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Pollen resources and trophic niche breadth of *Apis mellifera* and *Melipona obscurior* (Hymenoptera, Apidae) in a subtropical climate in the Atlantic rain forest of southern Brazil

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Abstract – Pollen sources that comprise the trophic niche of native bee species *Melipona obscurior* and introduced *Apis mellifera* and the breadth of this niche were studied in two areas in the Atlantic rain forest of southern Brazil. Pollen obtained from the forager bees during a period of 12 months showed that the richness of pollen types found in each sample varied from 5 to 21 for *A. mellifera* and from 1 to 10 for *M. obscurior*. In both areas, *A. mellifera* had higher niche breadth. *M. obscurior* demonstrated the temporal specialization, which was primarily related to the use of floral sources with poricidal anthers. The non-native pollen type *Eucalyptus* produced similar results for both bee species. Knowledge of plant species that sustain bee communities in the Atlantic rain forest of southern Brazil contributes toward the management and conservation of native bee populations and increases the beekeeping of stingless bees and honey bees in this region.

Meliponini / floral resources / pollinators / stingless bees / pollen

1. INTRODUCTION

Networks of species interactions are the backbone of biodiversity and directly affect community dynamics (Jordano et al. 2006). The heterogeneity of these relationships provides greater stability to

the system and allows for more adequate responses to different environmental changes (Aizen et al. 2012). Based on this assumption and because habitat loss can cause a decrease in the diversity and abundance of pollinators (Aizen and Feinsinger 1994; Steffan-Dewenter and Tschamtké 1999; Kremen et al. 2007; Nayak and Davidar 2010), the interactions between plants and their pollinators may be less susceptible to disruption when generalist species are involved compared with interactions with specialist species (Pigozzo and Viana 2010; Aizen et al. 2012). However, a disruption of native co-evolutionary system can occur when generalist species monop-

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olize the interactions at the network level (Santos et al 2012).

During this often mutualist interaction, bees are attracted to flowers primarily because of the nectar and pollen that are used as a food resource (Minckley and Roulston 2006). Approximately 20,000 species of bees are distributed throughout most of the world, and the social species of Apini and Meliponini are abundant in tropical and subtropical regions (Michener 2000). A generalist foraging habit is considered standard for many bees of the family Apidae. Perennial colonies of this family have high rates of offspring production and require food resources throughout the year (Cortopassi-Laurino and Ramalho 1988; Imperatriz-Fonseca et al. 1994). Additionally, these bees have extreme taxonomic versatility in collecting pollen from phylogenetically distant taxa (Antonini et al. 2006; Cane and Sipes 2006).

With origins in the Old World, *Apis* species occur predominantly in intertropical areas, with *Apis mellifera* Linnaeus advancing to temperate regions (Imperatriz-Fonseca et al. 1994). Subspecies from Europe and Africa were introduced to Brazil, where they hybridized and dispersed, and these subspecies are currently found in a large portion of the western hemisphere (Schneider et al. 2004). The colony size of these exotic species can reach 100,000 individuals, and these bees exhibit foraging strategies that allow them to survive in a wide variety of environments (Winston 2003). *Apis mellifera* can withstand extreme cold and heat and can forage in areas with high exposure to light that are far from their nests (Goulson 2003), which are advantages over other species. It is an important species in the bee–plant interaction network (Santos et al 2010), but its presence could cause a negative impact on local pollination network like observed by Santos et al (2012) in the Brazilian “Caatinga.”

In the Neotropics, native social bees are represented by approximately 400 species of Meliponini (Michener 2000), known popularly as stingless bees. In this context, *Melipona obscurior* Moure is common, occurring in Argentina (Misiones), Paraguay (Caaguazú), and Brazil, in the states of Mato Grosso, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (Camargo and

Pedro 2008). Unlike *A. mellifera*, *M. obscurior* colonies have hundreds of individuals (Imperatriz-Fonseca et al. 1994; Nogueira-Neto 1997), are sensitive to more extreme weather conditions, and may exhibit facultative reproductive diapause during periods of low temperatures (Borges and Blochtein 2005, 2006). Similar to other species of the genus, *M. obscurior* inhabits forested areas (Silveira et al. 2002), and due to habitat loss and destruction of their nests by predation, they are in a vulnerable situation in Rio Grande do Sul (Blochtein and Harter-Marques 2003).

Because of this vulnerability and lack of knowledge about the plant species that sustains this native bee species in southern Brazil, the objective of this study was to identify both the pollen sources that comprise the trophic niche of this highly eusocial bee and the breadth of this niche compared with non-native bee *A. mellifera*, over a year of pollen sampling under subtropical conditions. The results of this research will provide necessary information for the development of conservation plans and sustainable management of biodiversity in the Atlantic rain forest remnants of southern Brazil.

