

1 **Melissopalynology reveals the foraging preferences of the stingless bee *Melipona***
2 ***seminigra pernigra* Moure & Kerr 1950 (Apidae: Meliponini) in cangas of Serra**
3 **dos Carajás, southeastern Amazonia**

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27 ABSTRACT

28 The pollen content of honey samples collected in the years 2017 and 2019 from
29 experimental apiaries of *Melipona seminigra pernigra* Moure & Kerr 1950 installed in
30 campo rupestre on canga (CRC) vegetation of the Serra dos Carajás, southeastern
31 Amazonia, was analyzed to understand the local variability of floral resources occurring
32 on natural and disturbed areas. Around one hundred pollen types were identified mainly
33 belonging to Fabaceae, Myrtaceae and Euphorbiaceae (31, 6 and 5 types, respectively).
34 The N5 mine presented the highest pollen richness with 95 pollen types identified, almost
35 twice of those identified in the other areas, including the better preserved ones. Eighty
36 percent of the pollen types are rare with concentrations $\leq 2,000$ pollen grains/10 g; the
37 remaining types are the most abundant and frequent, and are considered the primary bee
38 sources (PBS). PBS correspond mostly to native plants such as *Tapirira guianensis* Aubl.,
39 *Protium* spp., *Aparisthium cordatum* (A.Juss.) Baill., *Mimosa acutistipula var. ferrea*
40 Barneby, *Periandra mediterrânea* (Vell.) Taub., *Miconia* spp., *Pleroma carajasense*
41 K.Rocha, *Myrcia splendens* (Sw.) DC., *Serjania* spp. and *Solanum crinitum* Lam. All
42 pollen types were identified during both seasons, but higher pollen concentration are
43 related to the dry period (June-September). The statistical analysis indicated that there
44 was no significant difference in honey pollen data between the natural and disturbed areas
45 since the plant species considered as PBS in this work are intensively used in revegetation
46 of degraded area (RDA) processes by mining activities.

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50 KEYWORDS

51 Stingless bees; honey; pollen; Serra dos Carajás; Amazônia; *Melipona*; Iron mining

52 1. Introduction

53 Social, native stingless bees – Meliponini tribe - are the main pollinators in neotropical
54 forests and contribute to the maintenance of the genetic diversity of their habitat (Roubik
55 1989; Imperatriz-Fonseca et al. 2012). In addition, stingless bees play an important role
56 in pollination of cultivated plants (Slaa et al. 2006; Giannini et al. 2015) and are used by
57 traditional people since many bee species store good quality honey that are historically
58 consumed (Quezada-Euán et al. 2018). In the last decades, apiculture with stingless bees
59 (called meliponiculture) grew considerably, especially for honey production (Jaffe et al.
60 2015); currently, this activity is an important example of native biodiversity associated to
61 raise income for traditional Amazonian communities (Cortopassi-Laurino et al. 2006).

62 Melissopalynological studies of stingless bees are important to identify the sources of
63 nectar explored by bees and, through this, improve the management of colonies and
64 landscape for a better honey production in both aspects: quality and quantity. Moreover,
65 it can potentially be used to characterize the local flora regarding its diversity and
66 phenology (Absy et al. 1984; Barth 1989, 1990; Martins et al. 2011).

67 The use of melissopalynology for identifying nectar resources used by stingless bees
68 on Brazil dates from 1960, according to an historical review (Barth 2004). Studies
69 analyzed floral preferences of single stingless bee species on different regions, such as
70 *Melipona asilvai* (Silva et al. 2018), *Melipona capixaba* (Luz et al. 2011), *Melipona*
71 *scutellaris* (Carvalho et al. 2001), *Tetragonisca angustula* (Novais and Absy 2015),
72 *Scaptotrigona aff. depilis* (Aleixo et al. 2017) and *Scaptotrigona postica* (Luz et al. 2019).
73 Other studies also presented floral preferences for more than one bee species, such as
74 *Melipona quadrifasciata anthidioides* and *Melipona scutellaris* (Oliveira et al. 2017),
75 *Apis mellifera* and *Melipona obscurior* (Hilgert-Moreira et al. 2014), or reviewed
76 information for multiple species (Ramalho et al. 1990, Freitas and Novais 2014, Souza et

77 al. 2018). Some studies have been developed specifically in the Amazon region, in natural
78 and disturbed areas, to identify the origin of pollen in loads carried by forager bees or in
79 the stored honey and beebread (Absy & Kerr, 1977; Absy et al. 1980; Carreira & Jardim
80 1994; Marques-Souza 1996; Marques-Souza et al. 1995, 1996, 2002; Rezende et al.,
81 2019). These are important contributions to understand the floral resources collected by
82 bees, especially considering the high diversity of stingless bees on Brazil and the
83 particularities of each biome. It is also key to practical applications on sustainable
84 development practices for rural communities (meliponiculture and honey production)
85 (Jaffe et al. 2015) and/or for the design of restoration strategies (Montoya et al. 2012).

