Introduction

In recent years, a growing number of studies have shown that the yields of many agricultural crops increase when pollinated by bees. The role of wild bees has garnered further attention due to the realization that human food security is directly dependent on this ecosystem service (Potts et al., 2016; Klein et al., 2018). According to Garibaldi et al. (2013), pollination by wild insects is more efficient than that carried out by honey bees alone; Mallinger et al. (2019) quantified the economic value of pollination by wild bees in sunflower crops in the United States at 56.7 million US dollars; two solitary bee species were identified as the most efficient pollinators of this crop. Crops such as strawberries (Herrmann et al., 2019; MacInnis & Forrest, 2019), rapeseed oil (Halinski et al., 2018; Perrot et al., 2018) and blueberry (Nicholson & Ricketts, 2019), among others, are also better pollinated by wild bees.

The anthropogenic drivers of pollinator decline are many (see Potts et al., 2010), but the loss of suitable habitats, among other effects of agricultural intensification, deserves special attention. Food and nesting resources are drastically reduced in intensively farmed landscapes because such areas have a high rate of land-use change and severe disturbances such as tillage, mowing, and grazing (Potts et al., 2010). Specialist species, whether habitat or dietary, experience the...
greatest population decline (Biesmeijer et al., 2006). As the proportion of a landscape’s agricultural cover increases, bee abundance and richness decrease, and much phylogenetic diversity is lost, leaving bee communities in such landscapes composed of more closely related species (Grab et al., 2019).

Reduction in the availability of floral resources, regardless of the responsible causes, affects bee communities negatively in terms of species composition, foraging behavior, corporal size, and fitness (Jha & Kremen, 2013; Campbell et al., 2018; Rollin et al., 2019). Larval development and offspring size suffer when females provide brood cells with little pollen or pollen of poor nutritional quality (Peterson & Roitberg, 2006; Vanderplanck et al., 2014; Moerman et al., 2015; Renauld et al., 2016). Since the amount and type of nutrients present in pollen and nectar tend to vary from one plant species to another (London-Shafir et al., 2003; Mao et al., 2013; Abbas et al., 2014) bees’ access to a diverse flora ensures better-nourished insects.

Sites within rural properties that harbor plant diversity can help maintain pollinator populations and thus provide pollination services in agricultural landscapes (Albrecht et al., 2007), for both crops and native plants. Ghazoul (2006) found that there were more pollinator visits to *Raphanus raphanistrum* L. flowers when individuals of this species occurred close to individuals of three more herbaceous species. According to the author, his study confirmed the hypothesis that pollination facilitation exists among co-flowering plants whose floral displays differ, attracting greater pollinator diversity. Thus, in addition to being an alternative source of food, ruderal plants also contribute to greater diversity in environments at the farm scale, which favors a greater abundance of pollinators (Chateil & Porcher, 2015).

Our study aims to understand whether the presence of herbaceous plants, acting as foraging sites, next to crops contributes to bee species richness in smallholder rural properties. We believe that the bee species richness and diversity sampled on ruderal plant flowers are greater than those sampled on crop plants; bee species composition also differs between these two types of plants.

**Material and Methods**

**Study area**

The study was carried out at three smallholding rural properties in Guapiara municipality, southern São Paulo state, Brazil (Fig 1). According to Köppen typology, the climate in Guapiara is Cwa (humid temperate with dry winter and wet summer). The mean temperature is 15.8°C in the coldest month (July) and 23.2°C in the hottest month (February); the average rainfall is 53.3 mm in the driest month (August) and 217.3 mm in the wettest month (January) (CEPAGRI, 2014). Guapiara contains part of the Intervales State Park and is in the heart of the region that comprises the Mosaic of Conservation Units of Serra de Paranapiacaba, which preserves the largest remaining area of Atlantic Forest in Brazil, with 120,000 hectares of protected areas (Fundação Florestal, 2019).

