

TOMATO (*SOLANUM LYCOPERSICUM*) SPECIALIZED POLLINATION IS ISOLATED FROM NEIGHBORING PLANTS AND POLLINATORS

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Journal of Pollination Ecology,
31(4), 2022, pp 29-38

DOI: [10.26786/1920-7603\(2022\)656](https://doi.org/10.26786/1920-7603(2022)656)

Received 16 July 2021,
accepted 7 March 2022

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Abstract—Tomato is one of the crops that require buzz pollination, for which a pollinator vibrates the tubular anthers for pollen to be released. This process is efficiently carried out by wild bees, whose distribution varies according to the geographical location and the particular characteristics of the different agroecosystems. The pollination network associated with tomato fields located in an agricultural area of Cuba was determined by field observations. In addition, it was studied whether pollination influences tomato yield, through exclusion experiments and comparing the characteristics of the fruits obtained in the presence or absence of pollinators. The pollination network consisted of 241 interactions between 12 plants, including tomato, adjacent crops such as papaya and pumpkin, and ruderal species, and 11 floral visitors, fundamentally bees, with 5 species involved. Tomato flowers were almost exclusively visited by the bee species *Exomalopsis pulchella*, capable of buzz pollination. Species of the genus *Exomalopsis* are frequent pollinators of tomato in the Neotropic. This denotes a temporary specialization in the use of tomato's floral resources by *Exomalopsis pulchella*. *Apis mellifera* was not detected visiting tomato flowers, despite being present in the pollination network associated with the studied agroecosystem. Pollination significantly increased the dimensions of tomato fruits. *Exomalopsis pulchella* also visited the ruderal plants *Asteraceae* sp., *Commelinaceae* sp. and *Millieria quinqueflora*. This should be taken into account in the management of the ruderal plant communities that surround the tomato fields, in order to promote and guarantee the presence of the main pollinator of this crop.

Keywords—buzz, Cuba, *Exomalopsis pulchella*, pollination network

INTRODUCTION

Pollination is a key process in the life cycles of angiosperms. Animals pollinate around 87.5% of flowering plants, and this number rises to 94% in tropical communities (Ollerton et al. 2011). Around 35% of crops require pollination by animals (Klein et al. 2007). Pollen must arrive to stigmas in a specific quantity, quality and time for successful pollination (Wilcock & Neiland 2002). However, interspecific pollen transfer is one of the causes of pollination failure because heterospecific pollen arrives to stigmas and reduces seed set by clogging stigmas or pistils (Moreira-Hernández & Muchhala 2019). Plants coevolved with pollinators to avoid this phenomenon by specialization of pollination systems (Rosas-Guerrero et al. 2014).

Some crops have a generalist pollination system and can be pollinated by a wide group of pollinator species, but others are extreme specialists and rely on few pollinator species for successful pollination (Roubik 1995). Among these specialist crops are tomato and pepper, which evolved buzz-pollination to ameliorate pollen limitation (Ashman et al. 2004).

Buzz-pollination is present in around 22,000 angiosperm species of 72 families and involves 58% of all bee species (Cardinal et al. 2018). The poricidal anthers of these plants are tubular, dehisce through a pore and bees must sonicate them to extract pollen (Buchmann, 1983). Bees use indirect flight muscles for this purpose (King et al. 1996). The sonication frequency needed for every

plant species is different and depends on the morphology of anthers and the size of the bee (De Luca et al. 2019). Smaller bees vibrate with higher frequencies and vice versa (De Luca et al. 2019). Several studies reported that native bees are the main pollinators that buzz-pollinate tomato flowers (Winfree et al. 2008; Silva-Neto et al. 2013; Vinicius-Silva et al. 2017; Franceschinelli et al. 2019), which increase tomato fruit yield (Cooley and Vallejo-Marín 2021). In the neotropics, species of *Exomalopsis*, *Bombus*, *Centris*, *Augochloropsis*, among others, perform buzz-pollination in tomato flowers (King 1993; Macias-Macias et al. 2009; Silva-Neto et al. 2017).

