
| S. bonariense | 7 | Zárate | 34.08 | 2.8 | 0.447 | 8 | 24.55 | 1.390 |
| S. bonariense | 7 | Zárate | 34.08 | 2.5 | 0.398 | 8 | 21.92 | 1.341 |
| S. bonariense | 7 | Zárate | 34.08 | 3 | 0.477 | 8 | 22.72 | 1.356 |
| S. bonariense | 8 | M. García | 34.16 | 2.4 | 0.380 | 6 | 28.73 | 1.458 |
| S. bonariense | 8 | M. García | 34.16 | 2.9 | 0.462 | 8 | 25.80 | 1.412 |
| S. bonariense | 8 | M. García | 34.16 | 2.7 | 0.431 | 8 | 25.00 | 1.398 |
| S. bonariense | 8 | M. García | 34.16 | 2.5 | 0.398 | 8 | 27.57 | 1.440 |
| S. bonariense | 8 | M. García | 34.16 | 2.6 | 0.415 | 8 | 24.68 | 1.392 |
| S. bonariense | 8 | M. García | 34.16 | 2.6 | 0.415 | 8 | 26.52 | 1.424 |
| S. bonariense | 8 | M. García | 34.16 | 3 | 0.477 | 8 | 25.30 | 1.403 |
| S. bonariense | 8 | M. García | 34.16 | 3 | 0.477 | 8 | 31.54 | 1.499 |
| S. bonariense | 8 | M. García | 34.16 | 2.7 | 0.431 | 6 | 18.44 | 1.266 |
| S. bonariense | 8 | M. García | 34.16 | 2.6 | 0.415 | 8 | 24.91 | 1.396 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.5 | 0.398 | 8 | 27.90 | 1.446 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.5 | 0.398 | 8 | 26.64 | 1.426 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.8 | 0.447 | 8 | 25.95 | 1.414 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.4 | 0.380 | 10 | 21.60 | 1.334 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.8 | 0.447 | 9 | 18.17 | 1.259 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.8 | 0.447 | 8 | 25.88 | 1.413 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.6 | 0.415 | 8 | 21.93 | 1.341 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.5 | 0.398 | 8 | 21.42 | 1.331 |
| S. bonariense | 9 | CABA | 34.58 | 2.3 | 0.362 | 8 | 16.83 | 1.226 |
| S. bonariense | 9 | C.A.B.A. | 34.58 | 2.7 | 0.431 | 9 | 23.66 | 1.374 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 3 | 0.477 | 8 | 28.37 | 1.453 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 24.11 | 1.382 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 22.38 | 1.350 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 26.15 | 1.417 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.7 | 0.431 | 8 | 25.29 | 1.403 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 24.11 | 1.382 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 26.15 | 1.417 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.7 | 0.431 | 8 | 25.29 | 1.403 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 2.8 | 0.447 | 8 | 22.38 | 1.350 |
| S. jatrophifolium | 1 | Iguazú | 25.68 | 3 | 0.477 | 8 | 28.37 | 1.453 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.5 | 0.398 | 8 | 23.19 | 1.365 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.6 | 0.415 | 8 | 23.85 | 1.377 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.7 | 0.431 | 8 | 25.41 | 1.405 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.8 | 0.447 | 8 | 19.36 | 1.287 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.5 | 0.398 | 8 | 18.71 | 1.272 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.6 | 0.415 | 8 | 18.08 | 1.257 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.5 | 0.398 | 8 | 23.16 | 1.365 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.7 | 0.431 | 8 | 20.15 | 1.304 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.6 | 0.415 | 8 | 25.17 | 1.401 |
| S. jatrophifolium | 10 | Cerro Corá | 27.48 | 2.7 | 0.431 | 8 | 20.33 | 1.308 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.5 | 0.398 | 8 | 22.06 | 1.344 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.2 | 0.342 | 8 | 21.72 | 1.337 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.4 | 0.380 | 8 | 21.92 | 1.341 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2 | 0.301 | 8 | 21.71 | 1.337 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.5 | 0.398 | 8 | 21.13 | 1.325 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.5 | 0.398 | 8 | 21.25 | 1.327 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.5 | 0.398 | 7 | 23.24 | 1.366 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.5 | 0.398 | 8 | 22.94 | 1.361 |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2.2 | 0.342 | 8 | 18.55 | 1.268 |

(Continued)

Table A1. (Continued).