86 Knowledge regarding bee flora in plant endemism hotspots (Kasecker et al. 2009;),
87 such as *campo rupestre* on *canga* at the Serra dos Carajás (Mota et al. 2018), are still
88 incipient (Barth 1987). This particular type of open vegetation consists mostly of herbs
89 and shrubs adapted to the edaphic conditions provided by iron-rich outcrops (Guimarães
90 et al. 2014; Schaefer et al. 2016; Viana et al. 2016; Mota et al. 2018) surrounded mostly
91 by evergreen tropical forest. The complexity of this plant-soil interaction is also
92 responsible for the development of different microhabitats with high beta diversity and
93 endemic plants (Nunes et al. 2015; Viana et al. 2016; Mota et al. 2018). Some Amazonian
94 stingless bees are also poorly known, as is the case with *Melipona seminigra pernigra*
95 Moure & Kerr 1950. This native, abundant species in eastern Amazonia (Moure & Kerr
96 1950; Silveira et al. 2002) is considered as one of the most popular species reared by
97 traditional populations for honey production (Nogueira-Neto 1997; Cortopassi-Laurino
98 et al. 2006), as seen also in the Carajás region.

99 Our aim is to understand the local variability of floral resources utilized by *M.*
100 *seminigra pernigra* in natural and disturbed areas. For this, we kept colonies of this
101 stingless bee species in experimental meliponaries on *canga*, forest and disturbed areas

102 in the region of Carajás and analyzed their honey samples through melissopalynology.
103 This is an important step for the conservation of bee species and their landscape,
104 providing knowledge about plant species used for honey production and also to help on
105 degraded land restoration strategies in the Carajás region.

106

107 **2. Study area**

108 The Carajás National Forest, a Federal Conservation Unit created in February 1998
109 comprises an area of approximately 3,930 km² (Figure 1A). Represented by discontinuous
110 table-top outcrops surrounded by a matrix of humid evergreen tropical forest (HETF) and
111 seasonally dry forest (SDF). The higher areas (600-800 m a.s.l.) are occupied by lateritic
112 plateaus with *campo rupestre on canga* (CRC) vegetation (Guimarães et al. 2014; Viana
113 et al. 2016; Mota et al., 2018). This mineral province includes one of the largest iron ore
114 deposits worldwide (Tolbert et al. 1971) and mining operations in the region began in
115 1985. The group of northern plateaus are known as Serra Norte, where two main areas
116 are being exploited, namely N4 and N5 mines.

117 The rainfall regime is characterized by a rainy season, regionally known as Amazonian
118 winter from November to May, followed by a dry Amazonian summer between June and
119 October (Lopes et al. 2013). The total annual rainfall of the Carajás region may vary
120 between 1,545 mm and 1,863 mm during the rainy season, with the dry season amounting
121 to values between 159 mm and 321 mm (Silva Júnior et al. 2017). The mean temperature
122 is 27.2°C, with a minimum annual temperature of 26.6°C in January and a maximum
123 annual temperature of 28.1°C in September (Tavares et al. 2018).

124

125 3. Materials and methods

126 Four experimental meliponaries were installed in natural and disturbed areas of Serra
127 Norte (Figure 1B, C). The natural area is located in the Trilha da Lagoa da Mata (1),
128 northeast of the N5 mine, Serra Norte. This area presents a narrow CRC area of around
129 33,000 m² surrounded by HETF (Figure 1B). Three disturbed areas were chosen as
130 follows: Viveiro Florestal (2), a plant nursery area for growing species of the Carajás
131 flora to provide plants for the revegetation of degraded areas (RDA), located ~ 1.2 km
132 southeast of area 1, covering an area of 26,500 m² surrounded by HETF and weedy plants;
133 2. an area close to the N5 mine (3), located 8.7 km southwest of area 1, consisting of
134 HETF and SDF towards the southern part of this area (Figure 1C); 3. a pit slope in RDA
135 process (4), mainly covered by CRC and weedy plants, located 5.5 km southwest of area
136 1 and 3.4 km distant of area 3. The main plant species in the four areas are given in
137 Supplementary Table S1. *Melipona seminigra* forage range is around 1 km (L. Costa,
138 personal communication), a flight ability similar to that of *Melipona mandacaia* Smith
139 (Kuhn-Neto et al., 2009), so it is unlikely that foraging activity overlapped between areas,
140 with exception to areas 1 and 2.

141 Due to the expansion dynamics of the N5 mine, the meliponary installed in this area
142 (3) was moved in March 2018, while the RDA apiary (4) started in June 2018. Monthly
143 samples were collected from the honey pots of fourteen hives of *Melipona seminigra*
144 *pernigra* from each apiary. The content, from five to ten honey pots (chosen randomly)
145 was removed during each collection event (Figure D, E). 46 samples covering a period of
146 16 months (September 2017 to January 2019) were harvested.

147 Honey samples weighing 10 g were diluted using 20 ml of distilled water according to
148 Maurizio and Louveaux et al. (1965). For each sample, a tablet containing 9,666 spores
149 of *Lycopodium clavatum* was added (Stockmarr 1971). These samples were acetolysed

150 following Erdtman (1952), and mounted on microscope slides using glycerin jelly. They
151 were deposited in the pollen library at Instituto Tecnológico Vale (PaliITV, Belém,
152 Brazil). Five hundred pollen grains were counted per sample using a Zeiss Axio Imager
153 M2. Pollen type identification was based on morphological comparisons with PaliITV.

