

Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years

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ABSTRACT. Bee fauna and associated flora from a grassland site in Brazil, surveyed 40 and 20 years ago, were newly surveyed with comparable methodology to evaluate changes in the bee fauna of this site, considering that human population and urbanization has exponentially increased in the last 40 years. In general, bee species richness has declined in 22%, as well as their abundance. Some of the previously abundant species are now absent, including *Bombus bellicosus* Smith, 1879, *Gaesischia fulgurans* (Holmberg, 1903) and *Thectochlora basiatra* (Strand, 1910). No particular trend of differential decrease among either taxonomic or functional groups was observed, except for a minor increase in the proportion of oligolectic species and a 50% reduction in the number of large species. The first two surveys were more similar to each other in species richness per bee genus, while the two most recent grouped together based on measures of anthropogenic impact. Furthermore, the number of plant species visited by bees increased, with a pronounced increase in ruderal and exotic species. Crop cultivation, competition with honeybees and climate changes may all be related to bee decline. Nevertheless, the effects of urbanization, in particular intense land occupation and few preserved natural areas can be pointed as the main causes of species decline. Due to continuing increase in human population, increased erosion in diversity is expected. Habitat protection is an additional challenge to bee conservation in the region, with no local conservation units set aside for grasslands. State and municipal agencies should urgently consider the establishment of reserves for the few remaining patches of natural grasslands.

KEY WORDS. Apidae; Apoidea; habitat fragmentation; pollinators; species richness; urban environments.

Bees play a fundamental role as pollinators of a large portion of plant species, affecting directly the maintenance and structure of biological communities. The association between bees and flowering plants represents the most important instance of mutualism in the Hymenoptera (LASALLE & GAULD 1993), and the disappearance of bees would be followed by the disappearance of many plant species (BIESMEIJER *et al.* 2006). Flowers are the main nutritional source for bees and, along with nesting materials, comprise their main habitat requirement (WESTRICH 1996). Thus, pollination is one of the most important ecological interactions for maintaining biodiversity, and one of the most economically valuable ecosystem services (KEVAN & PHILLIPS 2001, KLEIN *et al.* 2007, GALLAI *et al.* 2009). The maintenance of bee diversity along seasonal and annual cycles is essential for the efficient pollination of several crops (KLEIN *et al.* 2003, KREMEN *et al.* 2002).

Impacts caused by habitat loss and other anthropogenic changes on bee assemblages has been investigated through two basic approaches: 1) by comparisons between areas with varying degrees of human impact during the same time interval (e.g., ZANETTE *et al.* 2005, CANE *et al.* 2006), or 2) by comparisons

of changes in a specific area through time (e.g., MARLIN & LABERGE 2001, FRANKIE *et al.* 2009, KEARNS & OLIVERAS 2009a,b, BOMMARCO *et al.* 2012). These two types of monitoring, together with the study of plants that attract a large number of species or the use of trap-nests, were pointed out as essential for detection and control of the decrease in the number of pollinator populations (ALLEN-WARDEL *et al.* 1998, FRANKIE *et al.* 2002).

In the Neotropical region, the loss of habitat – due to deforestation or agricultural development – and the introduction of exotic species comprise the main threats to the bee fauna (FREITAS *et al.* 2009). However, well-documented examples of species decline are surprisingly uncommon (FREITAS *et al.* 2009) and only a single case of local extinction has been reported in Brazil (MARTINS & MELO 2009). The high diversity of the Brazilian bee fauna, with about 1,700 species (MELO 2007), is endangered due to a continuous process of urbanization and agricultural development. Here we provide the first documentation of negative impacts of anthropogenic development on the wild bee fauna in South America, based on three surveys conducted over the last 40 years in southern Brazil.

The first survey was conducted in the 1960s in a pioneer study of the bee fauna and associated flora in a grassland site in São José dos Pinhais (Paraná) (SAKAGAMI *et al.* 1967). This study was repeated two decades later and, although the number of species had remained the same, the number of genera and overall abundance both declined, dramatically for some species (BORTOLI & LAROCA 1990). A great increase in urbanization occurred around the study site between 1960 and 1980 and, in association with the increasing use of agricultural chemicals in the region, were pointed out as the main causes of the marked decline in bee abundance between the two surveys (BORTOLI & LAROCA 1990). Urbanization engenders serious consequences for the maintenance of bee diversity mainly due to the reduction of resources, including nesting sites and flower (food resource) abundance (LAROCA *et al.* 1982, ZANETTE *et al.* 2005, CANE 2005, FRANKIE *et al.* 2009).

To evaluate the current bee fauna and associated flora in this study area, we performed a one-year survey using the same collecting methodology after approximately 40 years since the first study. We identify the major changes in the richness and abundance of the wild bee fauna and flora, focusing on the main trends detected over the last 40 years of increasing urbanization and its impact on taxonomic and functional groups of wild bee fauna.

MATERIAL AND METHODS

The area of these surveys (SAKAGAMI *et al.* 1967, BORTOLI & LAROCA 1990) is a natural vegetation remnant, within the area of the Afonso Pena International Airport (25°32'S, 49°10'W), in São José dos Pinhais, Paraná, Brazil. The region comprises grassland (in the higher regions) and edaphic fields (in the lower regions subject to water overflow), and woodlands close to the rivers and patches of *Araucaria angustifolia* (Bertol.) Kunze forests (KLEIN & HATSCHBACH 1962). The climate is the Cfb type (Köppen), always humid, warm-mild pluvial, with more than five occurrences of frost each year.

The first survey in this area is hereafter referred to as S1 (SAKAGAMI *et al.* 1967), the second as S2 (BORTOLI & LAROCA 1990) and this study as S3. Significant urbanization occurred since S1 and S2, where the natural and agricultural areas were replaced by pavement or buildings (Figs 1-3). In addition to the urban matrix, the region around the study site is occupied by soybean fields within the airport area, and smaller plots of agricultural lands in the surroundings. Consequently our study site constitutes a patch of natural vegetation surrounded by urban or agricultural areas and is a likely refuge for the wild bee fauna.

Data on average temperature and precipitation in the study months during 2004 and 2005 were compiled from National Institute of Meteorology (INMET) database and compared to the normal climate records (1961-1990) for the region of São José dos Pinhais, from the Agronomical Institute of Paraná (IAPAR).



Figures 1-3. Aerial images of the study region in São José dos Pinhais, Brazil: (1) 1963; (2) 1980; (3) 2004. The airport runways are easily seen in the center of the images. Images from 1963 and 1980 are aerial photographs and that from 2004 is a Quikbird II satellite image (spatial resolution of 60 cm). The asterisks in Fig. 3 indicate the approximate center of the two sampling sites of the 2004-2005 study.

The collecting methodology of all three surveys consisted of sampling with entomological nets any bee visiting all flowering plants, in a predefined area during one year. In S3 the sampling took place at the warmest hours of the day, from 09:00-15:00 h, which includes the peak activity for most bee species (WILLIAMS *et al.* 2001), at two sites separated by about 2 km and comprising a total area of about 30,000 m² (Fig. 3). Collecting at each site was carried out by two collectors (ACM and RBG), once a month at each site, from August 2004 to July 2005. The collected specimens were combined into a single sample in our analysis, as in the previous studies. The total sampling hours varies among studies and was more similar between S1 (n = 134 hours) and S2 (n = 150 hours) performed by one collector, while in this study, 117 hours were performed by each of the two collectors during the sampling period (Table I).

In S3, numbers of *Trigona spinipes* (Fabricius, 1793) and *Apis mellifera* Linnaeus, 1758 were quantified in the field, since they are the most abundant species and are easily recognizable. Other bees were collected and further identified by RBG, GARM, and Danúncia Urban. Bee higher level classification follows MELO & GONÇALVES (2005). Bee vouchers were stored in the Coleção Entomológica Padre Jesus Santiago Moure (DZUP, Universidade Federal do Paraná) under accession numbers 23689 to 27388. Plant vouchers were deposited in the Botany Department herbarium (UPCB) of the Universidade Federal do Paraná, under accession numbers 58072 to 58179.

In addition to the original publications by SAKAGAMI *et al.* (1967) and BORTOLI & LAROCA (1990), data on the bee fauna of the 1960s were analyzed by SAKAGAMI & LAROCA (1971) and by S. Laroca in his unpublished master dissertation. We used these latter studies to complement some data not mentioned in the former studies. Taxonomic classification of the previous species lists was updated based on MOURE *et al.* (2007). Bee vouchers of S1 were not kept together in DZUP and the vouchers of S2 were not made available by the authors. For these reasons, we could not compare morphospecies among the three surveys and so most analyses were at the genus level, a solution adopted in other long-term studies (e.g., KEARNS & OLIVERAS 2009a). In S1 data of abundance were only provided for the most common species, which also limited our comparative analyses.

Bee species were placed in functional groups according to biological features most related with bee ecological habitat

requirements (WESTRICH 1996) and body size measured by intertegular distance (ITD) (CANE 1987). The defined groups of traits and respective states were: 1) Nest location (ground; pre-existing cavities); 2) Nesting behavior (solitary; eusocial; cleptoparasite); 3) Bee flower specificity (polylectic, generalist; oligolectic, specialist); and 4) Body size of females (ITD in mm) (1: 0.8-1.39; 2: 1.4-1.89; 3: 1.9-2.29; 4: 2.3-2.9; 5: > 3.0). Measurements of ITD for the bee genera were based on the species collected at the study site. The biological information was based mostly on MICHENER (2007). The biology of some genera is poorly known and, in those cases, traits were deduced from external morphological features, personal observations (GARM) or based on other closely related genera.

To establish a framework of anthropization in the area, we compiled data from the three sampling periods on 1) human population (BREMAEKER 2000, IPPUC 2006); 2) percentage of urban area; and 3) percentage of ruderal/exotic plant species.

Aerial photographs from 1963 and 1980 (Paraná's Environment State Agency – SEMA) and satellite image from 2004 (Urban Development Institute of São José dos Pinhais – IDU) were used to calculate the degree of urbanization in the three periods (Figs 1-3). The images were georeferenced and urban areas were delimited and their size calculated using the software ENVI 4.5 (ITT 2008). We considered as “urban” all areas presenting a regular matrix of buildings and roads, and the remaining non-urban areas were native grass fields, agricultural sites or non-paved roads.

To estimate the percentage of ruderal and exotic species we listed all plant species visited by the bee fauna in the three surveys and classified them by their original habitat and distribution: 1) native to the grasslands of southern Brazil, 2) native to *Araucaria* forests, and 3) widely spread ruderal native species or ruderal exotic species (non-native to the Brazilian flora). For plant sorting purposes, we were helped by botanists working in the herbariums of the Universidade Federal do Paraná (UPCB) and the Museu Botânico Municipal, Curitiba (MBM), familiar with Paraná's local flora.

The historical data from the previous surveys limited our options for analysis due to the lack of abundance information for most species in S1 and due to the impossibility of comparisons between morphospecies from the three surveys. Thus, for

Table I. Sampling effort (total number of hours per collector and total number of collectors in parenthesis), total number of species (S, in parenthesis, average number of species collected per hour, S/h), number of genera (G; in parenthesis, average number of genera per hour, G/h) and number of individuals (N), excluding *Apis mellifera* (in parenthesis, average number of specimens per hour, N/h), in the three surveys conducted in the airport at São José dos Pinhais. S1, 1962-1963 (SAKAGAMI *et al.* 1967), S2, 1981-1982 (BORTOLI & LAROCA 1990), S3, 2004-2005 (current study).