2. MATERIALS AND METHODS

2.1. Study areas

Fieldwork was conducted in the following two rural properties in southern Brazil, located in the Rio dos Sinos river basin: Rolante (29°38'3.20"S and 50°34'24.91"W), 70 m above sea level, and Riozinho (29°40'36.63"S and 50°27'32.58"W), 570 m above sea level. The regional climate is humid subtropical type Cfa according to the Köppen classification, with an average temperature above 22 °C for the warmest month and above 3 °C for the coldest month (Moreno 1961).

The phytophysiology of the region is characterized as a seasonal semideciduous forest (Oliveira-Filho 2009), with 143 tree species recorded. In both areas, there is also large-scale cultivation of exotic woody species, particularly *Eucalyptus* spp. and *Acacia mearnsii* De Wild, as well as subsistence farming.

2.2. Bee colonies

In each study area, three colonies of *A. mellifera* housed in Langstroth hives were used in addition to three *M. obscurior* colonies maintained in rational hives that were standardized according to the model proposed by Venturieri et al. (2003). The *A. mellifera* hives were separated by approximately 200 and 150 m from the hives of *M. obscurior* in Riozinho and Rolante, respectively, creating opportunities for foraging overlap of the two species. Hives of the same species were kept close to each other.

2.3. Pollen samples

The pollen analyzed in this study was obtained biweekly from April 2009 to March 2010 from the pollen loads of forager bees at the entrance of each hive. Because the flight activities of bees are conditioned to meteorological factors, there was no pollen collection during days of low temperature or rain. These periods are marked in the tables and graphs with an asterisk.

Pollen loads were obtained from *A. mellifera* using a pollen collector that is suitable for use in a Langstroth hive and was attached to each of the hives. This equipment consists of a wooden box with a collection drawer at the bottom. An acrylic plate with 221 openings, 4.6 mm in diameter, was placed in the upper portion of the hive at the front of the entrance. During the passage of the worker bees through the openings, the pollen basket loads fell into the collection drawer and were retained. The acrylic plates were placed in the pollen collectors only in the early morning of the sampling day and were removed at the end of the afternoon.

The pollen of *M. obscurior* was sampled simultaneously. For this species, the entry to each hive was blocked one at a time with a small wooden stick for 15 min each hour during the entire flight period. The returning foragers carrying pollen in their pollen baskets were captured with hand nets. The pollen loads were removed manually, and the bees were then released.

Each sample consisted of the total pollen loads of the three hives, which were obtained during one collection day for each bee species and each area, totaling 69 samples.

2.4. Preparation of pollen material in the laboratory and analysis of palynological slides

Each sample was crushed and homogenized with a magnetic stirrer at 10,000 rpm (adapted from Villanueva-Gutierrez and Roubik 2004). A volume of each sample suspension, corresponding to 0.1 g pollen, was then removed, and tablets of *Lycopodium clavatum* spores containing approximately 18,584 grains were added in each sub-sample with the purpose of obtaining an absolute number of pollen grains (Stockmarr 1971; Villanueva-Gutierrez and Roubik 2004). These sub-samples were acetolyzed (Erdtman 1952) with the subsequent assembly of slides for microscopy using glycerin gelatin stained with fuchsin as a mounting medium. Three slides were prepared for each sample.

Pollen analysis was performed using a Carl Zeiss light microscope under $\times 400$ to $\times 1,000$ magnification. In each sample, 1,200 pollen grains were counted (adapted from Kleinert et al. 2009) along transects distributed between the three slides. The classifications sought to include the pollen type within the lowest hierarchical taxon category possible. The terminology “type” used attached to some taxa refers to morphological similarity with this element. When identification was not possible, the pollen type was named “Undefined” followed by a number referring to the sample identification sequence (e.g., Undefined 1).

2.5. Data analysis

The indices of richness (S), evenness (J), and diversity (Shannon’s index H') of pollen types in each sample were calculated using the statistical program Paleontological Statistics Software Package for Education and Data Analysis (Hammer et al. 2001) considering that, in Riozinho, 18 pollen samples were obtained from *A. mellifera* and 15 from *M. obscurior*, and in Rolante, 19 samples were collected for *A. mellifera* and 17 for *M. obscurior*.

The pollen types were grouped based on the representation of each pollen type in the sample at the following four frequency class intervals: dominant pollen (DP), pollen frequently occurring in the samples with a frequency $>45\%$; accessory pollen (AP), with a frequency $>15\text{--}45\%$; isolated pollen (IP), with per-

centages between 15 and 3 %; and occasional pollen (OP), with percentages <3 % (Louveaux et al. 1978).