154 The distribution frequency of the pollen types followed Feller-Demalsy et al. (1987):
155 very frequent (>50%), frequent (20–50%), infrequent (10–20%) and rare (<10%); and
156 groups of pollen concentration according to Maurizio (1975): Group I (<20,000), Group
157 II (20,000–100,000), Group III (100,000–500,000), Group IV (500,000–1,000,000) and
158 Group V (>1,000,000) were adopted to classify pollen types per honey sample. The range
159 of the pollen types per honey sample was calculated using the Shannon–Weaver diversity
160 index (H' ; Ludwig and Reynolds 1988). Pielou's evenness index (J'), was calculated to
161 evaluate the degree of heterogeneity (0) or homogeneity (1) of pollen resources (Pielou
162 1977). Product moment correlation coefficient (PMCC) was applied between pollen
163 richness, H' and J' data.

164 For statistical analysis, the total pollen concentration (grains/cm³ unit) of four areas
165 (Trilha da Lagoa da Mata, Viveiro Florestal, N5 Mine and RDA) were counted based on
166 the definition of the seasonal rainfall pattern. The descriptive analyses were performed
167 using common and abundant taxa among sites, and Wilcoxon test for significance
168 difference of each site between periods. Bray-Curtis based non-metric multidimensional
169 scaling (NMDS) has been applied to evaluate species distribution and their relationship
170 between the sites. The NMDS analysis required the vegan R package (version 2.5.3;
171 Oksanen 2016), and visualization were carried out using the ggplot2 package (version
172 3.4.1; Wickham 2009)

173 Climatological data covering the collection years were obtained from the
174 meteorological station of Serra Norte de Carajás (OMM: 81860), which covers all studied
175 areas.

176

177 **4. Results**

178 *4.1. Climatological data*

179 The patterns of wind intensity and direction in the study site from January 2017 to January
180 2019 show slight variation of wind speed (~ 1 to 2 m/s) with prevailing direction from
181 the E and ENE (Figure 1A). The mean minimum and maximum air temperature for this
182 period was 23.8 °C and 27.7 °C, respectively, with the highest values in August to
183 September, while the lowest temperatures occurred in February and July (Figure 2A).
184 Based on the accumulated monthly rainfall (Figure 2A), the dry period extended from
185 June to September, ranging from 67 to 132 mm. The rainy period comprised October to
186 May, with values ranging from 1805 to 2300 mm. The total annual precipitation during
187 2017 was lower than that for 2018 with values of 1935 and 2367 mm, respectively. The
188 wettest month of the study period was February 2019 (approx. 700 mm) Relative
189 humidity follows the seasonal rainfall pattern, with the lowest values ($< 80\%$) observed
190 during in the dry period. Highest solar irradiance was detected in July with a mean of \sim
191 220 W/m², while the lowest occurred in December, with ~ 140 W/m² (Figure 2B).

192

193 *4.2. Pollen assemblage*

194 A total of 104 pollen types were identified in the 46 honey samples analyzed, belonging
195 to 35 families. Fabaceae, Myrtaceae and Euphorbiaceae were the most representative with
196 31 , 6 and 5 species, respectively (Supplementary Table S2).

197 In general, the N5 mine presented the highest pollen richness with 95 pollen types
198 identified. Trilha da Lagoa da Mata and Viveiro Florestal presented around 60 pollen
199 types each, while RDA had only 39 types. Maximum pollen concentration per area ranged
200 from 60,895 to 1,521,194 pollen grains/g, which were observed, respectively, in RDA
201 and Viveiro Florestal areas. 80% of the pollen types were found with values < 5,000
202 grains/10g and < 1%. Thus, the pollen types are generally rare (< 10%; Feller-Demalsy
203 et al., 1987) and belong to group I ($\leq 20,000$ pollen grains/10 g; Maurizio, 1975) (see
204 Supplementary Table S2; Supplementary Figure S1).

205 The remaining 20% of the pollen types are the most abundant and present in all areas
206 along the studied period (Supplementary Table S2; Supplementary Figure S2, S3, S4,
207 S5). These types were identified as *Tapirira guianensis* (Anacardiaceae), *Protium*
208 (Burseraceae), *Aparisthium cordatum* and *Alchornea* (Euphorbiaceae), *Mimosa*
209 *acutistipula var. ferrea* and *Periandra mediterranea* (Fabaceae), *Miconia* and *Pleroma*
210 *carajasense* (Melastomataceae), *Myrcia splendens* (Myrtaceae), *Serjania* (Sapindaceae)
211 and *Solanum crinitum* (Solanaceae) (Plate 1, 2). Abundances varied according to the year
212 of study.

213 Significantly higher pollen concentration was detected on 2018 (Supplementary Figure
214 S2, S3, S4, S5). Thus, for the Trilha da Lagoa da Mata, pollen types of *P. carajasense*,
215 *Miconia*, *Alchornea* and *M. acutistipula var. ferrea* abounded in March and April, while
216 *Protium* and *T. guianensis* in August and September (Supplementary Figure S2).

217 *Protium* and *T. guianensis* also abounded in June and July in the Viveiro Florestal,
218 where *A. cordatum* was very representative in October to December (Supplementary
219 Figure S3). *Protium* was abundant in June and November in the RDA area
220 (Supplementary Figure S5).

221 The pollen types *M. splendens* and *M. acutistipula* var. *ferrea* were significantly
222 present from September to December 2018, but not during the same period of the previous
223 year in N5 mine.