Survey	Periodicity	Sampling effort	S (S/h)	G (G/h)	N (N/h)
S1	weekly	134 (1)	167 (1.25)	45 (0.336)	4217 (32.4)
S2	weekly	150 (1)	167 (1.12)	37 (0.247)	1904 (12.9)
S3	fortnightly	117 (2)	131 (0.56)	39 (0.167)	1380 (5.9)

the most abundant species, we used Kato's method (KATO *et al.* 1952, LAROCA 1995), also employed by BORTOLI & LAROCA (1990) to compare the 1960s and 1980s faunas. This method consists of calculating the limits of relative abundance in percentage of dominant species, which are those presenting the lower confidence limit higher than the upper confidence limit for absent species based on the first survey (S1) (LAROCA 1995). The limits of relative abundance are calculated as follows: upper limit = $[(n1.fo)/(n2 + n1.fo)].100$, where $\{n1 = 2(K + 1); n2 = 2(N - K + 1)\}$ and lower limit = $[1 - (n1.fo)/(n2 + n1.fo)].100$, where $\{n1 = 2(N - K + 1); n2 = 2(K + 1)\}$, where "N" is the total amount of individuals collected, "K" is the number of individuals in each group and "fo" is obtained from the table of critical values of the F-distribution, at the 5% level of significance with n1 and n2 degrees of freedom.

The Bray-Curtis similarity index was used to compare the three surveys in relation to number of species per bee genus, as well as for degree of anthropization (see previous section), using the Vegan package version 1.8-8 (OKSANEN *et al.* 2007) implemented in the software R 2.5.0 (R DEVELOPMENT CORE TEAM 2007).

RESULTS

Current bee fauna and associated flora

The current assemblage of bees at the study site comprises 131 species, 130 of which are native, plus the exotic species *Apis mellifera* (Table I, Appendix 1). Seventy six (59%) were identified to species, while the other 53 were classified to morphospecies (Appendix 1). A total of 3,061 individuals were sampled, 1,681 (59%) were *A. mellifera*, and 1,380 native species, with *Trigona spinipes* (n = 173) being the most abundant, followed by *Augochlora iphigenia* Holmberg, 1886 (118), *Ceratina* (*Rhysozeratina*) sp. 1 (84), *Paroxystoglossa jocasta* (Schrottky, 1910) (80), *Ceratina asuncionis* Strand, 1910 (69), *Augochloropsis cleopatra* (Schrottky, 1902) (55), *A. iris* (Schrottky, 1902) (54), *Pseudagapostemon pruinosus* Moure & Sakagami, 1984 and *Bombus pauloensis* Friese, 1913 (49) (Appendix 1). Among the species collected, 99 (77%) are represented by fewer than 10 individuals, 20 (15%) by 11 to 49 individuals and eight (6%) by 50 or more individuals (Appendix 1).

A small portion of the 1,380 specimens, 73 individuals, were collected while they flew over the vegetation, and not on flowers. The remaining species were collected on 95 species of plants in 29 families (Appendix 2). Considering the flora visited by bees, Asteraceae was the most species-rich family, with 38 species, followed by Verbenaceae, with six species. Additionally, Convolvulaceae, Iridaceae, Lamiaceae, Rubiaceae, and Solanaceae stand out with four species each and the other families were represented by fewer than four species (Appendix 2).

Asteraceae had the largest number of bee visits followed by the next most visited families, in decreasing order of number of visits: Brassicaceae, Rosaceae, Malvaceae, Lamiaceae, Verbenaceae, and Apiaceae (Appendix 2). The families show-

ing the largest richness in visiting bee species are: Asteraceae (101 bee species), Apiaceae (22), Brassicaceae (21), Rosaceae (20), Malvaceae (19), Iridaceae (15), Verbenaceae (16), and Solanaceae (14) (Appendix 2). Some plant species stood out among those receiving a large number of visiting individuals: *Senecio oleosus* Vell., *Taraxacum officinale* Weber, *Baccharis myriocephala* DC., and *Raphanus raphanistrum* L. These four species, together with *Stevia veronicae* DC., are also those on which the largest richness of bee species were collected (Appendix 2).

Changes in the bee fauna and their associated flora

Species richness declined to the present survey, from 167 (S1 and S2) to 131, as well as a substantial decrease in number of individuals sampled, from 4217 (S1) to 1380 (S3) (Table I). S1 had a total of 167 species and 45 genera; S2, the same species richness, but only 37 genera; and S3 a total of 131 species and 39 genera (Appendix 3). In relative terms, taking into consideration the different sampling effort between the surveys, the reduction observed in S3 in both richness and abundance is much stronger, with the species capture rate in S3 reducing to less than 50% of that in S1 and to less than 20% in number of individuals collected per hour (Table I). Since the number of bee species remained unchanged in the interval of 20 years between S1 and S2 (Table I, Appendix 3), this suggests that events of population reduction precede the reduction in species richness, which was detected only in the current study.

The reduction in bee richness and abundance detected in S3 likely represents a long-term pattern and not the result of population fluctuation due to atypical climatic conditions prevalent during the sampling period, since the monthly climate variables (average temperature and precipitation) of the study months followed the averages expected for the region (data not shown; see Methods above).

Considering only the taxa identified to species, of a total of 113 species in the two previous surveys, 20 were absent in the present study (Appendix 4). Since there are no data on relative abundance for most of the species collected in S1 (Appendix 4), it is not possible to infer whether these 20 species are rare and consequently their absence in S3 would be simply a consequence of their rarity. However, some species cited as highly abundant in S1 or S2 are now absent, such as *Bombus bellicosus* Smith, 1879, *Gaesischia fulgurans* (Holmberg, 1903) and *Thectochlora basiatra* (Strand, 1910), and are apparently examples of local extinction (Fig. 4). Also, noticeable cases of population fluctuations were found, such as for *Trigona spinipes*, *Ceratina asuncionis* and *Bombus pauloensis* (Appendix 4, Fig. 4), as well as an increase in abundance of other species, including *Augochlora iphigenia*, *A. amphitrite* (Schrottky, 1910), *Augochloropsis iris* and *Bombus morio* Skorikov, 1922 (Appendix 4, Fig. 4).

Despite the decrease in richness and overall abundance, the relative proportions among the taxonomic groups are somewhat maintained, suggesting that the decrease in both richness and abundance are not taxonomic trends (Table II). Also, no particular trend is detected among the three surveys when

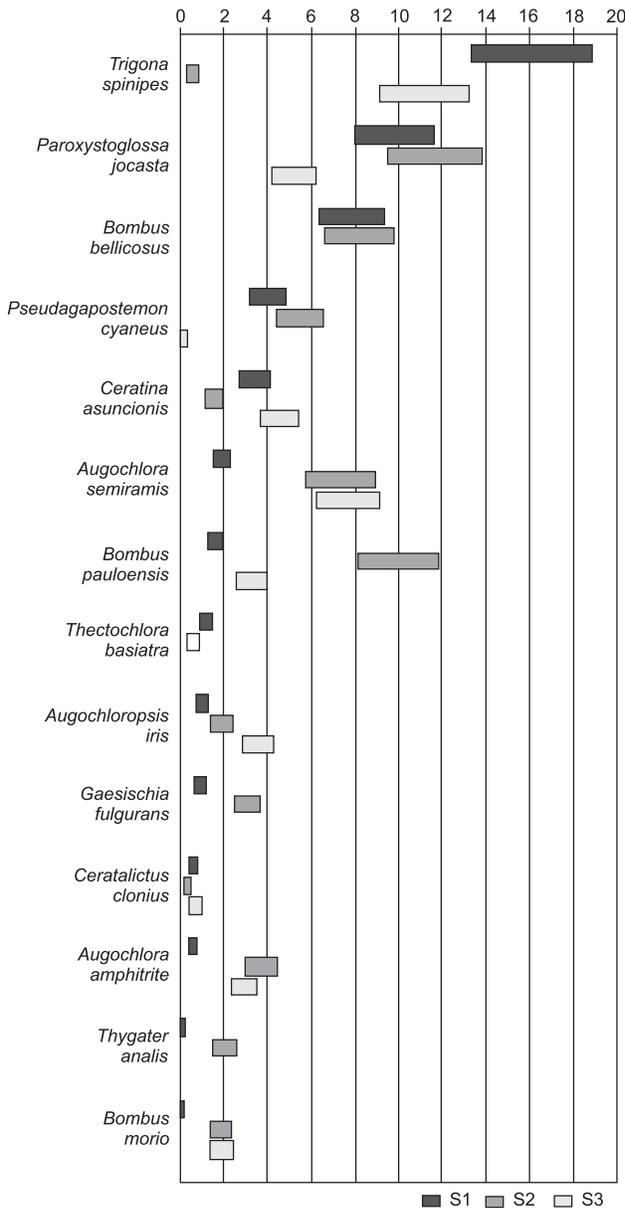


Figure 4. Graphical representation of the confidence limits of relative abundance (Kato index), in percentage, for the most abundant species in the three surveys conducted in the airport at São José dos Pinhais. Species are ordered, the most abundant at the top, based on the 1962-1963 survey. S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCA 1990); S3, 2004-2005 (current study).

comparing the variation in species diversity within functional groups (Table III). The proportion of species within each functional group seems to stay more or less constant across time, except perhaps for the small relative decrease in polylectic spe-

cies and a corresponding relative increase in oligolectic species, in the current survey (Table III). Female body size also maintained a similar proportion among the surveys, except for the group of large bees that had a decrease of about 50% from S1 to S3 (category 5 in Table III). Interestingly, the group of large bees (e.g., bumblebees and *Anthophora*) comprised only four species in S3 compared to 10 in S1 (Table III).

A total of 1681 honeybees were sampled in S3 (Appendix 1). Honeybee abundance was not quantified in the studies of SAKAGAMI *et al.* (1967) and BORTOLI & LAROCA (1990) and so its recent relative abundance cannot be compared with that of the previous studies. Approximate estimates in SAKAGAMI & LAROCA (1971) suggest (table 1 of that study) that honeybees in S1 were more abundant than all wild bees combined in 26 of the 36 collecting days.

Framework of anthropization

The human population in the municipality of São José dos Pinhais is ten times larger in S3 than it was in S1 (Table IV). At the time of S2 the human population had increased approximately three times, from 20,111 to 70,634 inhabitants in the two decades since S1, and in the 2000s population size was more than 200 thousand inhabitants (Table IV).

The portion occupied by urban areas around the study site grew considerably from the 1960s to 2000s (Figs 1-3). In the 1960s, the urban matrix comprised only ~5% of the total area, increasing to 32% in the 1980s and to 56% in the 2000s (Table IV). The remaining area was considered as non-urban and included crop and pasture fields, patches of native grasslands, small forest fragments, as well as unpaved roads.

The number of plant species visited by bees increased considerably from 67 species in the first survey to 92 species in S3 (Fig. 5). In reference to habitat preference of the plants, the number of species associated with grasslands and forest habitats has remained similar over all studies. On the other hand, the number of ruderal native and exotic plant species has tripled, from 10 (15%) in the first survey to 34 (37%) in this study (Table IV, Fig. 5).

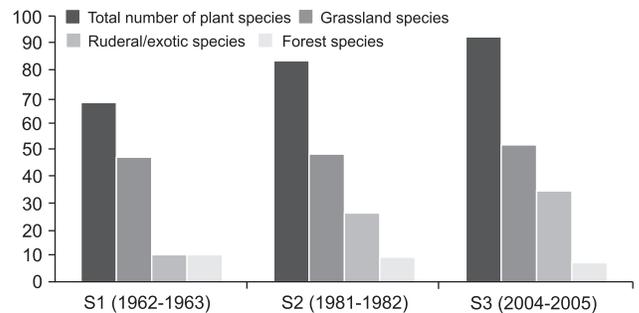


Figure 5. Total number of plant species visited by bees and number of species by category of habitat preference, in the three surveys conducted in the airport at São José dos Pinhais.