2.6. Trophic niche breadth

The range of food resources used by the two bee species was calculated using Shannon index ($H' = -\sum P_k \times \ln P_k$) according to Krebs (1999).

2.7. Statistical analysis

Data were analyzed comparing *A. mellifera*-Riozinho, *A. mellifera*-Rolante, *M. obscurior*-Riozinho, and *M. obscurior*-Rolante. Due to asymmetry of distributions as well as inequality of variances, the comparisons were done using Friedman nonparametric analysis of variance, the date of sampling being used as blocks. For these analyses, only the 14 sampling dates with no missing data for all four groups were used. *P* values were adjusted for multiple comparisons and were considered statistically significant if lower than 0.05.

3. RESULTS

3.1. Pollen type richness

Both *A. mellifera* and *M. obscurior* used a broad spectrum of pollen resources, which is characteristic of polylectic bee species. However, in both study areas, *A. mellifera* exploited the largest number of plant species represented by 75 pollen types in Riozinho and 92 in Rolante compared with *M. obscurior*, 37 pollen types in Riozinho, and 23 in Rolante. A subset of 21 pollen types in Riozinho and 19 in Rolante were common to both bee species.

The richness of pollen types of each sample throughout the year in Riozinho ranged from 5 to 21 for *A. mellifera* and from 2 to 10 for *M. obscurior*. In Rolante, the number of pollen types found in the samples ranged from 6 to 21 for *A. mellifera* and from 1 to 6 for *M. obscurior* (Figure 1).

The pollen sources used by both species of bees in Riozinho were distributed among 36 botanical families, with *A. mellifera* foraging on 33 of them and *M. obscurior* on 14 of them. In

Rolante, the pollen types identified in the samples belonged to 31 botanical families, all of which were exploited by *A. mellifera*, but only nine of them by *M. obscurior*. The most representative plant families for *A. mellifera* were Myrtaceae, Asteraceae, and Arecaceae in both areas. For *M. obscurior*, in Riozinho, the plant families Myrtaceae, Solanaceae, and Primulaceae had a greater representation within the pollen sources whereas, in Rolante, the most representative families were Myrtaceae and Arecaceae (Figure 2).

3.2. Evenness

The lowest evenness index in the pollen collections of *A. mellifera* in Riozinho occurred on April (Apr) 2 (0.53), whereas the largest (0.81) occurred on June (Jun) 2 (Table I). With regard to the distribution of pollen types collected by *M. obscurior* in Riozinho, the indices varied from 0.30 on November (Nov) 1 to 0.87 on Apr 2 (Table I). In Rolante, the lowest index for *A. mellifera* occurred on Jun 2 (0.34), whereas the largest occurred on January (Jan) 1 (0.77) (Table II). The collection of a single pollen type by *M. obscurior* on Apr 1, May 1, May 2, Jun 1, and Jun 2 was reflected by a lower evenness index between samples (0.0). February (Feb) 1 had the largest evenness index (0.94) (Table II).

3.3. Diversity and trophic niche breadth

Over the course of 1 year, the diversity of pollen types for *A. mellifera* according to Shannon's index ranged from 1.17 (Apr 2) to 2.16 (Dec 1 and 2), mean 1.67 ± 0.33 (mean \pm SD) ($n=18$), and for *M. obscurior*, it ranged from 0.41 (Nov 1) to 1.74 (Apr 1), 1.03 ± 0.36 ($n=15$), in Riozinho (Table I) (Figure 3). With regard to the diversity of resources exploited by *A. mellifera* in Rolante, Shannon's index ranged from 0.79 (Jun 2) to 2.08 (Nov 1), 1.5 ± 0.33 ($n=19$) and from 0.0 (Apr 1, May 2, Jun 1, and Jun 2) to 1.21 (March (Mar) 1), 0.58 ± 0.46 ($n=17$) for *M. obscurior* (Table II) (Figure 4).