| Species | Population |  | Latitude | Floral size |  | No. of elaiophores | Total area elaiophore |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  | (cm) | $\log$ |  | $\left(\mathrm{mm}^{2}\right)$ | $\log$ |
| S. jatrophifolium | 11 | Apóstoles | 28 | 2 | 0.301 | 8 | 22.21 | 1.347 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.2 | 0.342 | 7 | 18.32 | 1.263 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.3 | 0.362 | 8 | 18.31 | 1.263 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.8 | 0.447 | 8 | 21.45 | 1.331 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.5 | 0.398 | 8 | 21.26 | 1.328 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.4 | 0.380 | 7 | 18.19 | 1.260 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.5 | 0.398 | 8 | 21.60 | 1.334 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.3 | 0.362 | 8 | 16.32 | 1.213 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.3 | 0.362 | 8 | 21.21 | 1.327 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.3 | 0.362 | 8 | 19.40 | 1.288 |
| S. jatrophifolium | 4 | Yapeyú | 29.47 | 2.4 | 0.380 | 8 | 17.76 | 1.250 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.4 | 0.380 | 8 | 21.38 | 1.330 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.3 | 0.362 | 8 | 25.46 | 1.406 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.2 | 0.342 | 8 | 25.66 | 1.409 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.2 | 0.342 | 8 | 20.95 | 1.321 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.4 | 0.380 | 8 | 22.81 | 1.358 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.2 | 0.342 | 8 | 25.03 | 1.399 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.3 | 0.362 | 8 | 15.10 | 1.179 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2 | 0.301 | 8 | 15.26 | 1.183 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.7 | 0.431 | 8 | 21.65 | 1.336 |
| S. jatrophifolium | 5 | Concordia | 31.37 | 2.5 | 0.398 | 8 | 21.61 | 1.335 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2.2 | 0.342 | 8 | 16.73 | 1.223 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2.2 | 0.342 | 8 | 13.12 | 1.118 |
| S. jatrophifolium | 12 | Colón | 32.13 | 1.9 | 0.279 | 8 | 10.06 | 1.003 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2.4 | 0.380 | 8 | 18.70 | 1.272 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2.3 | 0.362 | 8 | 17.53 | 1.244 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2 | 0.301 | 8 | 17.72 | 1.249 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2 | 0.301 | 8 | 11.23 | 1.050 |
| S. jatrophifolium | 12 | Colón | 32.13 | 1.9 | 0.279 | 8 | 10.72 | 1.030 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2 | 0.301 | 8 | 12.78 | 1.107 |
| S. jatrophifolium | 12 | Colón | 32.13 | 2.1 | 0.322 | 8 | 19.84 | 1.298 |

Note: Population numbers correspond to those in Table 1.

Table A2. Data about visitation rate for Stigmaphyllon bonariense and S.jatrophifolium in studied sites.