![Fig 1. Smallholder rural properties overview. S1: property S1 showing cultivated and post-harvest areas. S2: property S2 showing a post-harvest area. S3: property S3 showing flat bean plantation.](image-url)
Property S1 is the largest in the area (8.67 ha), followed by property S2 (4.20 ha) and S3 (3.24 ha). The longest Euclidean distance between the properties is 8.63 km (S2-S3), with properties S1 and S2 being closer (4.61 km); S1 and S3 are 6.91 km apart (Fig 2). In all, six crops were grown on the three rural properties over a year (zucchini, kabocha squash, tomato, flat bean, peach, and cucumber). However, on S1 property five crops were grown (S1 = kabocha squash, tomato, flat bean, peach, and cucumber), blooming from July/2012 to March/2013 (Table 1). Properties S2 and S3 had three crops each (S2 = flat bean, cucumber, and zucchini; S3 = flat bean, tomato, and kabocha squash), but with only one crop in common and different blooming periods (Fig 3). Blooming period refers to the time when there were crop flowers on the property, as there were plantations of the same crop with different ages within the properties. A common practice in the properties studied is to allow the free growth of ruderal plants in post-harvest areas and crop borders so that throughout the year there is a turnover of areas that concentrate a greater abundance of these plants.

Fig 2. Study area location. South America, Brazil. Blue square indicating the study area in the São Paulo state.

| Crop               | RP*     | May/12 | Jun/12 | Jul/12 | Aug/12 | Sep/12 | Oct/12 | Dez/12 | Jan/13 | Feb/13 | Mar/13 |
|--------------------|---------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| Tomato             | S1, S3  |        |        |        |        |        |        |        |        |        |        |
| Zucchini           | S1, S2  |        |        |        |        |        |        |        |        |        |        |
| Kabocha Squash     | S1, S2  |        |        |        |        |        |        |        |        |        |        |
| Flat bean          | S1, S2, S3 |    |        |        |        |        |        |        |        |        |        |
| Cucumber           | S2      |        |        |        |        |        |        |        |        |        |        |
| Peach              | S1      |        |        |        |        |        |        |        |        |        |        |

*RP: Rural property

Fig 3. Crop plants blooming period at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013.

Data collection

For a period of ten months, from May 2012 to March 2013 (except November 2012), we collected bees at three rural properties. Bees were collected from 8 a.m. to 1 p.m., always by two collectors, with a change of collectors every sampling month. Using an entomological net one collector sampled the bees walking the crop lines, and the other one collected the bees on ruderal flowers present on the crop edges and in transects open in post-harvest areas. When there were no crops in bloom on any of the three rural properties, the two collectors sampled the bees on ruderal flowers in the post-harvest and surrounding areas. Each day of collection involved four to five 1-hour sampling cycles at 20-minute intervals, totaling 50 hours/property. At the time of insect collection were noted the plant type where the capture occurred (whether cultivated...
Table 1. Bee species sampled on crop flowers at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013.