Greenhouse tomato flowers require hand pollination or the introduction of bee nests for pollination (van Heemert et al. 1990). *Bombus terrestris* is a bumblebee used in many countries for this purpose (Morandin et al. 2001). This species is introduced in the neotropics and usually invades ecosystems and causes local extinctions of native bees (Dafni et al. 2010). However, native bees can be used in greenhouses to avoid the introduction of exotic bee species for greenhouse tomato pollination (Chávez et al. 2015).

Tomato and other crops flower massively, which offers a high amount of resources in a short time (Garibaldi et al. 2018). Native bee species require continuous food supply, which cannot be offered solely by crops (Russo et al. 2013). Diversified communities that include ruderal plants that offer pollen and nectar when tomato flowers are not available allow the temporal persistence of native bee species (Nicholls & Altieri 2013). Heterogeneous landscapes with diverse communities harbour complex networks of plant-pollinator interactions (Moreira et al. 2015). Diverse pollination networks offer a more stable pollination service in agroecosystems and influence stability of specialist pollinator populations (Guzman et al. 2019). Understanding interactions between plants and pollinators at the community level is a desired goal for management of natural resources and agroecosystems. With this study, we aim to characterize the pollination network around tomato fields and how important are pollinators for tomato yield in an agroecosystem of Cuba. This knowledge will be important for the agroecological management of the pollinators around tomato fields, and will

allow a better understanding of the connectivity of tomato crops with the surrounding biodiversity. The novelty of this study is the incorporation of the system perspective to the understanding of the pollination of tomato in Cuba.

MATERIALS AND METHODS

POLLINATION NETWORK

The characterization of the pollination network of tomato was conducted between November 2018 and March 2019, covering tomato planting season in Cuba. Sampling units were located in four tomato fields of the municipalities of San José de las Lajas (Field 1 (area: 8,567 m², coordinates: 22°98'17" N, 82°14'13" W); Field 2 (2,065 m², 22°98'94" N, 82°15'08" W); Field 3 (15,309 m², 23°00'98" N, 82°13'66" W)) and Jaruco (Field 4 (13,061 m², 23°02'34" N, 81°99'29" W)), in Mayabeque province (Fig. 1).

The sampling unit consisted of a tomato field and 50 meters around it. This distance is near the foraging range of small bees (Gathmann & Tschardt 2002), which are the main pollinators of tomato. The external matrix around fields includes other crops and ruderal plants, and it is highly homogeneous in plant species composition and abundance throughout the country (Ricardo et al. 2009). Every sampling unit was surveyed between 09:00 and 13:00, according with the moment of tomato anthesis and stigma receptivity, and when the activity of pollinators is higher (Silva-Neto et al. 2017). Two researchers walk several times over line transects that cover all tomato field and the external matrix, and recorded all interactions between flowers and floral visitors. An interaction was considered as the touch between the feeding structures of a floral visitor and the reproductive structures of the flowers. This design allowed obtaining a general description of the global agroecosystem network since the ruderal communities around fields are similar in species composition and abundance (Ricardo et al. 2009); and also a more accurate description of the pollinators of tomato. Pollinators and plants that were not accurately identified in the field were collected for posterior identification. Voucher specimens are deposited in the entomological collection of Faculty of Biology, University of Havana.