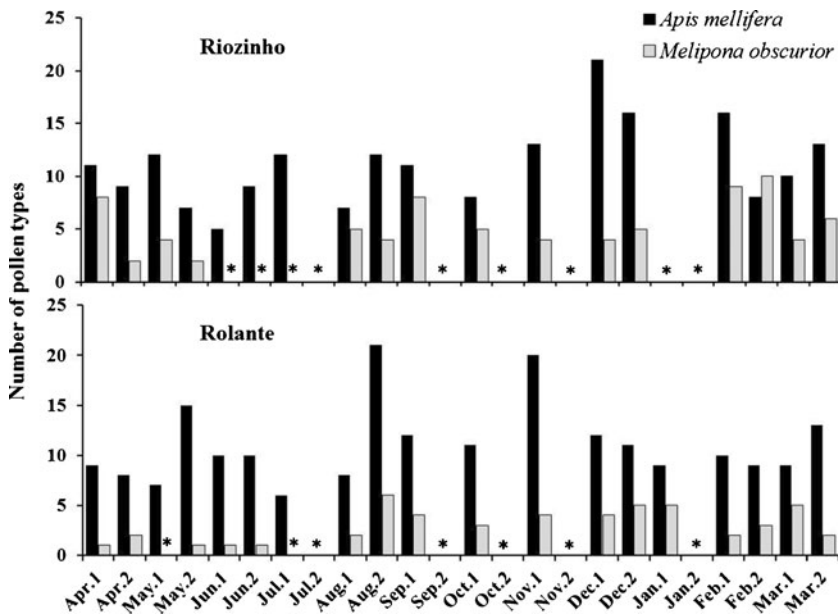


Figure 1. Number of pollen types in each sample collected from forager bees of *A. mellifera* and *M. obscurior*, from April 2009 to March 2010, in Riozinho and Rolante, RS, Brazil. Asterisk refers to the lack of collection to the respective period.

Friedman’s test for richness and Shannon index differ among the four groups of data ($P <$

0.001 in both cases). Although no differences were found between locality for the same

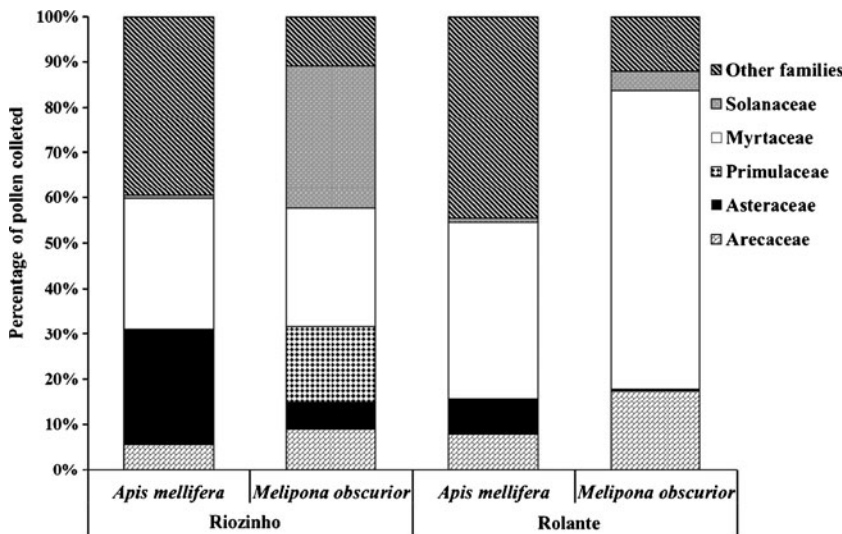


Figure 2. Representativeness of plant families in the samples of pollen collected by *A. mellifera* and *M. obscurior* with, at least, a single occurrence $\geq 15\%$, from April 2009 to March 2010, in Riozinho and Rolante, RS, Brazil

Table I. Indices of richness (S), evenness (J), and trophic niche breadth (Shannon H') of pollen types in each sample of pollen collected by *A. mellifera* and *M. obscurior*, from April 2009 to March 2010, in Riozinho, RS, Brazil.

Samples	Richness		Evenness		Shannon index	
	<i>A. mellifera</i>	<i>M. obscurior</i>	<i>A. mellifera</i>	<i>M. obscurior</i>	<i>A. mellifera</i>	<i>M. obscurior</i>
Apr 1, 2009	11	8	0.60	0.84	1.43	1.74
Apr 2	9	2	0.53	0.87	1.17	0.61
May 1	12	4	0.76	0.54	1.88	0.75
May 2	7	2	0.67	0.85	1.30	0.59
Jun 1	5	–	0.73	–	1.18	–
Jun 2	9	–	0.81	–	1.78	–
Jul 1	12	–	0.76	–	1.88	–
Jul 2	–	–	–	–	–	–
Aug 1	7	5	0.76	0.58	1.47	0.93
Aug 2	12	4	0.75	0.78	1.86	1.07
Sep 1	11	8	0.63	0.78	1.52	1.61
Sep 2	–	–	–	–	–	–
Oct 1	8	5	0.79	0.52	1.65	0.84
Oct 2	–	–	–	–	–	–
Nov 1	13	4	0.76	0.30	1.95	0.41
Nov 2	–	–	–	–	–	–
Dec 1	21	4	0.71	0.71	2.16	0.98
Dec 2	16	5	0.78	0.71	2.16	1.14
Jan 1, 2010	–	–	–	–	–	–
Jan 2	–	–	–	–	–	–
Feb 1	16	9	0.74	0.53	2.06	1.16
Feb 2	8	10	0.70	0.58	1.45	1.33
Mar 1	10	4	0.58	0.78	1.33	1.09
Mar 2	13	6	0.74	0.65	1.91	1.16