224 According to the mean values of pollen concentration of the most abundant pollen
225 types during the dry and rainy seasons, the pollen of all plant species was identified during
226 both seasons, however in variable abundance. Higher values are generally related to the
227 dry period (June-September). *M. acutistipula* var. *ferrea* is more abundant at the Viveiro
228 Florestal and N5 mine in the dry and wet season, respectively. *P. carajasense* abounded
229 during the wet season in the Trilha da Lagoa da Mata, while it was remarkably important
230 in the dry season in the Viveiro Florestal (Figure 3).

231 The Shannon-Weaver diversity (H') and Pielou's evenness (J') indexes have strong
232 PMCC (ρ -value ~ 0.7 to 0.9), and moderate to strong correlation with pollen richness (ρ -
233 value ~ 0.5 to 0.9) in each area (Figure 4). Thus, higher H' and J' were related to 2017,
234 while lower values were mainly found during June and July 2018.

235

236 4.3. Statistical analyses

237 Considering the statistical analysis, the overall mean of pollen concentration of all sites
238 shows an overlap of pollen concentration distribution (Figure 5A). RDA samples had the
239 lowest concentration than all other sites for both periods. Diversely, Viveiro Florestal had
240 different abundance for the two periods. Wilcoxon test was applied to evaluate differences
241 between climate periods for each site. The results show no statistically significant
242 difference on sites between periods, except for the Viveiro Florestal (ρ -value = 0.03). In
243 order to evaluate the pollen distribution and similarity among the sites, Non-metric
244 Multidimensional Scaling was the appropriate ordination method because the stress value
245 for two dimensional, which was 0.04 . NMDS, pointed to (dis)similarities on sites based

246 on pollen concentration (Figure 5B). RDA samples are more related on both periods due
247 to abundance of the pollen types of *Protium* and *Serjania*. N5 Mine samples are more
248 similar during both periods due to the abundance of *Mimosa acutistipula var. ferrea* and
249 *Myrcia splendens*, whereas the Trilha da Lagoa da Mata and Viveiro Florestal (rainy
250 period) have more contribution from *A. cordatum*, *Miconia* and *P. carajasense*. During
251 the dry period, Trilha da Lagoa da Mata and Viveiro Florestal differed from other samples
252 due to their pollen assemblages: the first is mainly composed by *T. guianensis* and
253 *Protium* and the latter has higher influence from several species. According to the
254 Wilcoxon test, Viveiro Florestal demonstrated significant statistical difference for both
255 periods, and therefore the NMDS is coherent with Wilcoxon test. Viveiro Florestal had
256 higher concentration of all pollen assemblages during the dry period, whereas, during the
257 rainy period it has a composition more comparable to the one at the Trilha da Lagoa da
258 Mata and N5 Mine in the same period.

259

260 5. Discussion

261 Considering the total pollen assemblage identified in honey samples of *M. seminigra*
262 *pernigra*, around 80% of the pollen types were found to be within the values < 5,000
263 grains/10g and < 1%. The remaining ~20% are the primary bee sources. The secondary
264 sources (less abundant) are continuously explored, providing a small amount of food that
265 is an alternative resource for the colony (Heinrich 1976). This is especially important
266 when other plants are saturated by other pollinators or flowering diminishes according to
267 seasonal changes. In some occasions, the secondary source moves to a central position in
268 the food supply (Novais & Absy 2013).

269 *Melipona* species are a successful generalist group of bees from tropical humid forests
270 that have a close relationship with tree crowns and mass flowering (Ramalho 2004), and

271 consequently play an important role in plant reproduction and natural forest regeneration
272 (Imperatriz-Fonseca et al. 1993). In the present experimental study developed at the
273 Carajás National Forest, the honey samples of *M. seminigra pernigra* were constituted
274 mostly by native species pollen.

275 Considered a native and abundant species, *Mimosa acutistipula var. ferrea* Barneby is
276 endemic to north and northeastern Brazil and abundant in the Serra dos Carajás region,
277 occurring on all CRC outcrops studied (Mattos et al. 2018). It features in the Brazilian
278 red list of plants as Data Deficient (DD) (Martinelli & Moraes 2013) and vulnerable (VU)
279 in the List of Threatened Species of Pará State (COEMA-PA, 2010). *M. acutistipula var.*
280 *ferrea* forms large single-species stands in both *canga* and altered barren areas (Giulietti
281 et al. 2018; Zappi et al. 2018). The clustered, long, pendulous, sweetly scented
282 inflorescences of *M. acutistipula var. ferrea* are very rich in pollen (Mattos et al., 2018).
283 This mass flowering is very attractive for *M. seminigra pernigra*. The abundance of the
284 *Mimosa*-type (small) pollen grains in honey samples can be related to the configuration
285 and relatively small pollen size, varying from 10-14 μm (Zappi et al. 2018 p. 149), which
286 are also released in large amounts according Ferreira and Absy (2017).

287 *P. carajasense* is a recently described endemic species from the CRC of Carajás
288 (Rocha et al. 2017), and it has been categorized as a possible Endangered (EN) species
289 according to the IUCN criteria (IUCN 2012). It occurs in large populations both on natural
290 and anthropic areas. This species has attractive short thyrsoid inflorescences with 7–25
291 campanulate flowers, lilac-pink to purple petals and poricidal anthers (Matos & Santos,
292 2017; Rocha et al. 2017). Vibrating bees (flower or anther buzzing) are favored by
293 poricidal anthers, limiting the access of competing pollinators (De Luca & Vallejo-Marín
294 2013). *M. seminigra pernigra* have body sizes exceeding the gap between anthers and
295 stigma in *P. carajasense*, and can be considered an efficient pollinator (Solís-Montero &

296 Vallejo-Marín 2017). Considering *Alchornea* spp., nectary stomata is commonly
297 observed on flowers, also in leaves, of *A. discolor* Poepp., *A. acutifolia* Müll. Arg., *A.*
298 *castaneifolia* (Willd.) A. Juss., *A. glandulosa* Poepp., *A. megalophylla* Müll. Arg., which
299 were extensively described for the study area (R. Secco personal communication; Secco,
300 2004).