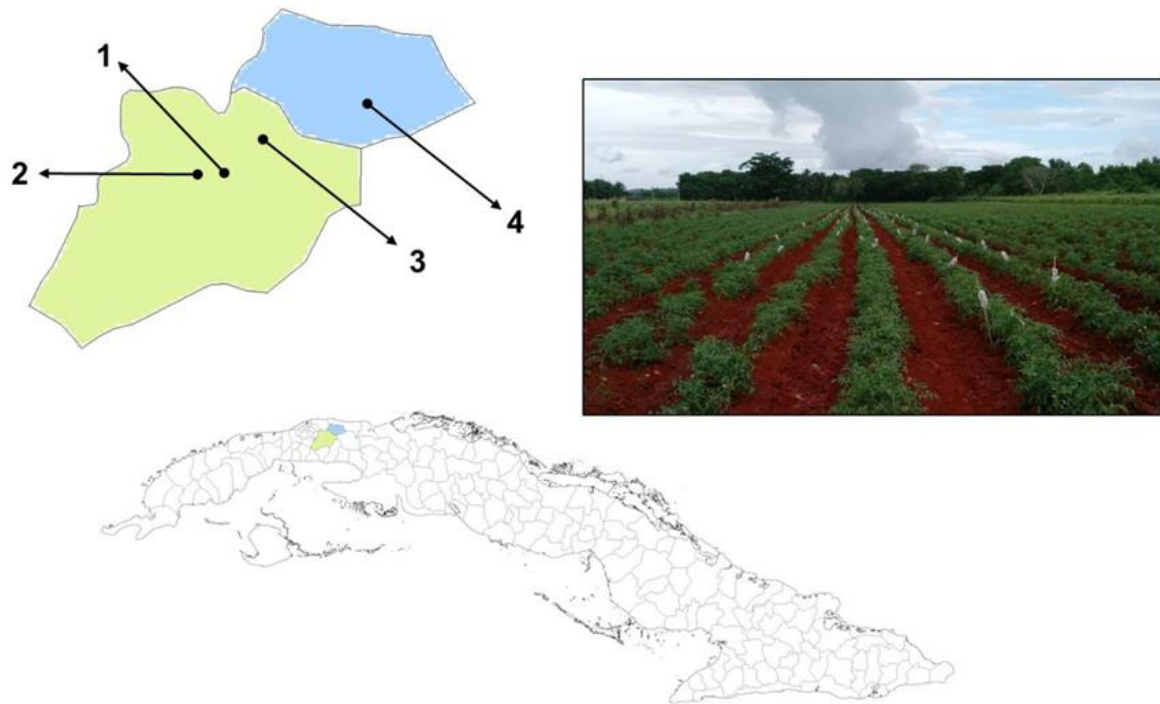


Figure 1. Location of the four tomato fields in the municipalities of San José de las Lajas (green) and Jaruco (blue) in the province of Mayabeque, Cuba. The picture shows the bagging experiments in the flowers of tomato plants.

We built an adjacency matrix with the data of all tomato fields: plants were located in rows, pollinators in columns and cells were filled with the number of interactions of every pair of species. Global network metrics were not calculated because of bias toward tomato pollinators introduced by the sampling design. Four species level metrics were used instead. The standardized Kullback-Liebler distance (d') measures how specialized or generalized a species is. This metric range from zero for generalized species to one for the most specialized ones (Blüthgen et al. 2006). Other metrics used were, species degree, which is the number of links per species (Jordano et al. 2003), and species strength, which is the sum of dependencies for each species. The latter is a measure of the importance of one species for the species of the other trophic level (Bascompte et al. 2006).

Specialization in pollination networks is usually asymmetric (Vázquez & Aizen 2004): while specialist species A depends highly on generalist species B, species B depends weakly on species A. To measure this dependence asymmetry, we used the index interaction push/pull, which ranges from

-1 to 1. Species with values of 1 have a significant influence in their interaction partners (“push their partners”), while species near -1 values depend heavily in their interaction partners (are “pulled” by their partners) (Vázquez et al. 2007). Observed indices were compared with those obtained by 1,000 null models using Patefield algorithm (Patefield 1981) implemented with nullmodel function of bipartite package. This null model (type I) maintains marginal totals identical to the original network and switch the links between species (Dormann et al. 2009).

BAGGING EXPERIMENTS

Bagging experiments were conducted to measure the importance of pollinators to tomato fruit yield. For this experiment, we used “Elbita” variety, developed in Cuba (Álvarez-Gil et al. 2018). Inflorescences were bagged when flowers fully formed and before anthesis. We selected the tip of shoots that contained less than 20 not-opened flowers. 80 shoots were bagged and other 80 not-bagged shoots were used as controls. Meshes were cylinders of 10 cm diameter and 40 cm height. Data was not collected from shoots that suffered any damage or when the mesh was removed

accidentally by wind or animals. Finally, we obtained data from 75 bagged shoots and 75 unbagged shoots. Twelve days after bagging the number of fruits formed was measured. At this moment, flowers had been pollinated or aborted. This variable was standardized by the number of not-opened flowers that the shoots contained at the beginning of the experiment. All meshes were removed after the twelve days period to allow normal development of fruits. A total of 37 bagged and 116 unbagged tomatoes were collected between days 29 and 35, when the seeds fully formed but the fruit had not ripened (stage “mature green” according to Gillaspay et al. 1993). Polar diameter, height, weight and number of seeds of every individual fruit were measured. Polar diameter and height were measured with a vernier caliper (accuracy of 0.1 cm), weight with a spring balance (accuracy of 10 g) and seeds manually counted. Shapiro-Wilk normality test was used to select appropriate tests to compare treatments for the five variables. If data follow a normal density we used t-tests, otherwise we employed two-sample Wilcoxon rank sum tests. All figures and analysis were performed in R 4.0.3 (R Core Team, 2020) using the packages *stats*, *bipartite* and *ggplot2*.