Table II. Comparative richness (R) and abundance (A), by bee subfamily, in the three surveys conducted in the airport at São José dos Pinhais; abundance data for *Apis mellifera* not included (see Appendix 1). S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCCA 1990); S3, 2004-2005 (current study).

Subfamilies	S1				S2				S3			
	R	%	A	%	R	%	A	%	R	%	A	%
Andreninae	17	10.1	137	3.2	20	11.9	76	4.0	12	9.1	70	5.1
Apinae	34	20.2	1515	35.9	36	21.4	659	34.6	33	25.2	474	34.3
Colletinae	10	5.9	43	1.0	7	4.2	17	0.9	8	6.1	21	1.5
Halictinae	88	52.4	2439	57.8	79	47.0	1088	57.1	64	48.9	766	55.5
Megachilinae	19	11.3	83	2.0	26	15.5	66	3.5	14	10.7	49	3.5
Total	167		4217		167		1906		131		1380	

Table III. Number of bee species (N) in each of the ecological functional groups. *Apis mellifera* excluded. S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCCA 1990); S3, 2004-2005 (current study). Body size measured by intertegular distance of females (in mm): 1: 0.8-1.39; 2: 1.4-1.89; 3: 1.9-2.29; 4: 2.3-2.9; 5: > 3.0.

Ecological functional group		S1		S2 ¹		S3	
		N	%	N	%	N	%
Nesting habit ²	Ground	118	76.1	116	70.7	92	76.0
	Cavity	37	23.9	48	29.3	29	24.0
Nesting behavior	Solitary ³	149	89.2	160	96.4	116	89.2
	Eusocial	6	3.6	4	2.4	5	3.9
	Cleptoparasite	12	7.2	2	1.2	9	6.9
Trophic specialization ²	Polylectic	132	85.2	142	86.6	97	80.2
	Oligolectic	23	14.8	22	13.4	24	19.8
Body size categories	1	68	40.7	63	38.0	47	36.2
	2	43	25.7	37	22.3	41	31.5
	3	16	9.6	20	12.0	12	9.2
	4	30	18.0	38	22.9	26	20.0
	5	10	6.0	8	4.8	4	3.1

¹A single species, identified only as "Gen. A", was left out; ²Cleptoparasitic species were not included; ³Some of these species might have communal or semisocial colonies.

Table IV. Degree of anthropization in the study site surroundings, as measured by human population (number of inhabitants in the city of São José dos Pinhais, Paraná, Brazil) and amount of urban area (in percentage of the total area; see Figs 1-3), and classification of plant species by habitat preference (in parenthesis, percentage of the total). S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCCA 1990); S3, 2004-2005 (current study).

Survey	Population	Urban area (%)	Plants			Total
			Grasslands	Ruderal/exotic	Forest	
S1	20,111	5.5	47 (70)	10 (15)	10 (15)	67
S2	70,634	32.0	48 (58)	26 (31)	9 (11)	83
S3	204,316	56.0	51 (55)	34 (37)	7 (8)	92

When the three factors analyzed above were taken together as a measure of the degree of anthropization the two most recent surveys (S2 and S3) are more similar to each other, based on Bray-Curtis similarity ($BC_{S2-S3} = 0.51$), than either is with S1 ($BC_{S1-S3} = 0.18$, $BC_{S1-S2} = 0.44$). In terms of bees (species per genus), S1 and S2 are more similar to each other ($BC_{S1-S2} = 0.79$) than to S3 ($BC_{S1-S3} = 0.74$, $BC_{S2-S3} = 0.67$).

DISCUSSION

The clear decline in both species richness and abundance over the past 40 years suggests that large impacts of urbanization may be common. While the current bee fauna is similar to that found in more preserved grassland sites in southern Brazil (GONÇALVES *et al.* 2009), some species have disappeared

(e.g., *Bombus bellicosus*, *Thectochlora basiatra* and *Gaesischia fulgurans*) yet all of the major bee groups and genera seem to have been affected similarly during the intervening period.

Previous studies indicated a differential decrease of functional bee groups subject to habitat loss, such as oligolectic species (BIJMEIJER *et al.* 2006, CANE *et al.* 2006). Contrary to what was expected, we found a slight increase in the overall percentage of oligolectic species in S3, and a concomitant decrease in the proportion of polylectic species. This observation should be treated cautiously because current understanding of flower specialization in these species is poor. In addition to polylectic species, large bee species declined in numbers by 50%, while no changes were detected for the other body size categories. Larger bees can forage greater distances than small bees (GREENLEAF *et al.* 2007), but success in resource acquisition is certainly affected by the quality of the matrix in which they forage, and which here has been strongly impoverished by intense urbanization. Cleptoparasitic bees are also susceptible to habitat disturbance and fragmentation (BORTOLI & LAROCA 1990, LAROCA & ORTH 2002, CALVILLO *et al.* 2010), but here we found no evidence of decline in this group. These different responses of functional categories among distinct habitats are influenced not only by the disturbance *per se*, but also by climate, land use history and landscape structure that may come as a consequence of disturbance (MORETTI *et al.* 2009).

Globally, mostly bee declines have been attributed to habitat fragmentation and loss, agrochemicals, pathogens, alien species, climate change and their interactions (POTTS *et al.* 2010 and references therein). We propose that the main causes of the accentuated declines that we observed in the wild bee fauna include: 1) habitat loss due to increased human occupation, 2) changes in species composition of the available flower sources due to introduction of exotic plants, 3) global climate changes, and 4) competition with exotic honeybees.

Habitat loss, by urbanization and agricultural development, is considered to be the main cause of bee decline worldwide (FREITAS *et al.* 2009, POTTS *et al.* 2010, PATINY *et al.* 2009, WILLIAMS & OSBORNE 2009). Urbanization results in decreased availability of exposed soil for nests, ground nesting species in particular (CANE 2005, CANE *et al.* 2006, ZANETTE *et al.* 2005) as well as for the establishment of food plants within the bee's flying radius. In some urban areas in North America no changes in overall species richness (KEARNS & OLIVERAS 2009a) or variable responses (depending on the functional group) have been observed, such as the increase in richness of bee species that nest in preexisting cavities (CANE *et al.* 2006, TSCHARNTKE *et al.* 1998). This response shows that, for some species, urbanization is not always detrimental to all bees.

Areas of natural vegetation remnants in large cities may serve as refuges, depending upon the quality of the surrounding matrix for foraging (McFREDERICK & LEBUHN 2006, STEFFAN-DEWENTER *et al.* 2002). Urbanization around our study site has been very intense, leaving almost nothing of the original habitats, as well

as with extensive modification of the surrounding matrix (Figs 1-3) due to exponential human population growth (Table IV). Within urban areas, habitat type is a very important influence on species composition, with residential areas and urban peripheries richer in species than city centers (LOSOSOVÁ *et al.* 2011). Comparing our study site (an urban periphery) to a nearby urban center park (Passeio Público Park in the city of Curitiba), we find a similar trend in which the central city park has a much more impoverished wild bee fauna (TAURA & LAROCA 2001).

Agricultural development at the study site, especially soybeans that today occupies more than 200 ha within the airport area, is likely to have negatively impacted the bees as well. Pesticides along with other agrochemicals may cause impoverishment of bee faunas (e.g., KEARNS *et al.* 1998, KREMEN *et al.* 2002) and was previously noted as one of the factors causing the decrease in bee abundance in S2 (BORTOLI & LAROCA 1990). Yet, despite changes in the original vegetation cover, agriculture and cattle ranching may maintain larger portions of suitable habitats for nests and food plants for bees (MARLIN & LABERGE 2001), with less impact than that due to urban sprawl (CANE 2005).

Long-term changes at the study site include floral composition visited by bees, and an increase in the number of visited plants as a consequence of the increase in the number of ruderal and exotic species. In the 1960s, ruderal plants comprised 15% of those visited by bees, while now they comprise 37% (Table IV). Also, the number of introduced plant species increased in S2 in the 20-year interval between the first two surveys (BORTOLI & LAROCA 1990: fig. 19). Functional diversity in plants may often be more important than species richness (DÍAZ & CABIDO 2001) and thus a substantial increase in the number of exotic plant species is likely to influence the availability of adequate food sources.

In the last few decades, global climate change caused by humans has threatened the survival of several species around the world (WILLIAMS *et al.* 2007). Although not widely studied in insects, climate change is likely to be a critical factor that will influence changes in species distribution and local extinction events. Climate change has been suggested as the main cause for local extinction of *Bombus bellicosus* at our study site and elsewhere in the state of Paraná (MARTINS & MELO 2009). This bumblebee is associated with regions with mild climates in southern South America, and Paraná is the northern limit of its original distribution (MARTINS & MELO 2009). Other factors, however, are also important causes of bumblebee decline worldwide (WILLIAMS & OSBORNE 2009), such as changing land use patterns, introduction of parasites from commercial colonies (MEEUS *et al.* 2011) and changes in the yearly supply of flower resources (CARVELL *et al.* 2006). Differences in tongue length and diet breadth of bumblebees living in the same region have been implicated in their differential decline (BOMMARCO *et al.* 2012). Nonetheless, because there are no records of exotic bumblebees, particularly *Bombus terrestris* (Linnaeus, 1758), in Brazil and since other bumblebee species in the area have not

been affected, the parasite hypothesis seems unlikely to be involved in the local extinction of *B. bellicosus* and so climate change remains as an important possibility.

Honeybees were reported from the study site since S1 (SAKAGAMI & LAROCA 1971) and were dominant in all three surveys. Potential and real impacts of *Apis mellifera* on the native bee fauna in the Neotropical region have not been conclusively resolved (e.g., PEDRO & CAMARGO 1991, WILMS & WIECHERS 1997, ROUBIK & WOLDA 2001). Honeybees as competitors is undeniable: populations are large, their foraging spectrum is vast and they remain active throughout the year (in tropical and subtropical regions), with extensive niche overlap with native species. This only implies competition for resources if their availability may be limiting (GOULSON 2003). Nevertheless, no studies have yet concluded that feral honeybees cause extinction of native bees (MORITZ *et al.* 2005) with a few exceptions, such as on islands (KATO *et al.* 1999, KATO & KAWAKITA 2004).

The long-term comparisons presented here document a steady decline in the diversity and abundance of the native bees at our study site and the negative effects of rapid urbanization taking place in most Brazilian cities. As the number of inhabitants is continually growing in the area – with already more than 250,000 in 2010 (IBGE 2010) – a continued impoverishment over time of the bee fauna is expected. The natural grasslands of southern Brazil are extremely endangered and poorly protected by few natural parks, especially in the state of Paraná (OVERBECK *et al.* 2009, VÉLEZ *et al.* 2009). Habitat protection is an additional challenge to bee conservation in the region, with no local conservation units set aside for grasslands. State and municipal agencies should urgently consider the establishment of reserves that include in addition to forest remnants, the few remaining patches of natural grasslands. Last but not least, to preserve these essential pollinators in the urban environments, Brazilian cities should include a larger portion of suitable places to wild bee fauna in their planning (e.g., city parks, squares and bee-friendly gardens).

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Appendix 1. Bee species collected in the period between August, 2004 and July, 2005 in two grassland sites within the Afonso Pena airport, in São José dos Pinhais, Paraná, Brazil. The number of individuals of each sex and also the number of individuals collected in each month are given. The last column indicates the plant species visited (see Appendix 2 for plant species ID).