| Crop                              | Bee species                                             | Rural properties |
|-----------------------------------|---------------------------------------------------------|------------------|
| Tomatos (Lycopersicon esculentum Mill.) | Anthrenoides meridionalis (Schrottky, 1906)             | X                |
|                                   | Augochloropsis cupreola (Cockerell, 1900)              | X                |
|                                   | Augochloropsis electra (Smith, 1853)                   |                 |
|                                   | Augochloropsis sp. 2                                   | X                |
|                                   | Augochloropsis sp. 3                                   | X                |
|                                   | Bombus (Fervidobombus) morio (Swederus, 1787)           | X                |
|                                   | Bombus (Fervidobombus) paveloensis Friese, 1913        | X                |
|                                   | Exomalopsis (Exomalopsis) analis (Spinola, 1853)       |                 |
|                                   | M. (Melipona) quadrifasciata quadrifasciata Lepeletier, 1836 | X                |
|                                   | Oxaea flavescens (Klug, 1807)                          | X                |
|                                   | Oxaea sp.                                               | X                |
|                                   | Paratrigona subnuda Moure, 1947                        | X                |
|                                   | Psaenythia bergii (Holmberg, 1884)                     | X                |
|                                   | Pseudaugochlora inordinata (Almeida, 2008)             | X                |
|                                   | Tetragonisca angustula (Lateille, 1811)                | X                |
|                                   | Trigona spinipes (Fabricius, 1793)                     |                 |
|                                   | Xylocopa (Neoxylocopa) suspeta (Moure & Camargo, 1988) | X                |
|                                   | Xylocopa (Stenoxylocopa) artifex (Smith, 1874)         | X                |
| Zucchini (Cucurbita pepo L.)       | Augochlorosa (Augochlorosa) amphitrite (Schrottky, 1909)| X                |
|                                   | Augochlorosa (Augochlorosa) foxtian (Cockerell, 1900)  |                  |
|                                   | Bombus (Fervidobombus) morio (Swederus, 1787)           | X                |
|                                   | Bombus (Fervidobombus) paveloensis Friese, 1913        | X                |
|                                   | Peponapis fervens (Smith, 1875)                        | X                |
|                                   | Trigona hyalinata (Lepeletier, 1836)                   | X                |
|                                   | Trigona spinipes (Fabricius, 1793)                     | X                |
| Kabocha Squash (Cucurbita maxima Duchesne) | Apis mellifera Linnaeus, 1758                         | X                |
|                                   | Bombus (Fervidobombus) paveloensis Friese, 1913        | X                |
|                                   | Melissopitla thoracica (Smith, 1854)                   | X                |
|                                   | Paratetrapedia fervida (Smith, 1879)                   | X                |
|                                   | Peponapis fervens (Smith, 1875)                        | X                |
|                                   | Trigona hyalinata (Lepeletier, 1836)                   | X                |
|                                   | Trigona spinipes (Fabricius, 1793)                     | X                |
| Flat bean (Phaseolus vulgaris L.)  | Apis mellifera Linnaeus, 1758                         | X                |
|                                   | Augochlorosa (Augochlorosa) amphitrite (Schrottky, 1909)| X                |
|                                   | Bombus (Fervidobombus) morio (Swederus, 1787)           | X                |
|                                   | Bombus (Fervidobombus) paveloensis Friese, 1913        | X                |
|                                   | Paratrigona subnuda Moure, 1947                        | X                |
|                                   | Peponapis fervens (Smith, 1875)                        | X                |
|                                   | Schwarziana quadrin punctata (Lepeletier, 1836)         | X                |
|                                   | Trigona spinipes (Fabricius, 1793)                     | X                |
| Cucumber (Cucumis sativus L.)      | Bombus (Fervidobombus) morio (Swederus, 1787)           | X                |
|                                   | Paratrigona subnuda Moure, 1947                        | X                |
| Peach (Prunus persica (L.) Batsch) | Trigona hyalinata (Lepeletier, 1836)                   | X                |
or ruderal), the identity of the rural property (if number 1, 2 or 3), the collector (identified by the first letter of the name) and the number of the insect (based on the amount that each collector sampled). Bee specimens collected were euthanized in ethyl acetate and stored in 70% alcohol. In the laboratory, the specimens were pressed, appropriately tagged, and stored in entomological drawers. Species identification was carried out by Dr. Silvia Pedro from Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Brazil. The specimens are currently stored in the collection of the Grupo de Estudos em Ecologia e Conservação de Abelhas Silvestres laboratory, São Paulo State University (UNESP), Rio Claro, São Paulo, Brazil. The sampling of ruderal plants present in rural properties was also carried out monthly. Each new ruderal plant that was identified in bloom was photographed, flower buds were collected for pollen analysis and a sample of the plant for the confection of exsiccates. The same procedure was adopted for crop plants in bloom.

**Pollen analysis**

To complement the data of which plants were used as a food source for the bees sampled in the three rural properties, we carried out the analysis of pollen grains adhered to the specimens’ bodies, scopes, and corbiciles. The pollen samples were obtained from the body of 115 individuals collected on crop flowers and 267 individuals collected on ruderal flowers and transferred to test tubes containing 50 mL of ethanol solution 70%. After 24 hours, the ethanol was discarded and the samples were placed in 4 mL of glacial acetic acid for 24 hours (Silva et al., 2010). After that, the pollen material was submitted to the acetylation process following the method described by Erdman (1960), and when the acetylation process was finished the samples were then put in an aqueous glycerine solution of 50%. After another 24 hours, small amounts of acetolized pollen were removed with cubes of glycerine jelly for the preparation of three microscopic slides per individual. Photomicrographs were taken and pollen types were identified by comparisons with the reference slides created with pollen samples collected from floral buds of the ruderal and crop plant species sampled in the three rural properties studied. Pollen grains removed from anthers contained in flower buds were submitted to the same process described above, with three microscopic slides per plant species. The ruderal plants sampled were identified using the book “Plantas daninhas do Brasil” (Lorenzi, 2008).