301 Other abundant plant species visited by *M. seminigra pernigra* in the study area, but
302 with wider geographical distribution, are *A. cordatum*, *M. splendens* and *T. guianensis*.
303 These species are commonly observed in forest margins, gallery forest, seasonally dry
304 forest (SDF) and humid evergreen tropical forest (HETF), as well as disturbed areas in
305 the Amazon and elsewhere. *A. cordatum* has racemose inflorescences with female flowers
306 closer to the foliage and distal male flowers, while the two latter are paniculate. All these
307 inflorescences provide large number of flowers per inflorescence. All species are good
308 source of pollen and nectar for bees, as well as resin in the case of *T. guianensis* (Matos
309 & Santos 2017). *P. mediterranea* has also a wide distribution with preference for open
310 ecosystems such as Amazonian savannas, high altitude grasslands, *campo rupestre* on
311 *canga* and other substrates (Mattos et al. 2018). It has racemose inflorescence with few,
312 showy blue to purplish open, zygomorphic pea-shaped flowers with conspicuous nectar
313 guides. These flowers provide both pollen and nectar for bees (Mateus 1998).

314 Pollen type of *Miconia* is frequently abundant in honey samples of *Melipona* bees in
315 the Amazon region (Absy & Kerr 1977; Absy et al. 1980; Marques-Souza 1996; Oliveira
316 et al. 2009; Ferreira & Absy 2017). The continuous flowering along both dry and wet
317 seasons provides an excellent source of pollen for bees (Renner 1989). *Miconia* has
318 poricidal anthers, supporting selective buzz pollination (Buchmann 1983). However, the
319 identification of *Miconia* to species level using honey samples was not possible due to
320 the stenopalynous pollen found in the genus, and there are at least 20 species of *Miconia*

321 cited for the CRC of Carajás (Rocha et al. 2017). This large genus, one of the biggest in
322 the Brazilian Flora, comprises 288 species in Brazil, 81 of them recorded for Pará state
323 (BFG 2020), and its species present considerable variation in the gap between anthers and
324 stigma. Therefore, it is not possible to be sure whether *M. seminigra pernigra* effectively
325 makes contact with the stigmas.

326 Pollen types of *Solanum crinitum* were present in lower frequency in honey samples
327 than *Miconia* but were well-represented in the study site. It has also poricidal anthers, but
328 in this case the stamens are fused into a cone and the anthers are almost in contact
329 (Giacomin and Gomes, 2018). Thus, bees can vibrate all anthers at once, performing
330 effective pollination (Solís-Montero & Vallejo-Marín 2017). *Melipona* has been
331 commonly observed visiting Solanaceae species in lowland Amazonian forest (Absy &
332 Kerr 1977; Absy et al. 1980), and, according to these authors, its pollen is of great
333 importance for the diet and maintenance of the *Melipona* hives. Extrafloral nectaries are
334 reported for *Solanum* (Anderson and Symon, 1985). Predominant occurrence of *Solanum*
335 pollen types with different sizes in the same honey sample of *Melipona* are also reported
336 in the northeastern Brazil (Barth et al., 2013; Ferreira & Absy 2015, 2017). However, it
337 is possible that the flowering of *Solanum crinitum* Lam., which is abundant in the study
338 site (Giacomin and Gomes, 2018) and certainly very rich in pollen, may have
339 concomitantly occurred with any other nectar provider species. As the pollen extraction
340 from the anthers of *Solanum* is done by vibration (buzz pollination; Buchmann and Cane,
341 1989), the body hairs of *M. seminigra pernigra* may be full of pollen, which are moved
342 to the corbicula. In the hives, the pollen is deposited into pots, but it is tasted by other
343 workers of the colony (Roubik, 1989). Likewise, the nectar collected is transferred
344 between workers by trophallaxis before its deposition into the pots. Thus, the

345 contamination of nectar collected from other source with the *Solanum* pollen that is
346 present in the digestive system of the workers may be also a plausible explanation.

347 Also well represented in honey samples were pollen types of *Protium* and *Serjania*,
348 chiefly at the Trilha da Lagoa da Mata, Viveiro Florestal and N5 mine areas. *Protium* is
349 the commonest component in the pollen assemblage of sampled honey at the RDA area.
350 These taxa present paniculate inflorescences with small, separate sex flowers that provide
351 bees with nectar, resin and pollen (male flowers only), while *Serjania* spp. is a rampant
352 liana with thyrsoid inflorescences with small, sweetly scented flowers that are considered
353 an excellent source of nectar (Matos & Santos 2017). Both genera are commonly
354 observed in transitional areas between CRC and HETF and SDF and provide great
355 availability of resources over a long flowering period (Absy & Kerr 1977; Oliveira et al.
356 2009).