RESULTS

Twelve plant species and 11 floral visitor species composed the pollination network, which established 241 interactions (Fig. 2). The plants were nine ruderal species and three crops, which include *Solanum lycopersicum* (tomato), *Cucurbita pepo* (pumpkin) and *Carica papaya* (papaya). The majority of floral visitor species were hymenopterans, five of which were bees. The interactions between *Solanum lycopersicum* and the bee *Exomalopsis pulchella* represented 45% of all interactions. This bee was the main floral visitor of tomato flowers and only visited two other plant species. We recorded just one interaction in tomato flowers with another bee, *Melipona beecheii*.

The plant species more specialized according to the index d' were the crops *Cucurbita pepo* ($d' = 0.85$), *Carica papaya* ($d' = 0.85$) and *Solanum lycopersicum* ($d' = 0.80$) (Tab. 1). Among the floral visitors, the species of Braconidae ($d' = 0.98$), *Exomalopsis pulchella* ($d' = 0.95$) and *Apis mellifera* ($d' = 0.90$) were the most specialized. *Cucurbita pepo* and *Apis*

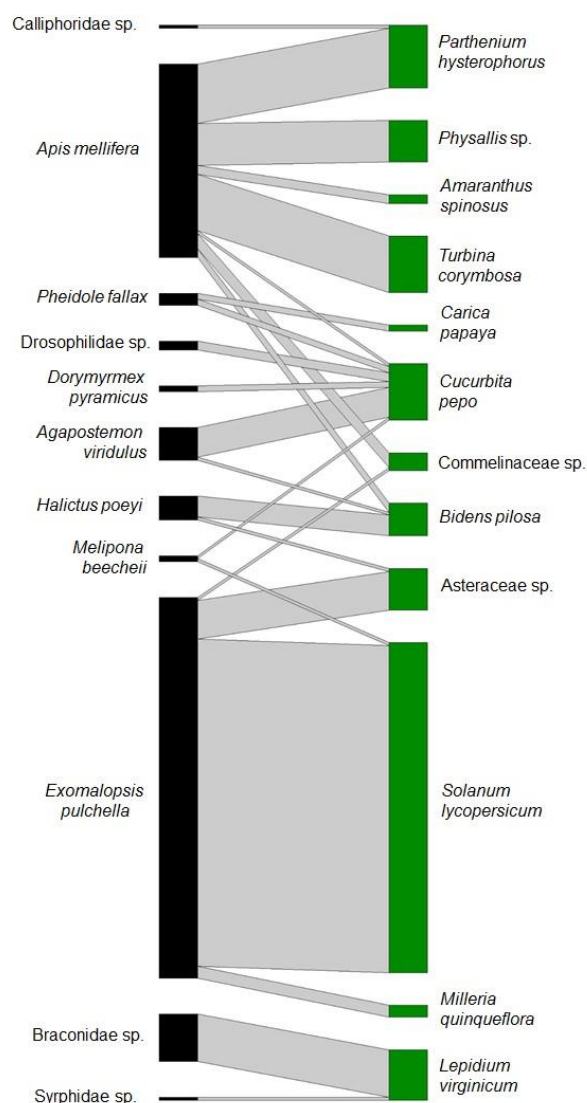


Figure 2. Pollination network around tomato fields in agroecosystems of Mayabeque, Cuba, between November 2018 and March 2019. Floral visitors are depicted in black squares, plants in green squares and interactions in grey lines between them. The thickness of grey lines indicates the abundance of every interaction.

mellifera were the species with the highest degree. Six species visited the flowers of *C. pepo*, while *A. mellifera* visited seven plant species. These two species also had the highest levels of species strength (Tab. 1).