Bee species	ID	F	M	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total	Plant species ID
Andreninae																	
Calliopsini																	
<i>Acamptopoeum prinii</i> (Holmberg, 1884)	1	1	0	-	-	-	-	-	-	-	-	1	-	-	-	1	87
Protandrenini																	
<i>Anthrenoides antonii</i> Urban, 2005	2	1	1	-	-	2	-	-	-	-	-	-	-	-	-	2	18
<i>Anthrenoides alvarengai</i> Urban, 2007	3	1	0	-	-	-	-	1	-	-	-	-	-	-	-	1	73
<i>Anthrenoides larocai</i> Urban, 2005	4	3	0	-	-	1	2	-	-	-	-	-	-	-	-	3	59,63,64
<i>Anthrenoides meridionalis</i> (Schrottky, 1906)	5	2	0	-	-	1	-	-	-	-	-	-	-	-	-	2	39
<i>Anthrenoides rodrigoii</i> Urban, 2005	6	1	0	-	-	-	1	-	-	-	-	-	-	-	-	1	43
<i>Anthrenoides politus</i> Urban, 2005	7	2	1	-	-	-	3	-	-	-	-	-	-	-	-	3	33,39
<i>Psaenythia annulata</i> Gerstaecker, 1868	8	14	8	-	-	2	8	6	-	5	1	-	-	-	-	22	2,14,29,34,37,3943,79
<i>Psaenythia bergii</i> Holmberg 1884	9	7	10	-	-	-	3	8	1	4	1	-	-	-	-	17	2,11,14,33,34,3943,47,78
<i>Psaenythia collaris</i> Schrottky, 1906	10	13	1	-	12	2	-	-	-	-	-	-	-	-	-	14	13,34,39,90,94
<i>Rhophitulus anomalus</i> (Moure & Lucas-de-Oliveira, 1962)	11	1	1	-	-	-	-	-	-	-	1	-	-	-	-	2	67,68
<i>Rhophitulus</i> sp. 1	12	2	0	-	-	-	-	-	1	1	-	-	-	-	-	2	11
Apinae																	
Apini																	
<i>Apis mellifera</i> Linnaeus, 1758	13	1681	-	206	127	261	43	22	198	304	65	190	16	145	104	1681	2,5,6,7,8,9,10,11,13,14,16,25,26,27,29,30,31,32,35,36,37,38,39,40,41,44,47,50,52,56,57,60,61,62,71,72,76,77,88,89,90,94
<i>Bombus pauloensis</i> Friese, 1913	14	40	9	2	3	8	4	3	7	13	-	9	1	2	2	49	2,11,19,23,34,37,39,41,42,43,50,55,56,78,63,64,82,88,89,94
<i>Bombus morio</i> (Swederus, 1787)	15	14	4	-	-	1	1	2	-	7	6	1	-	-	-	18	23,50,89
<i>Melipona quadrifasciata</i> Lepeletier, 1836	16	2	-	-	-	-	-	-	1	1	-	-	-	-	-	2	34,41
<i>Tetragonisca angustula</i> (Latreille, 1811)	17	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	34
<i>Trigona spinipes</i> (Fabricius, 1793)	18	173	-	23	59	-	2	2	10	4	2	2	32	20	17	173	7,10,27,30,34,3943,47,50,51,57,59,60,64,68,69,74,77,85,87,89,90,95
Emphorini																	
<i>Melitoma segmentaria</i> (Fabricius, 1804)	19	1	1	-	-	-	-	2	-	-	-	-	-	-	-	2	49
<i>Melitoma</i> sp. 1	20	0	1	-	-	-	-	1	-	-	-	-	-	-	-	1	86
Eucerini																	
<i>Melissodes nigroaenea</i> (Smith, 1854)	21	1	0	-	-	-	-	-	-	-	1	-	-	-	-	1	68
<i>Melissoptila aureocincta</i> Urban, 1968	22	0	1	-	-	-	-	1	-	-	-	-	-	-	-	1	39
<i>Melissoptila cnecomala</i> (Moure, 1944)	23	3	0	-	-	-	-	-	-	-	3	-	-	-	-	3	68
<i>Melissoptila minarum</i> (Bertoni & Schorrotky, 1910)	24	4	2	-	-	-	-	-	-	-	1	5	-	-	-	6	6,68,37
<i>Melissoptila paraguayensis</i> (Brèthes, 1909)	25	1	0	-	-	-	-	-	-	1	-	-	-	-	-	1	16
<i>Melissoptila setigera</i> Urban, 1998	26	2	0	-	-	-	-	-	-	-	-	2	-	-	-	2	72
<i>Melissoptila similis</i> Urban, 1988	27	1	0	-	-	-	-	-	-	-	-	1	-	-	-	1	29
<i>Melissoptila thoracica</i> (Smith, 1854)	28	3	2	-	-	-	-	-	-	-	3	2	-	-	-	5	47,68
<i>Thygater analis</i> (Lepeletier, 1841)	29	1	0	-	-	-	-	-	-	-	-	1	-	-	-	1	69
Exomalopsini																	
<i>Exomalopsis (Exomalopsis) analis</i> Spinola, 1853	30	3	0	-	-	-	-	-	-	-	-	3	-	-	-	3	23,37,38
<i>Exomalopsis (Phanomalopsis) trifasciata</i> Brèthes, 1910	31	5	0	-	-	-	1	1	1	-	-	2	-	-	-	5	31,37,54,88
Nomadini																	
<i>Brachynomada</i> sp. 1	32	0	1	-	1	-	-	-	-	-	-	-	-	-	-	1	34
<i>Brachynomada</i> sp. 2	33	0	1	-	-	-	1	-	-	-	-	-	-	-	-	1	39
<i>Nomada</i> sp. 1	34	0	1	-	-	-	1	-	-	-	-	-	-	-	-	1	33
<i>Nomada</i> sp. 2	35	0	1	-	-	-	-	-	-	-	-	1	-	-	-	1	37

Continues

Appendix 1. Continued.

Bee species	ID	F	M	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total	Plant species ID
Tapinotaspini																	
<i>Lanthanomelissa betinae</i> Urban, 1995	36	0	4	-	-	-	4	-	-	-	-	-	-	-	-	4	33,66
Xylocopini																	
<i>Ceratina (Ceratinula) cf. biguttulata</i> (Moure, 1941)	37	2	1	-	-	-	1	-	-	-	-	-	-	-	1	3	27,42,43
<i>Ceratina (Ceratinula) sp. 1</i>	38	3	3	2	-	-	1	-	1	1	-	-	1	-	-	6	34,43,47,68
<i>Ceratina (Ceratinula) sp. 2</i>	39	1	1	-	-	-	1	-	1	-	-	-	-	-	-	2	27,42
<i>Ceratina (Crewella) asuncionis</i> Strand, 1910	40	42	27	20	7	1	-	5	10	3	1	6	8	8	-	69	1,12,13,14,16,2223,27,29,31,34,35,37,38,39,41,42,45,49,68,80 84,89,90,94
<i>Ceratina (Crewella) rupestris</i> Holmberg, 1884	41	1	0	-	-	-	-	-	1	-	-	-	-	-	-	1	39
<i>Ceratina (Rhysoceratina) sp. 1</i>	42	59	25	21	10	4	7	1	17	2	1	-	1	-	3	84	2,11,12,13,15,1620,21,22,26,29,34,39,41,42,43,64,65,68,73,78, 79,80,83,86,94
<i>Ceratina (Rhysoceratina) sp. 2</i>	43	1	0	-	-	-	-	-	-	-	-	-	-	1	-	1	34
<i>Ceratina (Rhysoceratina) sp. 3</i>	44	0	3	2	-	-	-	1	-	-	-	-	-	-	-	3	21,34
<i>Xylocopa (Neoxylocopa) augusti</i> Lepeletier, 1841	45	4	1	-	3	1	1	-	-	-	-	-	-	-	-	5	55
Colletinae																	
Colletini																	
<i>Colletes rugicollis</i> Friese, 1900	46	0	1	-	-	-	-	-	1	-	-	-	-	-	-	1	27
Hylaeini																	
<i>Hylaeus (Hylaeopsis) sp. 1</i>	47	0	1	-	1	-	-	-	-	-	-	-	-	-	-	1	77
Neopasiphaeini																	
<i>Perditomorpha leaena</i> (Vachal, 1909)	48	0	1	-	-	-	-	-	-	-	1	-	-	-	-	1	68
<i>Belopria zonata</i> Moure, 1956	49	0	1	-	1	-	-	-	-	-	-	-	-	-	-	1	8
<i>Belopria sp. 1</i>	50	0	2	-	2	-	-	-	-	-	-	-	-	-	-	2	*
<i>Tetraglossula anthracina</i> (Michener, 1989)	51	1	2	-	-	-	-	-	-	-	-	3	-	-	-	3	72
Xeromelissini																	
<i>Chilicola (Oediscisca) sp. 1</i>	52	2	2	-	-	-	2	-	-	1	-	1	-	-	-	4	1,34,37
<i>Chilicola (Prospoides) sp. 1</i>	53	6	2	-	1	-	1	-	1	1	-	2	1	-	1	8	1,34,37,39
Halictinae																	
Augochlorini																	
<i>Augochlora amphitrite</i> (Schrottky, 1910)	54	42	2	4	10	2	1	8	11	2	-	-	3	2	1	44	34,36,39,43,47
<i>Augochlora iphigenia</i> Holmberg, 1886	55	113	5	15	31	15	11	22	7	1	3	3	3	6	1	118	12,16,20,21,24,29,34,36,37,39, 42,50,59,68,77,88,92,94
<i>Augochlora sp. 1</i>	56	7	2	-	-	-	-	-	-	-	1	6	-	2	-	9	1,23,34,37,48
<i>Augochlora sp. 2</i>	57	1	0	-	1	-	-	-	-	-	-	-	-	-	-	1	26
<i>Augochlora sp. 3</i>	58	4	2	-	3	-	1	1	-	-	-	-	-	-	1	6	8,39,43,74,90
<i>Augochlora ephyra</i> (Schrottky, 1910)	59	2	0	1	-	1	-	-	-	-	-	-	-	-	-	2	43,58
<i>Augochlora iopocila</i> Moure, 1950	60	1	0	-	-	-	-	-	-	-	-	1	-	-	-	1	84
<i>Augochloropsis anisitsi</i> (Schrottky, 1908)	61	1	0	-	-	-	-	-	-	-	-	-	-	-	1	1	34
<i>Augochloropsis aff. cleopatra</i> (Schrottky, 1902)	62	30	25	-	1	1	5	12	7	4	-	21	4	-	-	55	1,2,8,11,12,16,18,31,35,37,38, 39,88,89
<i>Augochloropsis cupreola</i> (Cockerell, 1900)	63	7	4	-	1	-	-	-	4	2	1	2	1	-	-	11	11,12,16,29,53,68,80,89
<i>Augochloropsis iris</i> (Schrottky, 1902)	64	26	28	-	5	1	10	5	9	6	2	16	-	-	-	54	1,2,7,11,16,27,29,31,34,37,38,59,69,77,87,88,92
<i>Augochloropsis liopelte</i> (Moure, 1940)	65	3	2	-	-	-	2	-	3	-	-	-	-	-	-	5	15,16,25,34,41
<i>Augochloropsis multiplex</i> (Vachal, 1903)	66	19	1	2	13	-	-	1	3	-	-	-	-	1	-	20	11,16,30,39,77,93
<i>Augochloropsis sympleres</i> (Vachal, 1903)	67	6	0	1	-	1	1	-	2	1	-	-	-	-	-	6	11,30,59,70
<i>Augochloropsis sp. 1</i>	68	11	2	-	4	-	-	1	2	1	-	3	-	-	2	13	1,8,11,14,27,38,39,41,77
<i>Augochloropsis sp. 2</i>	69	1	0	-	-	-	1	-	-	-	-	-	-	-	-	1	69
<i>Augochloropsis sp. 3</i>	70	13	1	2	2	-	-	1	2	1	2	3	1	-	-	14	4,11,29,30,34,36,37,39,51,68,77
<i>Augochloropsis sp. 4</i>	71	0	1	-	-	-	-	-	-	1	-	-	-	-	-	1	69
<i>Augochloropsis sp. 5</i>	72	3	1	1	2	-	-	-	-	-	-	-	-	1	-	4	27,30,85,93

Continues

Appendix 1. Continued.