357 Following the statistical analysis, there was no significant difference in honey pollen
358 data between the natural and disturbed areas. This is mainly due to the fact that all these
359 abundant and common native taxa are used in revegetation during RDA processes by
360 mining activities (Zappi et al. 2018). However, more studies are necessary to better
361 evaluate the prolonged effects of human interference over plant reproduction.

362 Regarding the importance of plants for honey production, income generation, and
363 conservation of pollinators, *T. guianensis*, *Protium* spp., *M. splendens*, *M. acutistipula*
364 *var. ferrea*, *Serjania* spp., *P. carajasense* and *A. cordatum* seem to be key species, as well
365 as *Miconia* spp. with some considerations. Indeed, most of *Miconia* species are
366 polliniferous, but it cannot be generalized (T. Vasconcelos, personal communication).
367 Most neotropical Melastomataceae have bee-pollinated flowers with poricidal anthers.
368 However, nectar rewards are known to be produced in about 80 species in eight genera,
369 including *Miconia* (Varassin et al. 2008; Brito et al., 2017). These authors using

370 anatomical methods based on scanning electron microscopy, and serial sections of
371 paraffin-embedded flowers precisely identified nectary stomata on the ovary apex in
372 *Miconia* spp.

373 These plant species can be used to help recover deforested areas (Zappi et al. 2018)
374 and help improve the resource provisions for the stingless bee populations. For local
375 beekeepers, the incorporation of these plants in the foraging area of beehives can help to
376 improve the amount of honey produced, reflecting positively on income generation.

377

378 6. Conclusions

379 *M. seminigra pernigra* uses, preferably, native plants from *cangas* and forests of the Serra
380 do Carajás as its primary sources. Main examples are *Tapirira guianensis* Aubl., *Protium*
381 spp., *Aparisthium cordatum* (A.Juss.) Baill., *Mimosa acutistipula* var. *ferrea* Barneby,
382 *Periandra mediterrânea* (Vell.) Taub., *Miconia* spp., *Pleroma carajasense* K.Rocha,
383 *Myrcia splendens* (Sw.) DC., *Serjania* spp., and *Solanum crinitum* Lam. However, these
384 primary bee sources (PBS) represent only 20% of the total pollen assemblage, which
385 suggest high dispersion rates of the colony members related to temporal flowering pattern
386 of the PBS. All pollen types were identified during both seasons, but higher concentration
387 values are related to the dry period (June-September). In fact, Shannon-Weaver diversity
388 (H') and Pielou's evenness (J') indexes substantially decrease when PBS are fully
389 available.

390 The PBS have different floral syndromes. The strategies included condensed spike-
391 shaped inflorescences offering abundant nectar and pollen in *M. acutistipula* var. *ferrea*
392 and *A. cordatum*; buzz pollinated anthers in *P. carajensis*, *Miconia* spp. and *S. crinitum*;
393 and separate sex flowers (*A. cordatum* and *Protium* spp.). The majority of the species had
394 small flowers grouped in inflorescences working as a flowering unit, while only *P.*

395 *mediterranea* and *P. carajasense* have large, attractive flowers. Of these species, the only
396 strongly zygomorphic flower with nectar guides was *P. mediterranea*.

397 No significant difference was statically found in honey pollen data between the natural
398 and disturbed areas, which may be related to the widespread use of PBS for mine land
399 rehabilitation, as well as in the remaining vegetation surrounding the mine. However,
400 longer-term data are necessary for better supporting such findings in mining land areas of
401 the study site, including climate change influences.