**Data analysis**

We compared the bee assemblages from flowers of ruderal and crop plants for each of the three properties. To estimate species richness, we used the Chao 1 index, which is based on abundance and is a function of the ratio of singletons to doubletons (Magurran, 2013). Average taxonomic breadth, ($\Delta+$; Clarke & Warwick, 1998; Andersson et al., 2013) and Shannon’s ($H'$) diversity index were calculated to estimate the sample diversity, while the dominance was calculated through the Simpson dominance index ($D$). Average taxonomic breadth is a diversity index that uses information from a Linnaean classification tree of the taxonomic relations between all sampled bee species. High $\Delta+$ values indicate a taxonomically broad, therefore taxonomically diverse, bee community; low $\Delta+$ values indicate a community composed of closely related species. Simpson dominance index ranges from 0, where all taxa are equally present, to 1, where one taxa dominates the community (Magurran, 2013). Finally, to verify whether bee species composition differed between the assemblage sampled from ruderal plants and that sampled from crop plants, we used the Jaccard’s dissimilarity index (Magurran, 2013). The analyses were performed using RStudio software version 3.6.3 (R Core Team, 2020) and the package vegan (Oksanen et al., 2019).

**Results**

A total of 61 bee species were identified (families Apidae, Halictidae, Megachilidae, Colletidae, and Andrenidae) among the 666 specimens collected across the three properties (Table 2). Property S2 harbored the greatest bee species richness ($n = 41$ species), followed by properties S3 ($n = 37$) and S1 ($n = 31$). *Bombus pauloensis* was the most abundant species in the three rural properties (S1 = 66 specimens; S2 = 65; S3 = 30), with *Trigona spinipes* the second most abundant in two properties (S2 = 23 specimens; S3 = 28) and *Bombus morio* the second most abundant in the S1 property (S1 = 40 specimens).

Twenty-nine bee species were collected on crop flowers, where the tomato was the crop with the greatest bee species richness visiting its flowers ($n = 18$ species) (Table 1) and the bee species *Bombus morio* that visited more varieties of crops. Twenty-eight species of ruderal plants were identified overall, with 25 species occurring on property S1, 20 species on property S2, and 15 species on property S3 (Table 3). Pollen analysis showed that *Leonurus sibiricus* and *Sonchus oleraceus* were the ruderal species visited by the largest number of bee species, 22 species each. Meanwhile, the rural property with the greatest ruderal plants species richness (S1 = 25 ruderal species) was not the place where there was the greatest bee species richness (S2 = 41 bee species), nor the place with the greatest bee species richness visiting ruderal plants (S2 = 39 bee species). There were nine bee species collected only on crop flowers and 32 bee species collected only on ruderal flowers (Table 2); however, 20 bee species were collected on both types of plants. In the Discussion section, we will pay special attention to species that have visited both ruderal and crop plants.

Pollen analysis also showed that of the 22 species of bees that were sampled only on flowers of ruderal plants, 9 species carried pollen of tomato and one species of bee carried pollen of kabocha squash, being *Augochloropsis* sp 1, *Dialictus* sp., *Exomalopsis* (Exomalopsis) *planiceps*, *Exomalopsis* sp 2, *Megachile* (*Chrysosaros*) *pseukanthidioides*, *Melissodes* (*Ecplectica*) *nigroaenea*, *Neocorynura oiospermi*, *Psanethyia* sp,
Thygater (Thygater) analis, and Exomalopsis sp 1, respectively. The same happened with the bee species that were collected only on crop flowers, of 9 species 5 carried pollen grains from ruderal plants: Augochlora (Augochlora) foxiana, Augochloropsis electra, Exomalopsis (Exomalopsis) analis, Oxaea sp., and Paratetrapedia fervida.