Bee species	ID	F	M	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total	Plant species ID
<i>Augochloropsis</i> sp. 6	73	1	0	–	–	–	–	–	–	–	–	–	1	–	–	1	47
<i>Augochloropsis</i> sp. 7	74	1	0	–	1	–	–	–	–	–	–	–	–	–	–	1	77
<i>Augochloropsis</i> sp. 8	75	1	0	–	–	–	–	–	–	–	–	1	–	–	–	1	37
<i>Ceratalictus clonius</i> (Brèthes, 1909)	76	7	2	–	1	1	–	3	3	1	–	–	–	–	–	9	1,2,27,31,39,77
<i>Ceratalictus psorasps</i> (Vachal, 1911)	77	11	0	–	–	7	–	–	–	2	–	1	1	–	–	11	1,11,12,13,37,59,79
<i>Neocorynura aenigma</i> (Gribodo, 1894)	78	13	7	–	10	–	–	5	1	2	–	2	–	–	–	20	2,11,16,37,39,77
<i>Neocorynura atomarginata</i> (Cockerell, 1901)	79	4	0	–	3	–	–	1	–	–	–	–	–	–	–	4	2,77
<i>Paroxystoglossa andromache</i> (Schrottky, 1909)	80	2	1	–	2	–	–	–	1	–	–	–	–	–	–	3	11,77
<i>Paroxystoglossa brachycera</i> Moure, 1960	81	1	0	–	1	–	–	–	–	–	–	–	–	–	–	1	39
<i>Paroxystoglossa jocasta</i> (Schrottky, 1910)	82	53	27	16	4	6	14	1	20	12	–	6	1	–	–	80	1,5,8,11,16,27,29,31,34,36,37,38,39,59,60,75,77
<i>Paroxystoglossa</i> sp. 1	83	1	0	1	–	–	–	–	–	–	–	–	–	–	–	1	36
<i>Pseudaugochlora</i> sp. 1	84	4	6	–	4	–	–	1	1	2	–	1	–	–	1	10	40,43,63,65,74,79,85,88
<i>Rhinocorynura viridis</i> Gonçalves & Melo, 2012	85	1	0	–	–	–	1	–	–	–	–	–	–	–	–	2	
<i>Temnosoma</i> sp. 1	86	1	0	–	–	–	–	–	–	–	–	–	–	–	1	1	27
Halictini																	
<i>Caenohalictus tessellatus</i> (Moure, 1940)	87	3	11	–	3	–	1	5	5	–	–	–	–	–	–	14	2,3,8,11,27,77
<i>Caenohalictus</i> cf. <i>palumbes</i> (Vachal, 1903)	88	1	0	–	–	–	–	–	–	–	–	–	1	–	–	1	[collected in flight]
<i>Dialictus nanus</i> (Smith, 1879)	89	11	0	2	1	–	3	1	3	–	–	–	1	–	–	11	3,11,12,39,43,75,77
<i>Dialictus autranellus</i> (Vachal, 1904)	90	1	0	–	1	–	–	–	–	–	–	–	–	–	–	1	77
<i>Dialictus bruneriellus</i> (Cockerell, 1918)	91	1	0	–	–	–	–	1	–	–	–	–	–	–	–	1	39
<i>Dialictus opacus</i> (Moure, 1940)	92	11	0	1	–	1	1	1	5	2	–	–	–	–	–	11	11,39,59,75
<i>Dialictus rostratus</i> (Moure, 1947)	93	1	0	–	–	–	–	–	–	–	1	–	–	–	–	1	17
<i>Dialictus</i> sp. 1	94	2	0	–	1	1	–	–	–	–	–	–	–	–	–	2	36,39
<i>Dialictus</i> sp. 2	95	1	0	–	–	–	–	–	–	–	–	–	–	–	1	1	43
<i>Dialictus</i> sp. 3	96	1	0	1	–	–	–	–	–	–	–	–	–	–	–	1	39
<i>Dialictus</i> sp. 4	97	2	0	–	–	1	–	–	–	–	1	–	–	–	–	2	39
<i>Dialictus</i> sp. 5	98	8	0	1	–	1	1	3	–	2	–	–	–	–	–	8	30,33,39,68
<i>Dialictus</i> sp. 6	99	1	1	–	1	–	–	–	1	–	–	–	–	–	–	2	27,77
<i>Dialictus</i> sp. 7	100	1	0	–	–	–	–	–	1	–	–	–	–	–	–	1	39
<i>Dialictus</i> sp. 8	101	9	0	3	4	–	–	–	–	–	–	2	–	–	–	9	36,38,39,43,47,77
<i>Dialictus</i> sp. 9	102	5	0	–	–	–	–	–	1	3	–	–	1	–	–	5	12,39,83
<i>Dialictus</i> sp. 10	103	34	0	1	1	5	6	12	4	3	–	–	2	–	–	34	3,12,29,36,39,43,75,79,83
<i>Dialictus</i> sp. 11	104	23	1	3	–	5	4	5	2	3	–	1	1	–	–	24	2,12,15,16,28,36,37,39,43,46,59,78,83
<i>Dialictus</i> sp. 12	105	10	0	6	–	–	–	2	2	–	–	–	–	–	–	10	14,36,39,43
<i>Dialictus</i> sp. 13	106	32	4	5	6	16	6	2	–	–	1	–	–	–	–	36	2,8,26,33,36,39,42,43,59,75,79,85
<i>Dialictus</i> sp. 14	107	10	1	–	3	–	3	4	1	–	–	–	–	–	–	11	33,39,43,60,77,85
<i>Dialictus</i> sp. 15	108	8	0	–	3	1	1	1	2	–	–	–	–	–	–	8	39,68,74,90
<i>Dialictus</i> sp. 16	109	0	1	–	–	–	1	–	–	–	–	–	–	–	–	1	33
<i>Dialictus</i> sp. 17	110	0	1	–	–	–	1	–	–	–	–	–	–	–	–	1	33
<i>Dialictus</i> sp. 18	111	0	2	–	–	–	–	–	–	–	–	–	2	–	–	2	12
<i>Dialictus</i> sp. 19	112	0	1	–	–	–	–	–	–	1	–	–	–	–	–	1	7
<i>Dialictus</i> sp. 20	113	0	1	–	–	–	–	–	–	1	–	–	–	–	–	1	57
<i>Dialictus</i> sp. 21	114	0	1	–	–	–	–	1	–	–	–	–	–	–	–	1	39
<i>Pseudagapostemon</i> (<i>Pseudagapostemon</i>) <i>cyaneus</i> Moure & Sakagami, 1984	115	1	0	1	–	–	–	–	–	–	–	–	–	–	–	1	39
<i>Pseudagapostemon</i> (<i>Pseudagapostemon</i>) <i>pruinosis</i> Moure & Sakagami, 1984	116	17	32	2	–	7	11	8	1	1	3	10	3	2	1	49	14,29,33,34,36,37,38,39,59,66,68,72
<i>Sphcodes</i> sp. 1	117	1	0	–	–	–	1	–	–	–	–	–	–	–	–	1	75

Continues

Appendix 1. Continued.

Bee species	ID	F	M	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total	Plant species ID
Megachilinae																	
Anthidiini																	
<i>Anthidium sertanicola</i> Moure & Urban, 1964	118	0	1	-	-	-	-	-	-	-	-	1	-	-	-	1	72
Megachilini																	
<i>Coelioxys praetextata</i> Haliday, 1836	119	2	3	-	-	1	-	-	-	-	-	2	1	1	-	5	34
<i>Coelioxys tolteca</i> Cresson, 1878	120	0	2	-	-	-	-	-	-	-	-	1	1	-	-	2	48
<i>Coelioxys chacoensis</i> Holmberg, 1903	121	2	0	-	-	-	-	-	-	-	1	1	-	-	-	2	81
<i>Megachile (Chrysosarus) pseudanthidioides</i> Moure, 1943	122	1	0	-	-	-	-	-	-	-	-	-	-	1	-	1	34
<i>Megachile (Leptorachis) paulistana</i> Schrottky, 1902	123	2	0	-	-	1	-	-	-	-	-	-	-	1	-	2	19
<i>Megachile (Moureapis) maculata</i> Smith, 1853	124	1	0	-	-	-	-	-	-	1	-	-	-	-	-	1	34
<i>Megachile (Moureapis) apicipennis</i> Schrottky, 1902	125	1	0	-	-	-	-	-	-	-	-	-	-	1	-	1	15,16,31,34,39,89
<i>Megachile (Pseudocentron) cf. framea</i> Schrottky, 1913	126	16	3	-	1	-	1	-	15	2	-	-	-	-	-	19	16,23,39,41
<i>Megachile (Moureapis) electrum</i> Mitchell, 1930	127	1	0	-	-	-	-	1	-	-	-	-	-	-	-	1	39
<i>Megachile (Pseudocentron) sp. 1</i>	128	4	1	-	-	-	-	-	1	2	-	2	-	-	-	5	39
<i>Megachile (Pseudocentron) sp. 2</i>	129	2	4	-	-	-	-	1	2	1	-	2	-	-	-	6	39
<i>Megachile (Pseudocentron) terrestris</i> Schrottky, 1902	130	1	0	-	-	-	-	1	-	-	-	-	-	-	-	1	24,31,39,68,78
<i>Megachile iheringi</i> Schrottky, 1913	131	2	0	-	-	1	1	-	-	-	-	-	-	-	-	2	34

Appendix 2. Plant species visited by bees in the period between August, 2004 and July, 2005, in two grassland sites within the Afonso Pena airport, in São José dos Pinhais, Paraná, Brazil. For identity of associated bees refer to Appendix 1.