En dash refers to the lack of collection

species of bee both for richness and Shannon index (*A. mellifera*, $P=1.000$ and 1.000 ; *M. obscurior*, $P=1.000$ and 0.644 , respectively), the two species differed when compared in the same locality (*A. mellifera* versus *M. obscurior*: Riozinho $P=0.010$; Rolante $P<0.001$ for richness; Riozinho $P=0.032$ and Rolante $P<0.001$ for Shannon). Values for *A. mellifera* were higher in both cases. As for evenness (J), no statistically significant difference among the four groups was observed ($P=0.510$ and $P=0.066$, respectively).

3.4. Representativeness of pollen types: frequency class intervals

With regard to the pollen types, the majority was present in low percentages (OP) in the samples collected ($n=69$ samples) by *A. mellifera* and *M. obscurior* throughout the year in both areas. By contrast, the number of DP types was lower compared with the other frequency classes for both bee species in both areas. Many types were present in more than one class interval. Therefore, in samples of

Table II. Indices of richness (S), evenness (J), and trophic niche breadth (Shannon H') of pollen types in each sample of pollen collected by *A. mellifera* and *M. obscurior*, from April 2009 to March 2010, in Rolante, RS, Brazil.

Amostras	Richness		Evenness		Shannon index	
	<i>A. mellifera</i>	<i>M. obscurior</i>	<i>A. mellifera</i>	<i>M. obscurior</i>	<i>A. mellifera</i>	<i>M. obscurior</i>
Apr 1, 2009	9	1	0.68	0.00	1.50	0.00
Apr 2	8	2	0.71	0.58	1.47	0.40
May 1	7	–	0.58	0.00	1.13	–
May 2	15	1	0.76	0.00	2.05	0.00
Jun 1	10	1	0.60	0.00	1.38	0.00
Jun 2	10	1	0.34	0.00	0.79	0.00
Jul 1	6	–	0.65	0.00	1.17	–
Jul 2	–	–	–	–	–	–
Aug 1	8	2	0.64	0.81	1.33	0.56
Aug 2	21	6	0.67	0.30	2.03	0.54
Sep 1	12	4	0.67	0.83	1.68	1.16
Sep 2	–	–	–	–	–	–
Oct 1	11	3	0.49	0.65	1.19	0.71
Oct 2	–	–	–	–	–	–
Nov 1	20	4	0.69	0.83	2.08	1.15
Nov 2	–	–	–	–	–	–
Dec 1	12	4	0.61	0.83	1.51	1.16
Dec 2	11	5	0.69	0.70	1.65	1.13
Jan 1, 2010	9	5	0.77	0.43	1.69	0.70
Jan 2	–	–	–	–	–	–
Feb 1	10	2	0.68	0.94	1.56	0.65
Feb 2	9	3	0.66	0.43	1.45	0.48
Mar 1	9	5	0.61	0.75	1.34	1.21
Mar 2	13	2	0.57	0.14	1.45	0.10

En dash refers to the lack of collection

pollen collected by *A. mellifera* in Riozinho, 72 % of the pollen types ($n=75$) occurred on the OP class interval, and 36 types (48 %; $n=75$) were present exclusively at frequencies below 3 % (OP), corresponding to 3.9 % of all grains analyzed from this species in this area. The other types, 46.7 % were IP, 26.7 % were AP, and 6.7 % were DP. The following species belonged to this latter class: *Eucalyptus*, *Piper* sp., *Mikania*-type, *Syagrus romanzoffiana*, and *Senecio*-type (Electronic supplementary information, Online Resource 1). The pollen types collected by *M. obscurior* in Riozinho had the

following distribution of 59.5 % ($n=37$) that occurred as OP, 17 types (45.9 %; $n=37$) were found only as OP, corresponding to 1.8 % of the total pollen collected by this species in this area. The other types analyzed, 35.1 % occurred as IP, 29.7 % as AP, and 16.2 % as DP. The dominant pollen type category included *Miconia*-type, *Eucalyptus*, *S. romanzoffiana*, *Solanum mauritianum*, Solanaceae sp. 1, and *Myrsine* (Electronic supplementary information, Online Resource 1).