Solanum lycopersicum, *Cucurbita pepo*, *Parthenium hysterophorus* and *Lepidium virginicum* were the plants with positive interaction push/pull index. All but *S. lycopersicum* show significant values when compared with those obtained by null models (Tab. 1). These plants have a strong

Table 1. Metrics for the species present in the pollination network in the agroecosystem of Mayabeque, Cuba, between November 2018 and March 2019. Values in bold are those significantly different from 1000 null models.

		<i>d'</i>	Degree	Species strength	Interaction push/pull
Plants	<i>Solanum lycopersicum</i>	0.8	2	1.35	0.18
	<i>Amaranthus</i> sp.	0.26	1	0.05	-0.95
	Asteraceae sp.	0.18	2	0.22	-0.39
	<i>Bidens pilosa</i>	0.61	3	1.01	0
	<i>Carica papaya</i>	0.85	1	0.5	-0.5
	Commelinaceae sp.	0.16	2	0.08	-0.46
	<i>Cucurbita pepo</i>	0.85	6	3.92	0.49
	<i>Parthenium hysterophorus</i>	0.53	2	1.31	0.15
	<i>Lepidium virginicum</i>	1	2	2	0.5
	<i>Milleria quinqueflora</i>	0.1	1	0.03	-0.97
	<i>Physallis</i> sp.	0.45	1	0.22	-0.78
	<i>Turbina corymbosa</i>	0.5	1	0.29	-0.7
	Floral visitors	<i>Exomalopsis pulchella</i>	0.95	4	3.09
<i>Agapostemon viridulus</i>		0.73	2	0.62	-0.19
<i>Apis mellifera</i>		0.9	7	5.11	0.59
Calliphoridae sp.		0.35	1	0.05	-0.95
Drosophilidae sp.		0.5	1	0.16	-0.84
<i>Dorymyrmex pyramicus</i>		0.44	1	0.11	-0.89
<i>Halictus poeyi</i>		0.77	2	0.71	-0.14
Braconidae sp.		0.98	1	0.94	-0.06
<i>Melipona beecheii</i>		0.05	2	0.06	-0.47
<i>Pheidole fallax</i>		0.68	2	1.11	0.05
Syrphidae sp.		0.4	1	0.06	-0.94

effect on the pollinators that visit them in offering food resources. Pollinators with positive values of interaction push/pull index were the bees *Exomalopsis pulchella* and *Apis mellifera*, and with a lower value the ant *Pheidole fallax*. This means that the plants more frequently visited by these bees (*Solanum lycopersicum* and *Turbina corymbosa*, respectively) highly depend on these insects for their pollination (Fig. 2).

Bagging experiments demonstrate that pollination increases tomato yield. Pollination increases the number of fruits produced ($W = 1.069$; $P < 0.001$). The average number of fruits formed standardized by the original number of flowers were higher in the open shoots (mean \pm S.D.; 0.45 ± 0.40) in comparison with the bagged ones (0.14 ± 0.30). Unbagged flowers that received free pollination developed into fruits with bigger

height ($t = 3.98$; $P < 0.01$), polar diameter ($W = 3,755.5$; $P < 0.01$), weight ($W = 3,658.5$; $P < 0.01$) and number of seeds ($W = 3,669.5$; $P < 0.01$) (Fig. 3).

DISCUSSION

The pollination network shows that there is a high connectivity between crops and the matrix around them. All species are integrated in a single web, where interspecific interactions are established. For example, facilitative interactions may occur between ruderal plants and crops (Russo et al. 2013). Ruderals can maintain the abundance of pollinator populations when crops are not flowered, which usually occur massively in a short time span (Roubik 1995). For instance, *Agapostemon viridulus*, a native bee that could be the main pollinator of the pumpkin according to our data, gathered nectar and pollen from *Bidens pilosa*, a

widespread species in Cuba (Oviedo & González-Oliva 2015) that produces high amounts of floral resources (Budumajji & Solomon 2018). The flowers of pumpkin are unisexual; pollen must be transported from male to female flowers by a pollinator. In fact, wild bees are more effective than *Apis mellifera* in pumpkin pollination (Knapp & Osborne 2019).