Plant species	ID	Habitat	Visiting bee species ID	Number of visits
Apiaceae				
<i>Eryngium floribundum</i> Cham. & Schldl	1	Grasslands	39,40,51,52,56,61,64,68,77,76,82	15
<i>Eryngium pandanifolium</i> Cham. & Schtdl. var. <i>chamissonis</i> (Urban) Math & Const.	2	Grasslands	8,9,13,14,42,61,64,64,76,78,79,84,87,104,106	43
<i>Foeniculum vulgare</i> Mill.	3	Exotic/Ruderal	87,89,103	3
Asteraceae				
<i>Achyrocline satureioides</i> (Lam.) DC.	4	Grasslands	70	1
<i>Austroeupeatorium inulaefolium</i> (Kunth.) R.M. King & H. Rob.	5	Grasslands	13,82	10
<i>Austroeupeatorium laetevirens</i> (Hook. & Arn.) R.M. King & H. Rob.	6	Grasslands	13,24	5
<i>Baccharidastrum triplinervium</i> (Less.) Cabrera	7	Grasslands	13,18,64,112	71
<i>Baccharis capraifolia</i> DC.	8	Grasslands	13,49,58,62,68,82,87,106	72
<i>Baccharis dracunculifolia</i> DC.	9	Grasslands	13	6
<i>Baccharis erioclada</i> DC.	10	Grasslands	13,18	34
<i>Baccharis myriocephala</i> DC.	11	Grasslands	9,12,13,14,41,61,62,64,66,67,68,70,77,78,80,82,87,89,92	222
<i>Baccharis pentodonta</i> Malme	12	Grasslands	40,41,55,61,63,77,89,102,103,104,111	17
<i>Baccharis uncinella</i> DC.	13	Grasslands	10,13,40,41,77	15
<i>Bidens pilosa</i> L.	14	Exotic/Ruderal	8,9,13,39,40,68,105,116	16
<i>Calea glabrata</i> Sch. Bip. & Krasch.	15	Grasslands	13,41,65,103,104,125	8
<i>Calea hispida</i> (DC.) Baker	16	Grasslands	13,14,25,39,40,41,55,61,62,64,65,66,78,82,92,104,125,126	72
<i>Calea</i> sp.	17	Grasslands	93	1
<i>Campovassouria cruciata</i> (Vell.) R.M. King & H. Rob.	18	Grasslands	2,13,62	8
<i>Campuloclinium macrocephalum</i> (Less.) DC.	19	Grasslands	14, 123	2
<i>Chromolaena ascendens</i> (Sch. Bip. ex Backer) R.M. King & H. Rob.	20	Grasslands	41,55	2
<i>Chromolaena congesta</i> (Hook. & Arn.) R. M. King & H. Rob.	21	Grasslands	41,44,55	6
<i>Chromolaena hirsuta</i> (Hook. & Arn.) & H. Rob.	22	Grasslands	39,40,41	2
<i>Chromolaena laevigata</i> (Lam.) R.M.King & H. Rob.	23	Grasslands	13,15,30,39,56,126	85
<i>Chromolaena pedunculosa</i> (Hook.& Arn.) R.M. King & H. Rob.	24	Grasslands	55,130	2
<i>Chrysoleaena platensis</i> (Spreng) H.Rob.	25	Grasslands	13, 65	1

Continues

Appendix 2. Continued.

Plant species	ID	Habitat	Visiting bee species ID	Number of visits
<i>Cirsium vulgare</i> (Savi) Ten.	26	Grasslands	13,41,57,106	4
<i>Conyza bonariensis</i> (L.) Cronquist	27	Ruderal	13,18,37,39,40,46,64,68,72,76,82 86,87,99	102
<i>Coreopsis tinctoria</i> Nutt.	28	Grasslands	13,104	2
<i>Disynaphia littoralis</i> (Cabrera) R.M. King. & H. Rob.	29	Grasslands	8,13,27,29,40,41,55,57,62,64,70,82,103,116	101
<i>Gnaphalium spicatum</i> Mill.	30	Grasslands	13,18,65,67,70,72,96,98	14
<i>Grazilia gaudichaudiana</i> (DC.) R.M. King & Rob.	31	Grasslands	13,14,31,33,40,62,64, 76,82,124,130	69
<i>Mikania micrantha</i> Kunth	32	Forest	13	5
<i>Perezia cubataensis</i> Less.	33	Grasslands	7, 9,64,34,36,37,98,106,107,109, 110, 116	15
<i>Senecio oleosus</i> Vell.	34	Ruderal	8,9,10,13,14,16,17,18,19,32 38,40,41,42,43,44,52,53,55,56,61, 64,65,70,82,116,119,122,125,131	538
<i>Solidago chilensis</i> Meyen	35	Ruderal	13,40,62	13
<i>Sonchus oleraceus</i> L.	36	Exotic/Ruderal	13,53,55,70,82,83, 94,101,103,104,106,116	46
<i>Stevia veronicae</i> DC.	37	Ruderal	8,13,24,14,26,30,31,32,33,35,40,52,53,56,61,62,64, 70,74,75,78,82,104,116	100
<i>Tagetes minuta</i> L.	38	Ruderal	13,30,32,40,62,64,68,82,101,116	21
<i>Taraxacum officinale</i> Weber	39	Exotic/Ruderal	5,7,8,9,10,13,14,18,20,24,33,40, 41,52,53,55,58,62,63,66,70,76, 78,81,82,87,89,91,92,94,96,97,98,100,101,102, 103,104,105,106,107, 108,116,115,124,125,126, 127,128,129,130	389
<i>Trixis verbaciformes</i> Less.	40	Grasslands	130	3
<i>Vernonanthura westiniana</i> (Less.) H. Rob	41	Grasslands	13,14,16,40,41,65,68,126	33
Boraginaceae				
<i>Moritzia dusenii</i> I. M. Johnst.	42	Grasslands	14,37,39,40,41,55,104	6
Brassicaceae				
<i>Raphanus raphanistrum</i> L.	43	Exotic/Ruderal	6,8,9,13,14,18,37,38,41,54,59,58,89,95,101,103, 104,105,106,107	185
Buddlejaceae				
<i>Buddleja vetula</i> Cham. & Schldt.	44	Grasslands	13,39	3
<i>Buddleja</i> sp. 1	45	Grasslands	39	1
Campanulaceae				
<i>Lobelia camporum</i> Pohl	46	Grasslands	104	1
Commelinaceae				
<i>Commelina elegans</i> Kunth	47	Ruderal	9,13,18,28,37,38,54,73,101	9
Convolvulaceae				
<i>Ipomoea indivisa</i> (Vell.) Hallier f.	48	Ruderal	56,120	2
<i>Ipomoea polymorpha</i> Griseb.	49	Ruderal	21,40,49	5
<i>Ipomoea purpurea</i> (L.) Roth	50	Ruderal	13,14,15,18,55	26
<i>Ipomoea ramosissima</i> (Poir.) Choisy	51	Ruderal	70	1
Cucurbitaceae				
<i>Cayaponia bonariensis</i> (Mill.) Mart. Crov.	52	Grasslands	13	3
Euphorbiaceae				
<i>Croton pallidulus</i> Baill.	53	Grasslands	63	2
Fabaceae				
<i>Eriosema crinitum</i> (Kunth) G. Don	54	Grasslands	31,33	1
<i>Spartium junceum</i> L.	55	Exotic/Ruderal	14,45	3
<i>Ulex europaeus</i> L.	56	Ruderal/Exotic	13,14	12
Iridaceae				
<i>Crocasmia crocosmiiflora</i> (W.A. Nicholson) N.E. Br.	57	Ruderal	13,18,113	34
<i>Cypella herbertii</i> Herb.	58	Grasslands	59	2
<i>Gelasine coerulea</i> (Vell.) Ravenna	59	Grasslands	4,55,64,67,77,82,92,106,116	23
<i>Sisyrinchium nidulare</i> (Hand. -Mazz.) Johnst.	60	Grasslands	18,82,105	4

Continues

Appendix 2. Continued.

Plant species	ID	Habitat	Visiting bee species ID	Number of visits
Lamiaceae				
<i>Cunila galioides</i> Benth.	61	Grasslands	13	2
<i>Peltodon rugosus</i> Tolm.	62	Grasslands	13	3
<i>Salvia lachnostachys</i> Benth.	63	Grasslands	4,14,84	3
<i>Stachys arvensis</i> L.	64	Ruderal/Exotic	4,13,14,18,41, 42	62
Loganiaceae				
<i>Spigelia martiana</i> Cham. & Schltld.	65	Grasslands	41,84	4
Lythraceae				
<i>Cuphea calophylla</i> Cham. & Schltld.	66	Grasslands	36,54,116	6
Malvaceae				
<i>Krapovickasia macrodon</i> (DC.) Fryxell	67	Grasslands	11	1
<i>Sida rhombifolia</i> L.	68	Ruderal	11,13,18,23,24,25,26,28 30,38,40,41,48,55, 63,70,98,108,116, 129,130	76
Melastomataceae				
<i>Acisanthera alsinaefolia</i> (DC.) Triana	69	Grasslands	18,29,64,69,71	7
<i>Tibouchina clavata</i> (Pers.) Wurd.	70	Forest	67	1
Myrtaceae				
<i>Myrceugenia euosma</i> (Berg.) Legr.	71	Forest	13	1
Onagraceae				
<i>Ludwigia sericea</i> (Cambess.) H.Hara	72	Ruderal	13,28,51,72,118	13
Oxalidaceae				
<i>Oxalis myriophylla</i> St. Hil.	73	Grasslands	3,41	2
<i>Oxalis paludosa</i> St. Hil.	74	Grasslands	13,18,58,84,108	13
Polygonaceae				
<i>Polygonum persicaria</i> L.	75	Ruderal	82,89,92,104,106,117	21
Rhamnaceae				
<i>Rhamnus sphaerosperma</i> var. <i>pupescens</i> (Reissek) M. C. Johnston	76	Forest	13	9
Rosaceae				
<i>Prunus brasiliensis</i> (Cham. & Schltld.) D. Dietr.	77	Ruderal	13,18,47,55,64,66, 68,70,74,76,78,79, 80,82,87,89,90,97,101,107	84
Rubiaceae				
<i>Borreria tenella</i> (Kunth) Cham & Schltld.	78	Grasslands	9,13,14,39,41,104,130	20
<i>Galianthe chodatiana</i> (Standl.) E.L. Cabral	79	Grasslands	8,41,77,84,103,106	12
<i>Galianthe verbenoides</i> (Cham. & Schltld.) Grisebach	80	Grasslands	40,41,63	4
<i>Mitracarpus hirtus</i> (L.) DC.	81	Ruderal	13,41,121	5
Saxifragaceae				
<i>Escallonia farinacea</i> St.- Hil.	82	Grasslands	14	1
Scrophulariaceae				
<i>Agalinis communis</i> (Cham. & Schltld.) D'Arcy	83	Grasslands	13,41,102,103,104	6
<i>Agalinis linarioides</i> (Cham. & Schltld.) D'Arcy	84	Grasslands	40,60	2
Solanaceae				
<i>Cestrum corymbosum</i> Schltld.	85	Ruderal	18,72,84,106,107	30
<i>Petunia linoides</i> Sendtn.	86	Grasslands	20,42	3
<i>Solanum americanum</i> Mill.	87	Ruderal	1,18,64, 64	4
<i>Solanum mauritianum</i> Scop.	88	Ruderal	13,14,31,33,55,63,62,64,84	14
Verbenaceae				
<i>Lantana camara</i> L.	89	Exotic/Ruderal	13,14,15,18,40,61,63,125	22
<i>Lantana fucata</i> Lindl.	90	Ruderal	10,13,18,39,58,108	21
<i>Lippia alba</i> var. <i>globiflora</i> (L'Her.) Moldenke	91	Ruderal	13	12
<i>Verbena bonariensis</i> L.	92	Ruderal	55,64	2
<i>Verbena brasiliensis</i> Vell.	93	Ruderal	66,72	2
<i>Verbena hirta</i> Spreng.	94	Grasslands	10,13,14,40,41,55	10
Zingiberaceae				
<i>Hedychium coronarium</i> Koenig	95	Exotic/Ruderal	13,18	2

Appendix 3. Comparative richness and abundance, by bee genus, in the three surveys conducted in the airport at São José dos Pinhais. S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCCA 1990); S3, 2004-2005 (current study) and biological characteristics of each genus. Nesting Behavior: (S) Solitary, (E) eusocial, (C) cleptoparasite. Nest location: (G) Ground, (C) Cavity. Trophic specialization: (P) Polylectic, (O) Oligolectic. Body size by intertegular distance (ITD, in mm) of female bees: (1) 0.8-1.39; (2) 1.4-1.89; (3) 1.9-2.29; (4) 2.3-2.9; (5) > 3.0.