402

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409

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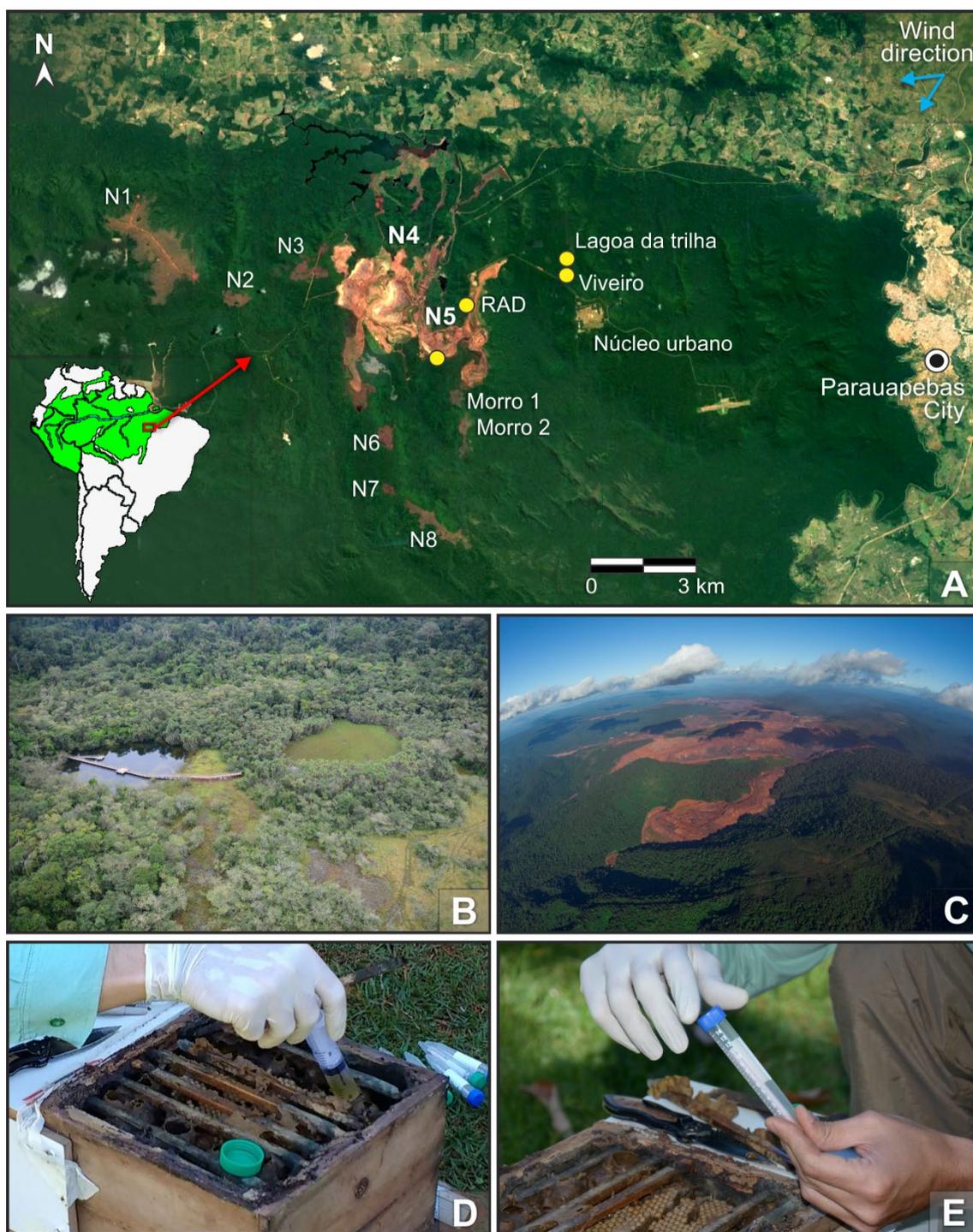
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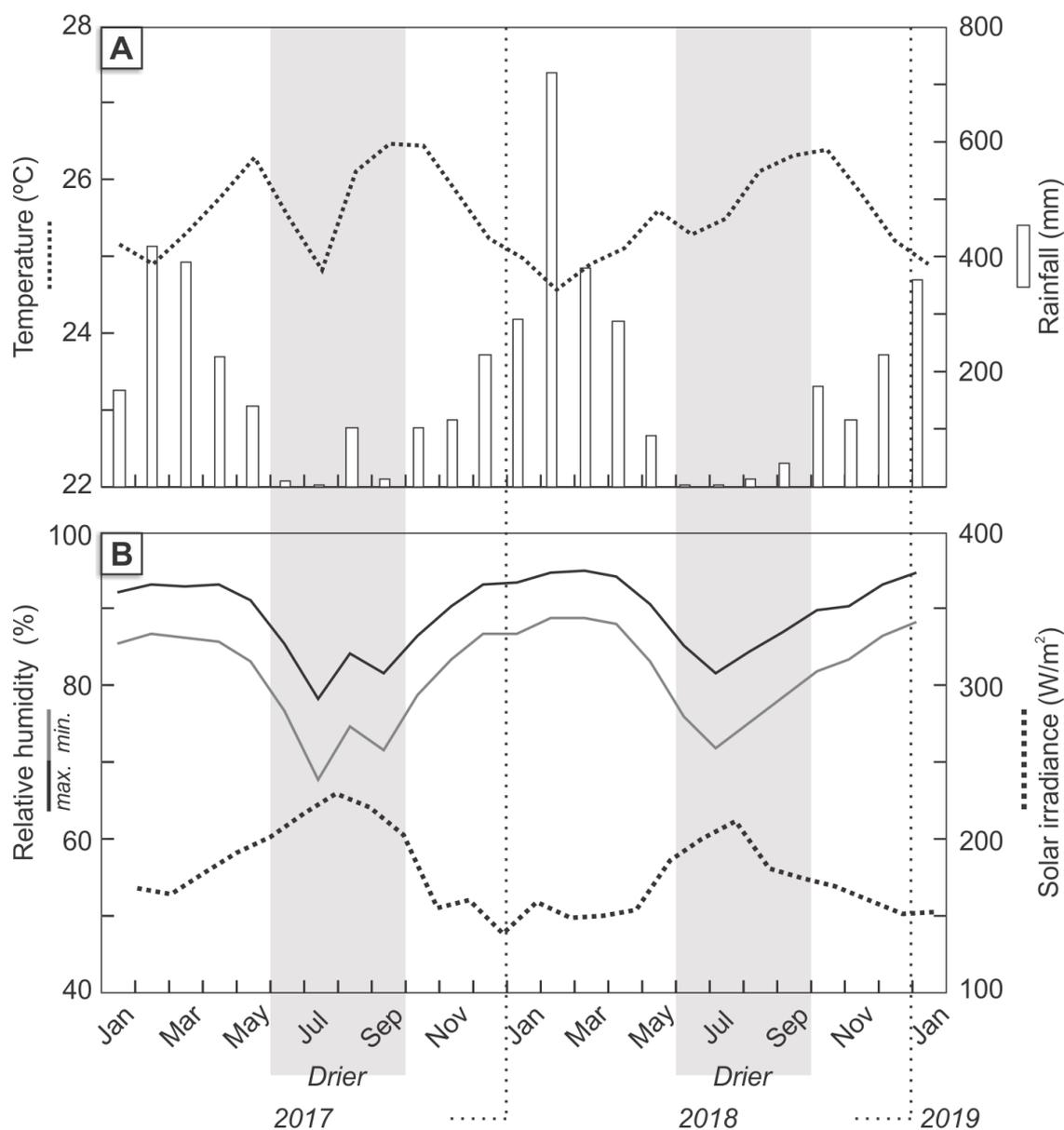
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639 **Figure 1.** (A) Study site inserted in the northern portion of the Carajás National Forest,
 640 southeast Amazonia (N1 to N8 are related mining areas codes). (B) Aerial photography
 641 of the Trilha da Lagoa da Mata (small area of canga vegetation surrounded by HETF and
 642 SDF). (C) Aerial photography showing the N4 and N5 mining areas surround by canga
 643 vegetation (open areas in the right side) and HETF and SDF. (D-E) sampling the honey
 644 pots.