Apis mellifera, the most cited pollinator, do not visited tomato or papaya, and only visited pumpkin once. Although this species is economically important for honey production, it is

not so efficient for pollination (Westerkamp 1991). Many management strategies of crop pollination focused on this species, when it could be cheaper and more stable maintaining diverse communities of plants and pollinators in the field margins (Garibaldi et al. 2013; Badillo-Montano et al. 2018). Agriculturally dominated landscapes reduce bee diversity and pollination service to crops (Grab et al. 2019). One of the main causes is the reduction of facilitative interactions between ruderal plants and crops (Carreck & Williams 2002). Pollinators

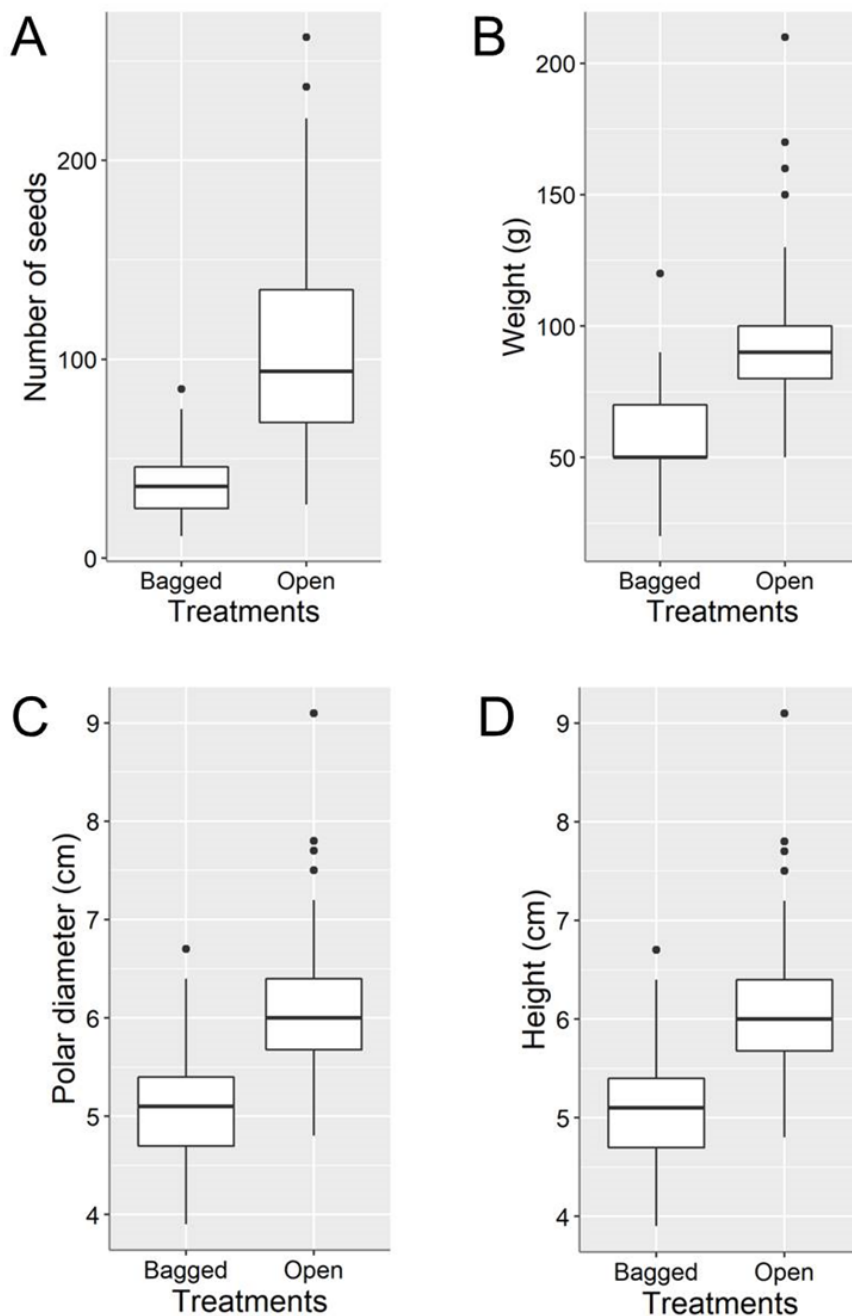


Figure 3. Fruit features of tomatoes obtained from open pollinated flowers and bagged flowers. The boxes depict the mean, 25th, and 75th percentiles. Black dots indicate outliers.

require stable supplies of pollen and nectar, which cannot be given by short-time flowering crops (Russo et al. 2013).