In Rolante, from the pollen types collected by *A. mellifera*, 84.8 % ($n=92$ types) occurred

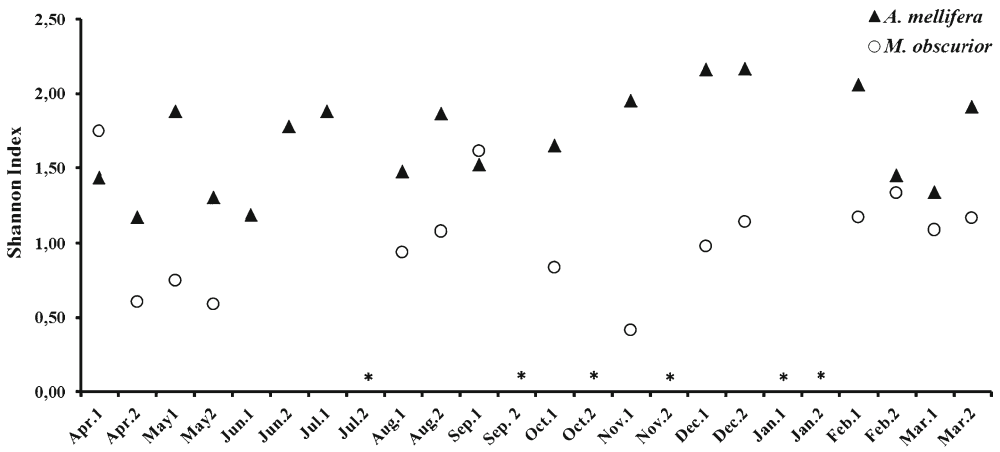


Figure 3. Trophic niche breadth, by Shannon index, used by *A. mellifera* and *M. obscurior*, from April 2009 to March 2010, in Riozinho, RS, Brazil. Asterisk refers to the lack of collection to the respective period for both bee species

on the OP class interval, 59 types (64.1 %; $n = 92$) exclusively at frequencies below 3 %. From the other pollen types collected, 26.1 % were IP, 21.7 % were AP, and 5.4 % were DP. Among the dominant plant species found in the samples were *Eucalyptus*, *Schinus terebinthifolius*, Poaceae sp. 1, Myrtaceae sp. 1, and *Dodonaea viscosa* (Electronic supplementary information, Online Resource 2). Together with *S. romanzoffiana*,

these pollen types comprised 65.4 % of the pollen in all samples analyzed. Poaceae sp. 1 is notable because it is present in 72.2 % of samples ($n = 15$) collected by *A. mellifera* in Riozinho (Electronic supplementary information, Online Resource 1) and in 63.1 % of the samples ($n = 19$) collected in Rolante (Electronic supplementary information, Online Resource 2). In the pollen type frequency classes of *M. obscurior*

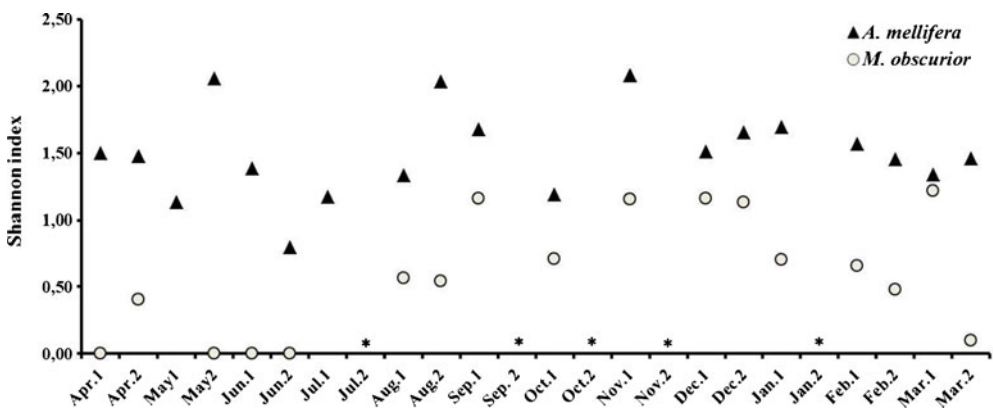


Figure 4. Trophic niche breadth, by Shannon index, used by *A. mellifera* and *M. obscurior*, from April 2009 to March 2010, in Rolante, RS, Brazil. Asterisk refers to the lack of collection to the respective period for both bee species

samples from Rolante, 52.2 % occurred as OP; eight types (34.8 %; $n=23$) were found only as OP, totaling 0.71 % of the pollen grains analyzed in the samples from *M. obscurior* in Rolante. Among the other pollen types, 21.7 % occurred as IP and 43.5 % as AP. The DP represented 17.4 % of the pollen types, including *Eugenia hiemalis*, *Eucalyptus*, Myrtaceae sp. 4, and *S. romanzoffiana* (Electronic supplementary information, Online Resource 2).