| Species | Population |  | Date | Observed flowers | Observed time | No. of legitimate visit | Visitation rate |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  |  |  |  |  |
| S. bonariense | 1 | Iguazú | 28 November 2015 | 21 | 10 | 2 | 0.0095 |
| S. bonariense | 1 | Iguazú | 28 November 2015 | 17 | 10 | 0 | 0.0000 |
| S. bonariense | 1 | Iguazú | 28 November 2015 | 19 | 10 | 1 | 0.0053 |
| S. bonariense | 1 | Iguazú | 29 November 2015 | 125 | 10 | 1 | 0.0008 |
| S. bonariense | 1 | Iguazú | 29 November 2015 | 78 | 10 | 1 | 0.0008 |
| S. bonariense | 1 | Iguazú | 29 November 2015 | 58 | 10 | 0 | 0.0000 |
| S. bonariense | 1 | Iguazú | 03 December 2014 | 71 | 10 | 2 | 0.0028 |
| S. bonariense | 1 | Iguazú | 03 December 2014 | 29 | 10 | 2 | 0.0069 |
| S. bonariense | 1 | Iguazú | 04 December 2014 | 56 | 10 | 0 | 0.0000 |
| S. bonariense | 1 | Iguazú | 04 December 2014 | 34 | 10 | 1 | 0.0029 |
| S. bonariense | 1 | Iguazú | 04 December 2014 | 59 | 10 | 3 | 0.0051 |
| S. bonariense | 1 | Iguazú | 05 December 2014 | 122 | 10 | 1 | 0.0008 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 132 | 10 | 4 | 0.0030 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 119 | 10 | 5 | 0.0042 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 119 | 10 | 3 | 0.0025 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 119 | 10 | 2 | 0.0017 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 145 | 10 | 0 | 0.0000 |
| S. bonariense | 1 | Iguazú | 03 March 2017 | 122 | 10 | 0 | 0.0000 |
| S. bonariense | 2 | San Ignacio | 02 December 2014 | 44 | 10 | 1 | 0.0023 |
| S. bonariense | 2 | San Ignacio | 02 December 2014 | 21 | 10 | 1 | 0.0048 |
| S. bonariense | 2 | San Ignacio | 06 December 2014 | 88 | 10 |  | 0.0034 |
| S. bonariense | 2 | San Ignacio | 02 December 2014 | 54 | 10 | 2 | 0.0037 |
| S. bonariense | 2 | San Ignacio | 02 December 2014 | 38 | 10 | 1 | 0.0026 |
| S. bonariense | 2 | San Ignacio | 02 December 2014 | 79 | 10 | 1 | 0.0013 |
| S. bonariense | 2 | San Ignacio | 08 December 2015 | 34 | 10 | , | 0.0000 |
| S. bonariense | 2 | San Ignacio | 08 December 2015 | 55 | 10 | 0 | 0.0000 |
| S. bonariense | 2 | San Ignacio | 08 December 2015 | 44 | 10 | 1 | 0.0023 |
| S. bonariense | 2 | San Ignacio | 08 December 2015 | 59 | 10 | 2 | 0.0034 |
| S. bonariense | 2 | San Ignacio | 09 December 2015 | 111 | 10 | 3 | 0.0027 |
| S. bonariense | 2 | San Ignacio | 09 December 2015 | 91 | 10 | 0 | 0.0000 |
| S. bonariense | 2 | San Ignacio | 26 January 2017 | 25 | 10 | 0 | 0.0000 |
| S. bonariense | 2 | San Ignacio | 26 January 2017 | 35 | 10 | 0 | 0.0000 |
| S. bonariense | 2 | San Ignacio | 26 January 2017 | 40 | 10 | 0 | 0.0000 |
| S. bonariense | 3 | Corrientes | 15 December 2015 | 73 | 10 | 3 | 0.0041 |
| S. bonariense | 3 | Corrientes | 15 December 2015 | 61 | 10 | 2 | 0.0033 |
| S. bonariense | 3 | Corrientes | 15 December 2015 | 31 | 10 | 1 | 0.0032 |
| S. bonariense | 3 | Corrientes | 15 December 2015 | 45 | 10 | 1 | 0.0022 |
| S. bonariense | 3 | Corrientes | 16 December 2015 | 65 | 10 | 3 | 0.0046 |
| S. bonariense | 3 | Corrientes | 16 December 2015 | 48 | 10 | 3 | 0.0063 |
| S. bonariense | 3 | Corrientes | 16 December 2015 | 24 | 10 | 0 | 0.0000 |
| S. bonariense | 3 | Corrientes | 17 December 2015 | 62 | 10 | 2 | 0.0032 |
| S. bonariense | 3 | Corrientes | 17 December 2015 | 39 | 10 | 0 | 0.0000 |
| S. bonariense | 3 | Corrientes | 05 February 2017 | 68 | 10 | 2 | 0.0029 |
| S. bonariense | 3 | Corrientes | 05 February 2017 | 92 | 10 | 4 | 0.0043 |
| S. bonariense | 3 | Corrientes | 08 April 2017 | 145 | 10 | 4 | 0.0028 |
| S. bonariense | 3 | Corrientes | 08 April 2017 | 184 | 10 | 3 | 0.0016 |
| S. bonariense | 3 | Corrientes | 08 April 2017 | 97 | 10 | 4 | 0.0041 |
| S. bonariense | 3 | Corrientes | 08 April 2017 | 74 | 10 | 0 | 0.0000 |
| S. bonariense | 4 | Yapeyú | 03 December 2013 | 17 | 10 | 1 | 0.0059 |
| S. bonariense | 4 | Yapeyú | 03 December 2013 | 25 | 10 | 1 | 0.0040 |
| S. bonariense | 4 | Yapeyú | 03 December 2013 | 47 | 10 | , | 0.0021 |
| S. bonariense | , | Yapeyú | 26 December 2013 | 67 | 10 | 1 | 0.0015 |
| S. bonariense | 4 | Yapeyú | 30 November 2014 | 41 | 10 | 0 | 0.0000 |
| S. bonariense | , | Yapeyú | 01 December 2014 | 28 | 10 | 1 | 0.0036 |
| S. bonariense | 4 | Yapeyú | 01 December 2014 | 33 | 10 | 2 | 0.0061 |
| S. bonariense | 4 | Yapeyú | 30 November 2014 | 41 | 10 | 0 | 0.0000 |
| S. bonariense | 5 | Concordia | 03 December 2014 | 23 | 10 | 2 | 0.0087 |
| S. bonariense | 5 | Concordia | 04 December 2014 | 84 | 10 | 3 | 0.0036 |
| S. bonariense | 5 | Concordia | 04 December 2014 | 67 | 10 | 2 | 0.0030 |
| S. bonariense | 5 | Concordia | 04 December 2014 | 53 | 10 | 0 | 0.0000 |
| S. bonariense | 5 | Concordia | 05 December 2014 | 52 | 10 | 3 | 0.0058 |