The most abundant interaction occurred between tomato and *Exomalopsis pulchella*. Both species are highly specialized in using each other niches, and show positive values of interaction push/pull index. This means that both of them depend highly on the other for pollination and food resources, respectively. According to the values of this index, *S. lycopersicum* depends more on *E. pulchella* for pollination than *E. pulchella* depends on *S. lycopersicum* for food resources. In other words, *E. pulchella* “push” more over *S. lycopersicum* than in the other sense. *E. pulchella* was reported as the main pollinator of tomato flowers in Cuba (Anais 1980). However, the other two species of *Exomalopsis* present in Cuba: *E. similis* and *E. bahamica* (Genaro 2007) could also pollinate tomato in other areas of the island.

Exomalopsis species are common pollinators of tomato in neotropical ecosystems (Vinicius-Silva et al. 2017). These species are able to buzz-pollinate the flowers of several plant species with poricidal anthers (Vallejo-Marín 2019). This specific pollination syndrome requires a bee with specialized indirect flight muscles that can produce vibrations with the required frequency to extract pollen from the pore in the tip of the anther (King & Buchmann 2003). Buzzing can only be performed by some bee species with this morphophysiological mechanism (Cardinal et al. 2018). For example, *Apis mellifera* do not buzz-pollinate (King & Buchmann 2003) and this could be the cause of the absence of interactions with tomato flowers, although another cause could be the absence of nectar in tomato flowers. In the agroecosystem studied, *Exomalopsis pulchella* preferentially uses tomato as the main food resource, but ruderal plants could provide nectar and pollen when tomato is not flowered. This also highlights the need to maintain diverse communities in agroecosystems (Nicholls & Altieri 2013).

Melipona beecheii was the other species that visited tomato flowers. This single visit can be considered as an occasional one, although it is able to buzz-pollinate. Other species of the genus, such as *Melipona quadrifasciata* from Brazil, had been reported as a common pollinator of tomato flowers

(Deprá et al. 2014; Silva-Neto et al. 2018). The species of Cuba (*Melipona beecheii*) had low interactions in the fields studied maybe because it had low abundance in this particular area or it uses other floral resources more attractive during the flowering period of tomato.

Tomato is hermaphroditic, but yield increases when pollinated (Deprá et al. 2014; Amala & Shivalingaswamy 2017; Salvarrey et al. 2020). Increase in fruit production due to pollinators can be attributed mainly to *Exomalopsis pulchella*, the main visitor of tomato flowers in the agroecosystem studied, although we do not corroborate which bee species pollinate the open-pollinated flowers. Our results can be used to improve tomato pollination in agroecosystems and greenhouses. Although tomato production in greenhouses is not a widespread practice in Cuba, it could be in the future. Tomatoes cultivated in greenhouses usually require a pollinator. In other countries, exotic bees had been introduced to perform this task, such as *Bombus terrestris*, which compete with native bee fauna and cause negative effect on pollinator communities (Dafni et al. 2010). Therefore, we encourage farmers and governmental institutions not to introduce exotic species in the future and to potentiate the use of *Exomalopsis pulchella* in greenhouses.

This study highlights the importance of wild bees for crop pollination, specifically the importance of *Exomalopsis pulchella* for tomato pollination. Wild pollinators better performed the service of pollination in the world than honeybees (Garibaldi et al. 2013). We proposed to increase ruderal plant areas that provide food resources for *E. pulchella* throughout the year. Management practices that include hedgerows near crops improve the pollinator community and maintain a stable pollination service to crops (Kremen et al. 2018).

ACKNOWLEDGEMENTS

Julio A. Genaro (Toronto, Canada) and Ana M. Hernández (La Habana, Cuba) made useful suggestions to the original manuscript. Julio A. Genaro also helped in identifying bees and sharing literature. Eldis R. Bécquer, Banessa Falcón and Rosalina Berazaín (National Botanical Garden, Cuba) helped with plant identification. Farm owners allow us to visit their farms and Rolando Casas kindly let us conduct bagging experiments in his farm. Idea Wild funded Diego

Alameda with equipment. Two anonymous reviewers made useful suggestions to the original manuscript.

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