4. DISCUSSION

In this study, a generalist foraging habit based on the number of pollen types exploited by *A. mellifera* and *M. obscurior* was observed. This foraging habit is characteristic of many bee species of Apidae as reported by Cortopassi-Laurino and Ramalho (1988), Roubik (1989), and Cane and Sipes (2006). The increased richness of floral sources observed in the pollen collections of *A. mellifera* relative to *M. obscurior* appears to be a characteristic of this exotic bee compared with Meliponini bees. This result was also observed by Wilms and Wiechers (1997) in a study with *A. mellifera*, *Melipona bicolor* Lepeletier, and *Melipona quadrifasciata* Lepeletier in the Atlantic rain forest in the state of São Paulo. This could also be observed by the largest number of interactions that *A. mellifera* maintained with plant species compared with other 69 species of bees that visited flowers in the arid Caatinga environment (Pigozzo and Viana 2010). Therefore, *A. mellifera* could strongly influence bee-plant interaction networks (Santos et al. 2010).

The variation in the number of pollen sources used by both species of bees throughout the year in both areas could be related to factors that are external to the colonies. For example, climatic factors that directly reflect phenology and influence the availability of flowers (Roubik 1989) and adverse weather conditions that may impair foraging activity of either bee species. These may be likely causes for the low pollen richness that was found for samples of *A. mellifera* for Jun 1 in Riozinho and for Jul 1 in Rolante, because these are months with low

temperatures in southern Brazil. Furthermore, during these periods, the increased representation of pollen from *Eucalyptus* spp., which produces abundant blossoms, may also explain the use of fewer pollen types. Low temperatures also influenced the absence of pollen collection by *M. obscurior* in June in Riozinho and in July in both areas and also the lowest richness index of pollen types in Rolante for the month of June. These results are validated by the observations of Borges and Blochtein (2005), who observed that temperatures above 13.7 °C during the autumn–winter were instrumental in initiating the flight activity of *M. obscurior*. Another possibility for the low richness of pollen types is a decrease in the external activities of the *M. obscurior* colonies related to a discontinuation (diapause) in reproductive activity resulting from low temperatures (Hilário and Imperatriz-Fonseca 2009). Facultative reproductive diapause was observed for the same species in this geographic region by Borges and Blochtein (2006). Pollen collection from only one or two floral sources recorded during certain periods for *M. obscurior*, despite the greater number of pollen types collected by *A. mellifera* that is indicative of a greater variety of blossoms available, seems to be a common behavior in Meliponini species (Oliveira et al. 2009), including species of *Melipona* (Ramalho et al. 1994; Fidalgo and Kleinert 2010). Kleinert et al. (2009) hypothesized that pollen collection from a few sources could be a way to maximize individual efficiency, which is a foraging strategy that involves floral preference.

The increase in the richness of pollen types in the samples from August could be a result of milder weather conditions that promote greater foraging activity. This result is corroborated by an increase in the intensity of external activities in Meliponini hives during the spring and summer in the south of Brazil observed for *Plebeia saiqui* (Holmberg) (Pick and Blochtein 2002), *M. obscurior* (Borges and Blochtein 2005, 2006), and *Melipona bicolor schencki* Gribodo (Ferreira Júnior et al. 2010). Additionally, a greater pollen range associated with a less favorable period as was observed in July for *A.*

mellifera in Riozinho and may indicate a resource shortage that triggers the search for floral pollen from many sources.

The constant presence of Myrtaceae pollen in the diet of *A. mellifera* and *M. obscurior* throughout the year in both areas is consistent with other studies that identify this family as one of the pollen sources most exploited by bees in Brazil (Wilms and Wiechers 1997; Carvalho et al. 2001; Antonini et al. 2006; Ramalho et al. 2007; Luz et al. 2011). The pollen type *Eucalyptus*, which is a representative of the Myrtaceae family found in most samples, in some cases as a dominant pollen, was used similarly by *Melipona marginata marginata* Lepeletier (Kleinert-Giovannini and Imperatriz-Fonseca 1987) and *Melipona capixaba* Moure and Camargo (Luz et al 2011) in other Brazilian states. *S. romanzoffiana* (Arecaceae) was another resource exploited by both species in both areas and in some cases was the dominant pollen in several samples throughout the year. The importance of Arecaceae pollen as a resource for other *Melipona* species was cited by Oliveira et al. (2009), and for *A. mellifera* by Ramalho et al. (2007) and Boff et al. (2011). Other plant families, however, were more frequently exploited by one of the bee species, such as Poaceae and Asteraceae. These pollens were a constant presence in the collections of *A. mellifera* and were present in a few collections of *M. obscurior*, similar to other studies of *Melipona quadrifasciata anthidioides* Lepeletier (Antonini et al. 2006) and *Melipona scutellaris* Latreille (Ramalho et al. 2007). However, *A. mellifera* displays some preference for foraging on herbs (Moretti and Marchini 1998), which include the majority species of Poaceae and Asteraceae (Boff et al. 2011). Conversely, Solanaceae species, particularly *S. mauritianum*, were heavily exploited by *M. obscurior* in Riozinho and were present in a few *A. mellifera* collections as occasional pollen. Similarly, the *Miconia*-type (Melastomataceae) was an important floral resource in some samples of *M. obscurior* in both areas. The presence of *Miconia* in samples from *M. obscurior* was also observed