Table A2. (Continued).

| Species | Population |  | Date | Observed flowers | Observed time | No. of legitimate visit | Visitation rate |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  |  |  |  |  |
| S. bonariense | 5 | Concordia | 05 December 2014 | 65 | 10 | 0 | 0.0000 |
| S. bonariense | 5 | Concordia | 19 January 2017 | 52 | 10 | 0 | 0.0000 |
| S. bonariense | 5 | Concordia | 19 January 2017 | 35 | 10 | 0 | 0.0000 |
| S. bonariense | 5 | Concordia | 19 January 2017 | 48 | 10 | 1 | 0.0021 |
| S. bonariense | 6 | Ibicuy | 09 December 2012 | 25 | 10 | 0 | 0.0000 |
| S. bonariense | 6 | Ibicuy | 09 December 2012 | 124 | 10 | 2 | 0.0016 |
| S. bonariense | 6 | Ibicuy | 21 December 2013 | 131 | 10 | 3 | 0.0023 |
| S. bonariense | 7 | Zárate | 10 December 2014 | 55 | 10 | 3 | 0.0055 |
| S. bonariense | 7 | Zárate | 10 December 2014 | 41 | 10 | 1 | 0.0024 |
| S. bonariense | 7 | Zárate | 10 December 2014 | 38 | 10 | 0 | 0.0000 |
| S. bonariense | 7 | Zárate | 11 December 2014 | 29 | 10 | 0 | 0.0000 |
| S. bonariense | 7 | Zárate | 11 December 2014 | 71 | 10 | 1 | 0.0014 |
| S. bonariense | 7 | Zárate | 11 December 2014 | 53 | 10 | 0 | 0.0000 |
| S. bonariense | 8 | M. García | 14 February 2014 | 41 | 10 | 2 | 0.0049 |
| S. bonariense | 8 | M. García | 14 February 2014 | 19 | 10 | 0 | 0.0000 |
| S. bonariense | 8 | M. García | 14 February 2014 | 77 | 10 | 3 | 0.0039 |
| S. bonariense | 8 | M. García | 14 February 2014 | 81 | 10 | 4 | 0.0049 |
| S. bonariense | 8 | M. García | 27 February 2014 | 44 | 10 | 0 | 0.0000 |
| S. bonariense | 8 | M. García | 27 February 2014 | 49 | 10 | 1 | 0.0020 |
| S. bonariense | 8 | M. García | 16 December 2014 | 34 | 10 | 2 | 0.0059 |
| S. bonariense | 8 | M. García | 16 December 2014 | 21 | 10 | 0 | 0.0000 |
| S. bonariense | 8 | M. García | 17 December 2014 | 51 | 10 | 1 | 0.0020 |
| S. bonariense | 8 | M. García | 17 December 2014 | 33 | 10 | 1 | 0.0030 |
| S. bonariense | 8 | M. García | 28 December 2016 | 51 | 10 | 2 | 0.0039 |
| S. bonariense | 8 | M. García | 28 December 2016 | 23 | 10 | 0 | 0.0000 |
| S. bonariense | 9 | Caba | 12 February 2014 | 58 | 10 | 2 | 0.0034 |
| S. bonariense | 9 | Caba | 12 February 2014 | 124 | 10 | 0 | 0.0000 |
| S. bonariense | 9 | Caba | 15 February 2014 | 78 | 10 | 1 | 0.0013 |
| S. bonariense | 9 | Caba | 15 February 2014 | 69 | 10 | 0 | 0.0000 |
| S. bonariense | 9 | Caba | 28 December 2014 | 75 | 10 | 3 | 0.0040 |
| S. bonariense | 9 | Caba | 29 December 2014 | 48 | 10 | 1 | 0.0021 |
| S. bonariense | 9 | Caba | 29 December 2014 | 55 | 10 | 0 | 0.0000 |
| S. bonariense | 9 | Caba | 30 December 2014 | 29 | 10 | 1 | 0.0034 |
| S. bonariense | 9 | Caba | 18 December 2016 | 19 | 10 | 0 | 0.0000 |
| S. bonariense | 9 | Caba | 20 December 2016 | 29 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 04 December 2014 | 25 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 04 December 2014 | 31 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 04 December 2014 | 36 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 05 December 2014 | 44 | 10 | 1 | 0.0023 |
| S. jatrophifolium | 1 | Iguazú | 05 December 2014 | 28 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 05 December 2014 | 17 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 30 November 2015 | 22 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 30 November 2015 | 25 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 1 | Iguazú | 30 November 2015 | 44 | 10 | 1 | 0.0023 |
| S. jatrophifolium | 1 | Iguazú | 01 December 2015 | 22 | 10 | 1 | 0.0045 |
| S. jatrophifolium |  | Iguazú | 01 December 2015 | 19 | 10 | 0 | 0.0000 |
| S. jatrophifolium |  | Iguazú | 01 December 2015 | 34 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 10 | Cerro Corá | 04 December 2014 | 22 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 10 | Cerro Corá | 04 December 2014 | 19 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 10 | Cerro Corá | 04 December 2014 | 31 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 11 | Apóstoles | 08 December 2013 | 18 | 10 | 1 | 0.0056 |
| S. jatrophifolium | 11 | Apóstoles | 08 December 2013 | 14 | 10 | 1 | 0.0071 |
| S. jatrophifolium | 11 | Apóstoles | 09 December 2013 | 29 | 10 | 2 | 0.0069 |
| S. jatrophifolium | 11 | Apóstoles | 09 December 2013 | 38 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 11 | Apóstoles | 09 December 2013 | 31 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 4 | Yapeyú | 03 December 2012 | 92 | 30 | 1 | 0.0004 |
| S. jatrophifolium | 4 | Yapeyú | 03 December 2012 | 105 | 10 | 1 | 0.0010 |
| S. jatrophifolium | 4 | Yapeyú | 26 February 2013 | 117 | 10 | 1 | 0.0009 |
| S. jatrophifolium | 4 | Yapeyú | 26 February 2013 | 25 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 4 | Yapeyú | 20 December 2013 | 18 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 4 | Yapeyú | 30 November 2014 | 51 | 10 | 2 | 0.0039 |