Genera	Richness			Abundance			Biological characteristics			
	S1	S2	S3	S1	S2	S3	Nesting behavior	Nest location	Bee flower specificity	ITD
Andreninae										
Calliopsini										
<i>Acamptopoeum</i>	1	1	1	6	10	1	S	G	P	2
<i>Callonychium</i>	1	0	0	4	0	0	S	G	O	1
Protandrenini										
<i>Anthrenoides</i>	6	5	6	47	31	12	S	G	O	2
<i>Parapsaenythia</i>	0	2	0	0	3	0	S	G	P	3
<i>Psaenythia</i>	6	9	3	52	26	53	S	G	P	3
<i>Rhophitulus</i>	2	1 ¹	2	17	3	4		G	O	1
Apinae										
Anthophorini										
<i>Anthophora</i>	1	1	0	1	11	0	S	G	P	5
Apini										
<i>Apis</i>	1	1	1	?	?	1681	E	C	P	4
<i>Bombus</i>	3	3	2	396	375	85	E	C	P	5
<i>Melipona</i>	1	0	1	11	0	2	E	C	P	4
<i>Plebeia</i>	1	0	0	1	0	0	E	C	P	1
<i>Tetragonisca</i>	0	0	1	0	0	1	E	C	P	1
<i>Trigona</i>	1	1	1	675	9	173	E	C	P	2
Centridini										
<i>Centris</i>	1	0	0	1	0	0	S	C	O	5
Emphorini										
<i>Melitoma</i>	0	0	2	0	0	3	S	G	O	4
Eucerini										
<i>Gaesischia</i>	4	3	0	51	63	0	S	G	O	4
<i>Melissodes</i>	0	1	1	0	1	1	S	G	P	4
<i>Melissoptila</i>	3	4	7	57	30	19	S	G	O	4
<i>Thygater</i>	1	1	1	3	37	1	S	G	P	5
Exomalopsini										
<i>Exomalopsis</i>	3	2	2	18	9	8	S	G	P	2
Isepeolini										
<i>Isepeolus</i>	2	0	0	12	0	0	C	–	–	3
Nomadini										
<i>Brachynomada</i>	0	0	2	0	0	2	C	–	–	2
<i>Trophocleptria</i>	1	0	0	2	0	0	C	–	–	2
<i>Nomada</i>	1	0	2	1	0	2	C	–	–	2
Tapinotaspidini										
<i>Lanthanomelissa</i>	1	2	1	3	19	4	S	G	O	2
<i>Paratetrapedia</i>	0	1	0	0	1	0	S	C	O	3
<i>Tapinotaspoides</i>	1	1 ²	0	7	17	0	S	G	O	3
Xylocopini										
<i>Ceratina</i>	5	11	7	264	72	168	S	C	P	1
<i>Xylocopa</i>	3	3	1	12	14	5	S	C	P	5
Colletinae										
Colletini										
<i>Colletes</i>	3	4	1	17	4	1	S	C	P	4
Diphaglossini										
<i>Ptiloglossa</i>	1	0	0	1	0	0	S	G	P	5

Contiues

Appendix 3. Continued.

Genera	Richness			Abundance			Biological characteristics			
	S1	S2	S3	S1	S2	S3	Nesting behavior	Nest location	Bee flower specificity	ITD
Hylaeini										
<i>Hylaeus</i>	3	0	1	19	0	1	S	C	P	1
Neopasiphaeini										
<i>Belopria</i>	0	0	2	0	0	3	S	G	O	3
<i>Hexanthes</i>	0	1	0	0	3	0	S	G	O	3
<i>Perditomorpha</i>	0	1	1	0	7	1	S	G	O	2
<i>Tetraglossula</i>	3 ³	1 ⁴	1	2	3	3	S	G	O	3
Xeromelissini										
<i>Chilicola</i>	1 ⁵	0	2	3	0	12	S	C	O	1
Halictinae										
Augochlorini										
<i>Augochlora</i>	4	3	5	148	203	181	S	G	P	3
<i>Augochlorella</i>	4	4	2	17	9	2	S	G	P	1
<i>Augochlorodes</i>	2	0	0	40	0	0	S	G	P	1
<i>Augochloropsis</i>	15	18	15	363	116	188	S	G	P	2
<i>Ceratalictus</i>	2	1	2	132	5	20	S	G	P	1
<i>Neocorynura</i>	3	1	2	48	2	24	S	G	P	2
<i>Paroxystoglossa</i>	4	2	4	599	235	86	S	G	P	2
<i>Pseudaugochlora</i>	1 ⁶	1 ⁶	1	10	13	11	S	G	P	3
<i>Rhinocorynura</i>	2	0	1	4	0	1	S	G	P	2
<i>Temnosoma</i>	1	0	1	1	0	1	C	–	–	2
<i>Thectochlora</i>							S	G	P	1
Halictini										
<i>Agapostemon</i>	0	1	0	0	1	0	S	G	P	3
<i>Caenohalictus</i>	1	1	2	148	8	15	S	G	P	1
<i>Dialictus</i>	41 ⁷	41	26	554	315	186	S	G	P	1
<i>Oragapostemon</i>	1 ⁸	0	0	0	0	0	S	G	P	2
<i>Pseudagapostemon</i>	3	4	2	325	170	50	S	G	P	2
<i>Sphecodes</i>	3	1	1	3	2	1	C	–	–	1
Megachilinae										
Anthidiini										
<i>Anthidium</i>	0	0	1	0	0	1	S	C	P	4
<i>Epanthidium</i>	1	0	0	1	0	0	S	C	P	4
Megachilini										
<i>Coelioxys</i>	4	1	3	17	1	9	C	–	–	4
<i>Megachile</i>	14	25	10	65	65	39	S	C	P	4
Total	167⁹	167¹⁰	131	4217⁹	1906¹⁰	1380				

Taxonomic notes: ¹Identified as "*Heterosarellus*" in the original paper; ²Identified as *Tapinotaspis*; ³Identified both as *Hoplocolletes* and *Tetraglossula*; ⁴Identified as *Hoplocolletes*; ⁵Identified as *Oediscelisca*; ⁶Identified as *Pseudaugochloropsis*; ⁷Includes also *Rhynchalictus*; ⁸Included in *Pseudagapostemon*; ⁹Total number includes one species, with 11 individuals, of an unidentified genus ("Panurginae") of Andreninae not listed here in the table; ¹⁰Total number includes two species, with three specimens, of an unidentified genus ("Panurginae") of Andreninae and one species, with one individual, of an unidentified genus ("Gen.A") of Apinae.

Appendix 4. Compilation of bee species collected in the three surveys conducted in grassland sites within the Afonso Pena airport, in São José dos Pinhais, Paraná, Brazil. Taxa not identified to species level could not be compared between the surveys and are indicated only as number of species per genus. The values in the last three columns are number of specimens collected in each survey. Abundance data lacking for species in S1 are indicated with a question mark. S1, 1962-1963 (SAKAGAMI *et al.* 1967); S2, 1981-1982 (BORTOLI & LAROCCA 1990); S3, 2004-2005 (current study).

Species	Presence/Abundance in surveys			Species	Presence/Abundance in surveys		
	S1	S2	S3		S1	S2	S3
Andreninae				<i>Melissoptila setigera</i> Urban, 1998	0	0	2
Calliopsini				<i>Melissoptila similis</i> Urban, 1988	0	0	1
<i>Acamptopoeum prinii</i> (Holmberg, 1884)	6	10	1	<i>Melissoptila thoracica</i> (Smith, 1854)	0	0	5
<i>Callonychium petunia</i> ¹ Cure & Wittmann, 1990	4	0	0	<i>Thygater analis</i> (Lepeletier, 1841)	3	37	1
Protandrenini				Exomalopsini			
<i>Anthrenoides antonii</i> Urban, 2005	0	0	2	<i>Exomalopsis (Exomalopsis) analis</i> Spinola 1853	0	0	3
<i>Anthrenoides alvarengai</i> Urban, 2007	0	0	1	<i>Exomalopsis (Phanomalopsis) trifasciata</i> Brèthes, 1910	0	0	5
<i>Anthrenoides larocai</i> Urban, 2005	0	0	3	<i>Exomalopsis</i> spp.	3	2	–
<i>Anthrenoides meridionalis</i> (Schrottky, 1906)	0	0	2	Isepeolini			
<i>Anthrenoides politus</i> Urban, 2005	0	0	3	<i>Isepeolus viperinus</i> (Holmberg, 1886)	1	0	0
<i>Anthrenoides rodrigo</i> Urban, 2005	0	0	1	<i>Isepeolus</i> sp. ²	1	0	0
<i>Anthrenoides</i> spp.	5	5	–	Nomadini			
<i>Parapsaenythia serripes</i> (Ducke, 1908)	0	2	0	<i>Brachynomada</i> spp.	0	0	2
<i>Psaenythia annulata</i> Gerstaecker 1868	?	4	22	<i>Nomada</i> spp.	1	0	2
<i>Psaenythia bergii</i> Holmberg 1884	?	5	17	<i>Trophocleptria variolosa</i> Holmberg, 1886	2	0	0
<i>Psaenythia capito</i> Gerstaecker, 1868	?	3	0	Tapinotaspidini			
<i>Psaenythia collaris</i> Schrottky, 1906	10	3	14	<i>Lanthanomelissa betinae</i> Urban, 1995	0	0	4
<i>Psaenythia nomadoides</i> Gerstaecker, 1868	?	3	0	<i>Lanthanomelissa</i> sp.	3	2	–
<i>Psaenythia quadrifasciata</i> Friese, 1908	?	2	0	<i>Paratetrapedia fervida</i> ³ (Smith, 1879)	0	1	0
<i>Rhopitulus anomalus</i> (Moure & Lucas de Oliveira, 1962)	0	0	2	<i>Tapinotaspoides serraticornis</i> ⁴ (Friese, 1899)	7	17	0
<i>Rhopitulus</i> spp.	2	0	1	Xylocopini			
Apinae				<i>Ceratina (Ceratinula) cf. biguttulata</i> (Moure, 1941)	0	0	3
Anthophorini				<i>Ceratina (Ceratinula) oxalidis</i> Schrottky, 1907	13	0	0
<i>Anthophora paranensis</i> Holmberg, 1903	1	11	0	<i>Ceratina (Ceratinula) sp.</i>	1	4	8
Apini				<i>Ceratina (Crewella) asuncionis</i> Strand, 1910	136	20	69
<i>Apis mellifera</i> Linnaeus, 1758	?	?	1681	<i>Ceratina (Crewella) rupestris</i> Holmberg, 1884	0	0	1
<i>Bombus pauloensis</i> Friese, 1913	?	186	49	<i>Ceratina (Rhysoaceratina) spp.</i>	0	0	88
<i>Bombus bellicosus</i> Smith, 1879	328	151	0	<i>Ceratina</i> spp.	2	6	–
<i>Bombus morio</i> (Swederus, 1787)	?	34	18	<i>Xylocopa (Nanoxycopa) ciliata</i> Burmeister, 1876	?	3	0
<i>Melipona quadrifasciata</i> Lepeletier, 1836	11	0	2	<i>Xylocopa (Neoxycopa) augusti</i> Lepeletier 1841	?	10	5
<i>Plebeia emerina</i> (Friese, 1900)	1	0	0	<i>Xylocopa (Neoxycopa) frontalis</i> (Olivier, 1789)	0	10	0
<i>Tetragonisca angustula</i> (Latreille, 1811)	0	0	1	<i>Xylocopa (Stenoxycopa) artifex</i> Smith, 1874	?	0	0
<i>Trigona spinipes</i> (Fabricius, 1793)	675	9	17	Colletinae			
Centridini				Colletini			
<i>Centris (Hemisiella) tarsata</i> Smith, 1874	1	0	0	<i>Colletes kerri</i> Moure, 1956	?	0	0
Emphorini				<i>Colletes michenerianus</i> Moure, 1956	?	0	0
<i>Melitoma segmentaria</i> (Fabricius, 1804)	0	0	2	<i>Colletes rugicollis</i> Friese, 1900	?	1	1
<i>Melitoma</i> sp.	0	0	1	<i>Colletes rufipes</i> Smith, 1879	0	1	0
Eucerini				Diphaglossini			
<i>Gaesischia aurea</i> Urban, 1968	?	5	0	<i>Ptiloglossa hemileuca</i> Moure, 1944	1	0	0
<i>Gaesischia flavoclypeata</i> Michener, LaBerge & Moure, 1955	?	1	0	Hylaeini			
<i>Gaesischia fulgurans</i> (Holmberg, 1903)	43	43	0	<i>Hylaeus rivalis</i> (Schrottky, 1906)	?	0	0
<i>Gaesischia nigra</i> Moure, 1968	?	0	0	<i>Hylaeus (Hylaeopsis) spp.</i>	2	0	1
<i>Melissodes nigroaenea</i> (Smith, 1854)	0	1	1	Neopasiphaeini			
<i>Melissoptila aureocincta</i> Urban, 1968	12	0	1	<i>Perditomorpha leaena</i> (Vachal, 1909)	0	7	1
<i>Melissoptila bonaerensis</i> Holmberg, 1903	?	2	0	<i>Belopria zonata</i> Moure, 1956	0	0	1
<i>Melissoptila cnecomala</i> (Moure, 1944)	0	4	3	<i>Belopria</i> sp.	0	0	2
<i>Melissoptila minarum</i> (Bertoni & Schorrotky, 1910)	?	9	6	<i>Hexanthea missionica</i> Ogloblin, 1948	0	3	0
<i>Melissoptila paraguayensis</i> (Brèthes, 1909)	0	0	1	<i>Tetraglossula anthracina</i> (Michener, 1989)	2	3	3
<i>Melissoptila richardiae</i> Bertoni & Schrottky, 1910	0	15	0	<i>Tetraglossula bigamica</i> (Strand, 1910)	1	0	0