Table 2. Bee species, abundance and type of plant visited at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013.

| Species | Plants | Abundance/ Rural Property |
|---------|--------|---------------------------|
|         | Crop   | Ruderal | S1 | S2 | S3 |
| ANDRENIDAE |        |          |    |    |    |
| OXAEINI |        |          |    |    |    |
| Oxaea flavescens Klug, 1807 | X | 1 |
| Oxaea sp | X | 6 |
| PANURGINAE |        |          |    |    |    |
| PROTANDRENNI |        |          |    |    |    |
| Anthrenoides meridionalis (Schrottky, 1906) | X | X | 9 | 1 |
| Anthrenoides jordanensis Urban, 2007 | X | 1 |
| Cephalurgus anomalis Moure & Lucas de Oliveira, 1962 | X | 3 |
| Psacnythia bergii Holmberg, 1884 | X | X | 1 | 1 | 2 |
| Psacnythia sp | X | 3 |
| Rophitulus sp | X | 1 |
| APIDAE |        |          |    |    |    |
| APINAE |        |          |    |    |    |
| APINI |        |          |    |    |    |
| Apis mellifera Linnaeus, 1758 | X | X | 42 | 18 | 10 |
| BOMBINI |        |          |    |    |    |
| Bombus (Fervidobombus) brasiliensis Lepeletier, 1836 | X | 1 | 1 |
| Bombus (Fervidobombus) morio (Svederus, 1787) | X | X | 40 | 10 | 5 |
| Bombus (Fervidobombus) pauloensis Friese, 1913 | X | X | 66 | 65 | 30 |
| EMPHORINI |        |          |    |    |    |
| Melitoma segmentaria (Fabricius, 1804) | X | 1 |
| EUCERINI |        |          |    |    |    |
| Melissodes (Eclectica) nigroaenea (Smith, 1854) | X | 3 | 4 | 2 |
| Melissoptila richardiae Bertoni & Schrottky, 1910 | X | 1 |
| Melissoptila thoracica (Smith, 1854) | X | X | 4 | 3 |
| Peponapis fervens (Smith, 1875) | X | X | 7 | 3 | 5 |
| Thygater (Thygater) analis (Lepeletier, 1841) | X | 2 |
| Trichocerapis mirabilis (Smith, 1865) | X | 1 |
| EUGLOSSINI |        |          |    |    |    |
| Eulaema (Apeulaema) nigrita Lepeletier, 1841 | X | 1 |
| EXOMALOPSINI |        |          |    |    |    |
| Exomalopsis (Exomalopsis) analis Spinola, 1853 | X | 9 | 11 |
| Exomalopsis (Exomalopsis) planiceps Smith, 1879 | X | 1 |
| Exomalopsis (Exomalopsis) sp 1 | X | 3 |
| Exomalopsis (Exomalopsis) sp 2 | X | 1 |
| MELIPONINI |        |          |    |    |    |
| Geotrigona subterranea (Friese, 1901) | X | 4 | 3 |
| M. (Melipona) quadriglumis quadriglumis Lepeletier, 1836 | X | X | 2 | 3 |
| Paratrigona subnuda Moure, 1947 | X | X | 28 | 22 | 10 |
| Schwarziana quadririgulata (Lepeletier, 1836) | X | X | 10 | 6 | 1 |
| Tetragonisca angustula (Latreille, 1811) | X | X | 1 | 1 |
| Trigona hyalinata (Lepeletier, 1836) | X | X | 12 | 3 |
Table 2. Bee species, abundance and type of plant visited at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013. (Continuation)