by Harter et al. (2002) in an Araucaria forest of Rio Grande do Sul. The use of sources with poricidal anthers, which is the case of many species of Melastomataceae and Solanaceae, seems to be common in *Melipona* bees (Imperatriz-Fonseca et al. 1994; Wilms and Wiechers 1997; Harter et al. 2002; Antonini et al. 2006; Nunes-Silva et al. 2010). The release of pollen from this anther type occurs by vibration of the bee thorax muscles (Nunes-Silva et al. 2010), which is an innate ability of *Melipona* bees, but is absent in *A. mellifera*. The presence of Solanaceae pollen in *A. mellifera* samples from Riozinho and Rolante was related to the opportunistic behavior of collecting pollen left on previous visits by other bee species.

The Shannon index values for niche breadth observed for *A. mellifera* were greater than those of *M. obscurior*, compatible with the results found by Oliveira et al. (2009) for *A. mellifera* (ranged from 1.59 to 3.0) and for *M. marginata marginata* Moure (0.88 and 0.95). Higher values for *A. mellifera* in relation to other stingless bees were also found by Aguiar (2003) and Aguiar and Santos (2007)).

A greater range of trophic niche associated with the greater richness of pollen types and evenness coincided with a period of improved weather in this area. The association of a lower breadth with a greater concentration of collection from a few pollen types (lower evenness) that was observed for *M. obscurior* demonstrates that these bee species may have a tendency to specialize. This can be observed in *M. obscurior* samples from Nov 1 in Riozinho, in which *S. mauritianum* comprised 90.4 % of the collected pollen, leading to the lowest levels of evenness and trophic niche breadth of all samples throughout the year. Similarly, in Rolante, the presence of only one pollen source in the samples from Apr 1, May 2, Jun 1, and Jun 2, led to a zero index of evenness and niche breadth. This behavior of temporal specialization is likely to be a result of economic decisions (Ramalho et al. 1994).

The trophic niche of *A. mellifera* and *M. obscurior* in the Atlantic Forest of southern

Brazil showed generalist feeding behavior common to social bees, which demonstrates plasticity in pollen resource use. The variation in richness and the representation of pollen resources used during the year may have been influenced by factors related to the environment and the behavioral and biological aspects that are typical of each species. Therefore, the low niche breadth associated with low evenness that characterized some pollen samples demonstrated a trend toward temporal specialization through more intense exploitation of a few floral sources, such as Myrtaceae, Solanaceae, Melastomataceae, and Primulaceae by *M. obscurior*, and species of Myrtaceae, Asteraceae, Poaceae, and Arecaceae by *A. mellifera*. These results are consistent with the results of other authors (Imperatriz-Fonseca et al. 1994; Wilms and Wiechers 1997; Aguiar 2003; Oliveira et al. 2009). Temporal specialization, as with *M. obscurior* foraging on floral resources, are not used by the exotic bee species; moreover, collecting pollen from plant species with intense flowering, like *Eucalyptus* spp., could lead to a lower interspecific competition and reducing a potential impact on native bee species. In this threatened ecosystem, *M. obscurior* has an important role in the maintenance of plant species that need bee pollinators with special characteristics to extract pollen from poricidal anthers.

It is hypothesized that the results obtained in this study could be used to support meliponiculture in Rio Grande do Sul, thereby encouraging the cultivation of important pollen source plants for *M. obscurior*. Similarly, it is argued that, in areas of the Atlantic rain forest with apiculture activity, measures are necessary for the conservation and restoration of plant species with floral sources that comprise a portion of the pollen diet of *M. obscurior* to reduce the vulnerability of this species.

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Ressources en pollen et étendue de la niche trophique d'*Apis mellifera* et de *Melipona obscurior* (Hymenoptera, Apidae) en climat subtropical, dans la forêt pluviale atlantique du sud du Brésil

Meliponini / ressources florales / pollinisateurs / abeille / pollen

Pollenquellen und Umfang trophischer Nischen bei *Apis mellifera* und *Melipona obscurior* (Hymenoptera, Apidae) unter subtropischen Klimabedingungen im atlantischen Regenwald Südbrasilens

Meliponini / Blütenangebot / Bestäuber / stachellose Bienen / Pollen

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