Table A2. (Continued).

| Species | Population |  | Date | Observed flowers | Observed time | No. of legitimate visit | Visitation rate |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. | Name |  |  |  |  |  |
| S. jatrophifolium | 4 | Yapeyú | 01 December 2014 | 29 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 4 | Yapeyú | 01 December 2014 | 44 | 10 | 1 | 0.0023 |
| S. jatrophifolium | 4 | Yapeyú | 01 December 2014 | 45 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 4 | Yapeyú | 25 January 2017 | 12 | 10 | 1 | 0.0083 |
| S. jatrophifolium | 4 | Yapeyú | 25 January 2017 | 17 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 5 | Concordia | 03 December 2014 | 46 | 10 | 2 | 0.0043 |
| S. jatrophifolium | 5 | Concordia | 04 December 2014 | 38 | 10 | 3 | 0.0079 |
| S. jatrophifolium | 5 | Concordia | 04 December 2014 | 22 | 10 | 2 | 0.0091 |
| S. jatrophifolium | 5 | Concordia | 04 December 2014 | 47 | 10 | 3 | 0.0064 |
| S. jatrophifolium | 5 | Concordia | 04 December 2014 | 36 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 5 | Concordia | 04 December 2014 | 36 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 5 | Concordia | 25 January 2017 | 45 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 5 | Concordia | 25 January 2017 | 45 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 12 | Colón | 15 February 2015 | 47 | 10 | 3 | 0.0064 |
| S. jatrophifolium | 12 | Colón | 15 February 2015 | 26 | 10 | 1 | 0.0038 |
| S. jatrophifolium | 12 | Colón | 16 December 2015 | 28 | 10 |  | 0.0000 |
| S. jatrophifolium | 12 | Colón | 16 December 2015 | 40 | 10 | 0 | 0.0000 |
| S. jatrophifolium | 12 | Colón | 16 December 2015 | 38 | 10 | 1 | 0.0026 |
| S. jatrophifolium | 12 | Colón | 25 January 2017 | 25 | 10 | 0 | 0.0000 |

[^3]
[^0]:    *Corresponding author. Email: torretta@agro.uba.ar

[^1]:     Gualeguaychú. ${ }^{\mathrm{d}}$ Ciudad Autónoma de Buenos Aires. ${ }^{\text {e}}$ Oberá. ${ }^{\mathrm{f}}$ Concepción del Uruguay.

[^2]:    

[^3]:    Note: Population numbers correspond to those in Table 1.