| Species | Plants | Abundance/ Rural Property |
|---------|--------|---------------------------|
|         | Crop   | S1 | S2 | S3 |
| Trigona spinipes (Fabricius, 1793) | X | X | 23 | 23 | 28 |
| TAPINOTASPIDINI | | | | |
| Paratetrapedia fervida (Smith, 1879) | X | 1 | | |
| TETRAPEDIINI | | | | |
| Tetrapedia aff. diversipes Klug, 1810 | X | 1 | | |
| XYLOCOPINAE | | | | |
| CERATINI | | | | |
| Ceratina (Ceratinula) cf. oxalidis Schrottky, 1907 | X | 1 | | |
| XYLOCOPINI | | | | |
| Xylocopa (Neoxylocopa) brasiianorum (Linnaeus, 1767) | X | X | 2 | 1 | |
| Xylocopa (Neoxylocopa) frontalis (Olivier, 1789) | X | X | 5 | 4 | 1 |
| Xylocopa (Neoxylocopa) suspecta Moure & Camargo, 1988 | X | X | | 2 | |
| Xylocopa (Stenoxylocopa) artifex Smith, 1874 | X | X | 3 | 3 | 2 |
| COLLETIDAE | | | | |
| COLLETINAE | | | | |
| Colletes rugicollis Friese, 1900 | X | 1 | | |
| HALICTIDAE | | | | |
| HALICTINAE | | | | |
| AUGOCILORIN | | | | |
| Augochlora (Augochlora) amphitrite (Schrottky, 1909) | X | X | 2 | 1 | 7 |
| Augochlora (Augochlora) foxiana Cockerell, 1900 | X | X | 1 | | |
| Augochlora (Oxystoglossella) morae Strand, 1910 | X | 1 | 1 | 1 | |
| Augochlora (Oxystoglossella) sp | X | | 1 | | |
| Augochloropsis cupreola (Cockerell, 1900) | X | X | 3 | 2 | 2 |
| Augochloropsis electra (Smith, 1853) | X | | | 2 | |
| Augochloropsis nasuta Moure, 1944 | X | | | 1 | |
| Augochloropsis notophos (Vachal, 1903) | X | | 1 | | |
| Augochloropsis sp 1 | X | | 2 | | |
| Augochloropsis sp 2 | X | X | 7 | 3 | 2 |
| Augochloropsis sp 3 | X | X | | 1 | 1 |
| Neocorynura oiospermi (Schrottky, 1909) | X | 3 | 4 | 1 | |
| Pseudaugochlora indistincta Almeida, 2008 | X | | | 1 | |
| HALICTINI | | | | |
| Dialictus creusa (Schrottky, 1909) | X | | 1 | | |
| Dialictus sp 1 | X | | 1 | | |
| Dialictus sp | X | X | 1 | 2 | 3 |
| Pseudagapostemon (Neagapostemon) cf. cyanomelas Cure, 1989 | X | | | 1 | |
| MEGACHILIDAE | | | | |
| MEGACHILINAE | | | | |
| ANTHIDII | | | | |
| Anthidium manicatum (Linnaeus, 1758) | X | 1 | 1 | |
| MEGACHILINI | | | | |
| Megachile (Chrysosarus) pseudanthidioides Moure, 1943 | X | | 1 | 1 | |
| Megachile (Melanosarus) sp | X | | 2 | | |
| Megachile sp 1 | X | | 2 | | |
| Megachile sp 2 | X | 1 | | |
A comparison between the richness estimator Chao 1 and the sampled species’ richness values indicates that there may be even more bee species in the study area (Table 4) and there were greater bee species on ruderal flowers than on crops. The assemblages of bees collected on ruderal plants are not more diverse than those of crop plants, nor are they taxonomically more diverse (Table 4). Property S2 differs from these results, due to a smaller number of bee species collected on crop plants; this difference may be a consequence of not having planted tomatoes that year, a mass-flowering crop and prevalent in the Guapiara municipality. Property S3 was the only one that showed greater dominance in the bee assemblage collected on ruderal plants. However, the composition of bee species differs between crop and ruderal for the three properties (Table 4).

Table 3. Ruderal plant species, resource available for pollinators according to literature data (P: pollen; N: nectar), and number of floral visiting bee species (according to pollen analysis) at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013. In bold are the ruderal plant species visited by the greatest number of bee species.