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Appendix 4. Continued.

Species	Presence/Abundance in surveys			Species	Presence/Abundance in surveys		
	S1	S2	S3		S1	S2	S3
Xeromelissini				<i>Dialictus bruneriellus</i> (Cockerell, 1918)	0	0	1
<i>Chilicola</i> (<i>Oediscelisca</i>) <i>dalmeidai</i> (Moure, 1946)	3	0	0	<i>Dialictus flavipes</i> Moure, 1950	0	75	0
<i>Chilicola</i> (<i>Oediscelisca</i>) sp.	0	0	4	<i>Dialictus opacus</i> (Moure, 1940)	21	8	11
<i>Chilicola</i> (<i>Prosopoides</i>) sp.	0	0	8	<i>Dialictus phleboleucus</i> (Moure, 1956)	33	3	0
Halictinae				<i>Dialictus rostratus</i> (Moure, 1947)	?	1	1
Augochlorini				<i>Dialictus rhytidophorus</i> (Moure, 1956)	?	10	0
<i>Augochlora amphitrite</i> (Schrottky, 1909)	21	69	44	<i>Dialictus travassosi</i> (Moure, 1940)	?	4	0
<i>Augochlora semiramis</i> (Schrottky, 1910)	79	141	118	<i>Dialictus ypirangensis</i> (Schrottky, 1910)	?	0	0
<i>Augochlora thalia</i> Smith, 1879	0	?	0	<i>Dialictus</i> spp.	34	34	21
<i>Augochlora</i> spp.	2	0	16	<i>Oragapostemon divaricatus</i> (Vachal, 1903)	?	0	0
<i>Augochlora ephra</i> (Schrottky, 1910)	0	3	2	<i>Oragapostemon</i> (<i>Braslagapostemon</i>) <i>larocai</i> Cure, 1989 ⁹	?	11	0
<i>Augochloraella iopocila</i> Moure, 1950	?	3	1	<i>P.</i> (<i>Pseudagapostemon</i>) <i>cyaneus</i> Moure & Sakagami, 1984	?	104	1
<i>Augochloraella</i> spp.	4	2	0	<i>P.</i> (<i>Pseudagapostemon</i>) <i>ochromerus</i> (Vachal, 1904)	?	2	0
<i>Augochlorodes</i> spp. ⁵	2	0	0	<i>P.</i> (<i>Pseudagapostemon</i>) <i>pruinus</i> Moure & Sakagami, 1984	?	53	49
<i>Augochloropsis anisitsi</i> (Schrottky, 1908)	?	2	1	<i>Sphecodes</i> spp.	3	1	1
<i>Augochloropsis brachycephala</i> Moure, 1943	?	0	0	Megachilinae			
<i>Augochloropsis cleopatra</i> (Schrottky, 1902)	0	14	55	Anthidiini			
<i>Augochloropsis cupreola</i> (Cockerell, 1900)	?	11	11	<i>Anthidium sertanicola</i> Moure & Urban, 1964	?	0	1
<i>Augochloropsis deianira</i> (Schrottky, 1910)	0	9	0	<i>Epanthidium nectarinioides</i> (Schrottky, 1902)	1	0	0
<i>Augochloropsis iris</i> (Schrottky, 1902)	29	63	54	Megachilini			
<i>Augochloropsis liopelte</i> (Moure, 1940)	0	12	5	<i>Coelioxys pampeana</i> Holmberg, 1887	?	0	0
<i>Augochloropsis multiplex</i> (Vachal, 1903)	0	1	20	<i>Coelioxys praetextata</i> Haliday, 1836 ¹⁰	?	1	5
<i>Augochloropsis rufisetis</i> (Vachal, 1903)	0	1	0	<i>Coelioxys tolteca</i> Cresson, 1878	?	0	2
<i>Augochloropsis sympleres</i> (Vachal, 1903)	0	0	6	<i>Coelioxys chacoensis</i> Smith, 1854	?	0	2
<i>Augochloropsis terrestris</i> (Vachal, 1903)	?	0	0	<i>Coelioxys</i> spp.	1	1	0
<i>Augochloropsis</i> spp.	10	10	36	<i>Megachile</i> (<i>Acentron</i>) <i>eburnipes</i> Vachal, 1904 ¹¹	0	1	0
<i>Ceratalictus clonius</i> (Brèthes, 1909)	?	5	9	<i>Megachile</i> (<i>Acentron</i>) <i>itapuae</i> Schrottky, 1908 ¹²	?	1	0
<i>Ceratalictus psoraspi</i> (Vachal, 1911)	0	0	11	<i>Megachile</i> (<i>Acentron</i>) <i>lentifera</i> Vachal, 1909	?	2	0
<i>Ceratalictus</i> sp.	1	0	0	<i>Megachile</i> (<i>Acentron</i>) sp.	0	1	0
<i>Neocorynura aenigma</i> (Gribodo, 1894)	?	2	20	<i>Megachile</i> (<i>Austromegachile</i>) <i>susurrans</i> Haliday, 1836	?	1	0
<i>Neocorynura atromarginata</i> (Cockerell, 1901)	0	0	4	<i>Megachile</i> (<i>Austromegachile</i>) <i>recta</i> Mictchell, 1930	?	0	0
<i>Neocorynura polybioides</i> (Ducke, 1906)	?	0	0	<i>Megachile</i> (<i>Austromegachile</i>) <i>trigonaspis</i> Schrottky, 1913	?	0	0
<i>Paroxystoglossa andromache</i> (Schrottky, 1909)	?	0	3	<i>Megachile</i> (<i>Austromegachile</i>) sp.	0	1	0
<i>Paroxystoglossa brachycera</i> Moure, 1960	0	15	1	<i>Megachile</i> (<i>Chrysosarus</i>) <i>inquirenda</i> Schrottky, 1913	0	7	0
<i>Paroxystoglossa jocasta</i> (Schrottky, 1910)	263	220	80	<i>Megachile</i> (<i>Chrysosarus</i>) <i>pseudanthidioides</i> Moure, 1943	0	0	1
<i>Paroxystoglossa mimetica</i> Moure, 1950	?	0	0	<i>Megachile</i> (<i>Chrysosarus</i>) sp. ¹³	0	1	0
<i>Paroxystoglossa</i> spp.	1	0	0	<i>Megachile</i> (<i>Leptorachis</i>) <i>aetheria</i> Mitchell, 1930	0	3	0
<i>Pseudaugochlora</i> ⁶ spp.	1	1	10	<i>Megachile</i> (<i>Leptorachis</i>) <i>aureiventris</i> Schrottky, 1902	?	4	0
<i>Rhinocorynura vernoniae</i> (Schrottky, 1914) ⁷	?	0	0	<i>Megachile</i> (<i>Leptorachis</i>) <i>paulistana</i> Schrottky, 1902	0	0	2
<i>Rhinocorynura viridis</i> Gonçalves & Melo, 2012	1	0	1	<i>Megachile</i> (<i>Moureapis</i>) <i>apicipennis</i> Schrottky, 1902	0	8	1
<i>Temnosoma</i> spp.	1	0	1	<i>Megachile</i> (<i>Moureapis</i>) <i>electrum</i> Mitchell, 1930	0	0	1
<i>Thectochlora basiatra</i> (Strand, 1910) ⁸	47	9	0	<i>Megachile</i> (<i>Moureapis</i>) <i>maculata</i> Smith, 1853	?	1	1
Halictini				<i>Megachile</i> (<i>Moureapis</i>) <i>nigropilosa</i> Schrottky, 1902	?	4	0
<i>Agapostemon</i> aff. <i>chapidensis</i> Cockerell, 1900	0	1	0	<i>Megachile</i> (<i>Moureapis</i>) <i>pleuralis</i> Vachal, 1909	?	0	0
<i>Caenohalictus implexus</i> Moure, 1950	68	0	0	<i>Megachile</i> (<i>Moureapis</i>) sp. ¹⁴	0	1	0
<i>Caenohalictus</i> cf. <i>palumbes</i> (Vachal, 1903)	0	0	1	<i>Megachile</i> (<i>Pseudocentron</i>) <i>curvipes</i> Smith, 1853	?	1	0
<i>Caenohalictus tessellatus</i> (Moure, 1940)	0	8	14	<i>Megachile</i> (<i>Pseudocentron</i>) cf. <i>framea</i> Schrottky, 1913	?	0	19
<i>Dialictus nanus</i> (Smith, 1879)	20	8	11	<i>Megachile</i> (<i>Pseudocentron</i>) <i>terrestris</i> Schrottky, 1902	?	11	1
<i>Dialictus autranellus</i> (Vachal, 1904)	?	0	1	<i>Megachile</i> (<i>Pseudocentron</i>) spp.	0	1	11
Continues next column				<i>Megachile</i> <i>iheringi</i> Schrottky, 1913	0	3	2

Notes: ¹Cited as *Callonychium* sp. in S1; ²Cited as *Isepeolus "modestior"* nomen nudum; ³Cited as *Paratetrapedia flaviventris*; ⁴Cited as *Tapinotaspis tucumana*; ⁵The two species were referred by unpublished manuscript names; ⁶ Cited previously as *Pseudaugochloropsis graminea*; ⁷ Cited as *Rhinocorynura inflaticeps*; ⁸ Cited as *Thectochlora alaris*; ⁹ Cited also as *Pseudagapostemon* sp. 10. Identified as *Coelioxys vidua* in S1. 11. Cited as *Megachile bernardina*; 12. Cited as *Megachile dilatata* and *M. hastigera*; 13. Cited as *Megachile* (*Dactylomegachile*) sp.; 14. Cited as *Megachile* (*Acentrina*) sp.