| Family          | Species                      | Resource | Floral visiting bee species (N) | Rural properties |
|-----------------|------------------------------|----------|--------------------------------|------------------|
|                 |                              |          | S1                | S2 | S3 |
| Apocynaceae     | Aselepias curassavica        | N/P      | -                 | X  | X  | X  |
| Asteraceae      | Ageratum conyzoides          | N/P      | 7                 | X  | X  | X  |
|                 | Bidens alba                  | N/P      | 6                 | X  | X  |   |
|                 | Bidens pilosa                | N/P      | 11                | X  | X  | X  |
|                 | Emilia fosbergii             | N/P      | 4                 | X  |   | X  |
|                 | Galinsoga paviflora          | N/P      | 1                 | X  | X  |   |
|                 | Senecio brasiliensis         | N/P      | 4                 | X  | X  |   |
|                 | Sonchus oleraceus            | N/P      | 22                | X  | X  | X  |
|                 | Synderella nodiflora         | N/P      | 2                 | X  |   | X  |
|                 | Tithonia baccata             | N/P      | 2                 | X  | X  |   |
|                 | Tithonia diversifolia        | N/P      | -                 | X  |   |    |
|                 | Vernonon westiniana          | N/P      | -                 | X  | X  |   |
| Bignoniaceae    | Pyrostegia venusta           | N/P      | -                 |    |    | X  |
| Boraginaceae    | Cordia curassavica           | N        | -                 |    |    | X  |
| Brassicaceae    | Brassica rapa                | N/P      | 6                 | X  |   |    |
| Convolvulaceae  | Ipomea nill                  | N/P      | -                 | X  | X  | X  |
|                 | Ipomea triloba               | N/P      | -                 | X  |   |    |
| Euphorbiaceae   | Ricinus communis             | P        | 1                 | X  | X  |   |
| Lamia ce        | Leonurus sibiricus           | N        | 22                | X  | X  | X  |
| Malvaceae       | Sida rhombifolia             | P        | 4                 | X  | X  |   |
| Phytolaccaceae  | Phytolacca americana         | N/P      | -                 | X  |   | X  |
| Primulaceae     | Anagallis arvensis           | P        | -                 |    | X  | X  |
| Rosaceae        | Rubus rosifolius             | N/P      | 1                 | X  | X  | X  |
| Solanceae       | Solanum americanum           | P        | -                 | X  | X  |   |
|                 | Solanum erianthum            | P        | 1                 | X  | X  |   |
|                 | Solanum paniculatum          | P        | 2                 | X  | X  | X  |
| Verbenaceae     | Lantana camara               | N        | -                 | X  | X  | X  |
|                 | Stachytarpheta cayennensis   | N        | 4                 | X  | X  | X  |
| **Total species** |                              |          | **25**            | **20**| **15** |

Discussion

As we expected, species richness of bees visiting ruderal flowers was greater than the richness of bees visiting crop flowers, as well as differences in species composition. But we did not expect that there will be no differences concerning diversity (Shannon index) and average taxonomic breadth (Δ+). However, our results reinforce the importance of ruderal flora for increasing plant diversity on rural properties and thus contributing to bee diversity in agricultural landscapes. Studies conducted mostly in Europe and the United States have already evaluated the importance of plant diversity in agricultural areas, mainly in set-aside systems, and its positive effects on pollinator diversity (Carreck & Williams, 2002; Potts et al., 2003; Hopwood, 2008; Kuussaari et al., 2011; Tscharntke et al., 2011; Kovács-Hostyánszki et al., 2011; Torné-Noguera et al., 2014; Venturini et al., 2017).
Ruderal plants can provide an alternative food resource for pollinators, enabling these insects to remain in or be attracted to, crop areas where they visit the cultivated plant flowers as well as the ruderal plant flowers (Nicholls & Altieri, 2013). Our pollen analysis shows that both bee species that were sampled only on crop or ruderal flowers carried pollen grains from both types of plants, together with the result that 20 bee species were sampled in both types of plants, it strengthens the argument that ruderal plants are an alternative food source in agricultural landscapes (Luz et al., 2011; Luz et al., 2018; Santos et al., 2020). However, there is a lot of concern about ruderal plants competing with crop plants for pollinator visitation. For some crops, though, studies are showing that such competition does not occur (Lundin et al., 2017; Alomar et al., 2018; Knapp et al., 2019); instead, the presence of a richer ruderal plant community at the field scale favored a more diverse bee community (Norris et al., 2018; Knapp et al., 2019). In sunflower crops, for example, the presence of a diverse ruderal plant community within the crop field was responsible for increasing the diversity of flower visitors while also mitigating the negative effects of isolation on crops that were far from native vegetation remnants (Carvalheiro et al., 2011).

Of the 20 bee species in common between crop and ruderal plants (Table 1), some are well-studied crop pollinators. As is the case of bee genera Apis, Bombus, Melipona, Trigona, and Xylocopa, which are among effective pollinators of various crops, including those planted in our three rural properties studied (Giannini et al., 2015). Apis mellifera, Bombus morio, Bombus pauloensis, Melipona quadridiastica, Trigona spinipes, and Xylocopa frontalis are among the 14 most important bee species for the pollination of Brazilian crops, considering the economic value of the pollination and the number of pollinated crops by them (Giannini et al., 2020). For good agricultural production, a diverse pollinator fauna is necessary (Garratt et al., 2014), which in turn is maintained by a diverse flora at crop scale and adjacent off-crop habitats (Medeiros et al., 2017; Thompson et al., 2019).

Tomato is the predominant crop in the Guapiara municipality, the longest time flowering period (6 months) and also with the greatest bee species richness as floral visitors. Due to its long flowering period and wide distribution in the municipality, it can be considered a mass-flowering crop and an important pollen source, mainly for native bee species since they are the only ones capable of performing buzz pollination releasing pollen from the poricidal anthers of its flowers (Nunes-Silva et al., 2010). Although studies indicate positive and negative effects of mass-flowering crops on bee species richness and abundance (Holzschuh et al., 2011; Holzschuh et al., 2013; Diekotter et al., 2014; Holzschuh et al., 2016), it is recognized that a diversified flora in the region provide food resources in periods when the crops are not blooming, favoring pollinator populations permanence.

Plant diversity at crop scale is crucial for providing bees with diverse food sources, especially in agricultural regions with few remnants of native vegetation. Simplified landscapes, such as those dominated by monocultures, tend to harbor lower plant diversity and, therefore, lower quantity and quality of available food resources, which can compromise the fitness of bee individuals in the region. Renauld et al. (2016) verified that the offspring from the solitary bee Andrena nasonii Robertson, 1895 in homogeneous landscapes had a smaller body size than those born in landscapes with lower percentages of agricultural occupation. The availability of food resources throughout the seasons is closely related to plant diversity, which positively influences the fitness and population growth of social bees as well (Kaluza et al., 2018).

At the rural properties sampled in the present study, it is common practice for farmers to allow the free growth of ruderal plants in the post-harvest areas (Fig 4 C, E) and at the borders of the crop fields (Fig 4 A). Even though the practice is not intended to provide foraging places for bees, such sites are widely used by apicultural fauna (Fig 4 D, F). Measures such as those adopted by the farmers of Guapiara municipality favor the permanence of wild bee populations in agricultural areas, and they can potentially be replicated in other localities. Allowing ruderal plants to coexistence with crops, provided that the issues of plant health are observed, is a simple and low-cost measure for farmers and provides both economic and environmental benefits, as already presented by Carvalheiro et al. (2011). Our study has led us to conclude that ruderal plants help to enhance plant diversity at crop scale, which is crucial for providing bees with diverse food sources contributing to the permanence of these pollinators in agricultural landscapes.

### Table 4. Richness estimators, diversity and dominance indexes for bees sampled from crop and ruderal plants at three smallholder rural properties in Guapiara, São Paulo state, Brazil, between May 2012 and March 2013.

|                      | Property S1 | Property S2 | Property S3 |
|----------------------|-------------|-------------|-------------|
|                      | Crop        | Ruderal     | Crop        | Ruderal     | Crop        | Ruderal     |
| Species richness     | 19          | 23          | 6           | 39          | 18          | 28          |
| Chao 1               |             |             |             |             |             |             |
| Shannon-Wiener (H’)  | 2.35        | 2.4         | 1.76        | 2.69        | 2.3         | 2.95        |
| Simpson (D)          | 0.85        | 0.87        | 0.8         | 0.86        | 0.84        | 0.92        |
| Average taxonomic breadth (Δ+) | 80.46 | 80.15 | 58.83 | 87.66 | 80.63 | 80.86 |
| Jaccard (J)          | 0.7142      | 0.9052      | 0.7709      |             |             |             |
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Authors Contribution

P. C. M. carried out the fieldwork and performed the statistical analysis; M. J. O. C. participated in the design of the study and, P. C. M. and M. J. O. C. drafted the manuscript. All authors gave final approval for publication.

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