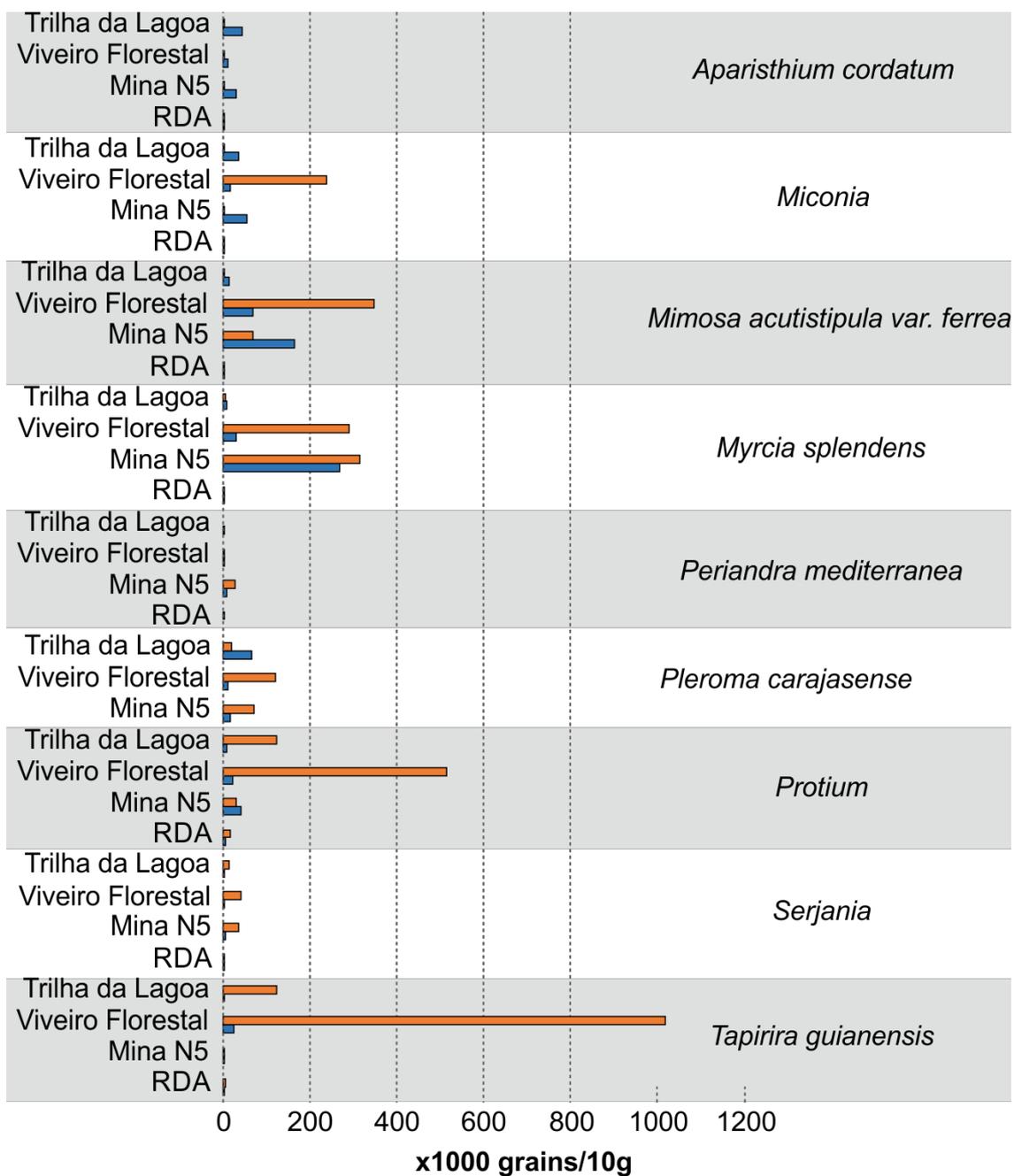


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646 **Figure 2.** (A) Accumulated monthly rainfall data (mm; right side) and mean air
 647 temperature (°C; left side) at the Carajás Meteorological Station from January 2017 to
 648 January 2019. (B) Monthly mean solar irradiance (W/m²; right side) and Maximum and
 649 minimum relative humidity (%; left side). Gray bands indicate the drier climate periods.

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■ Dry ■ Rainy

653 **Figure 3.** Total pollen concentration of the most abundant, frequent and common plant

654 species of all studied areas considering the different climate periods.

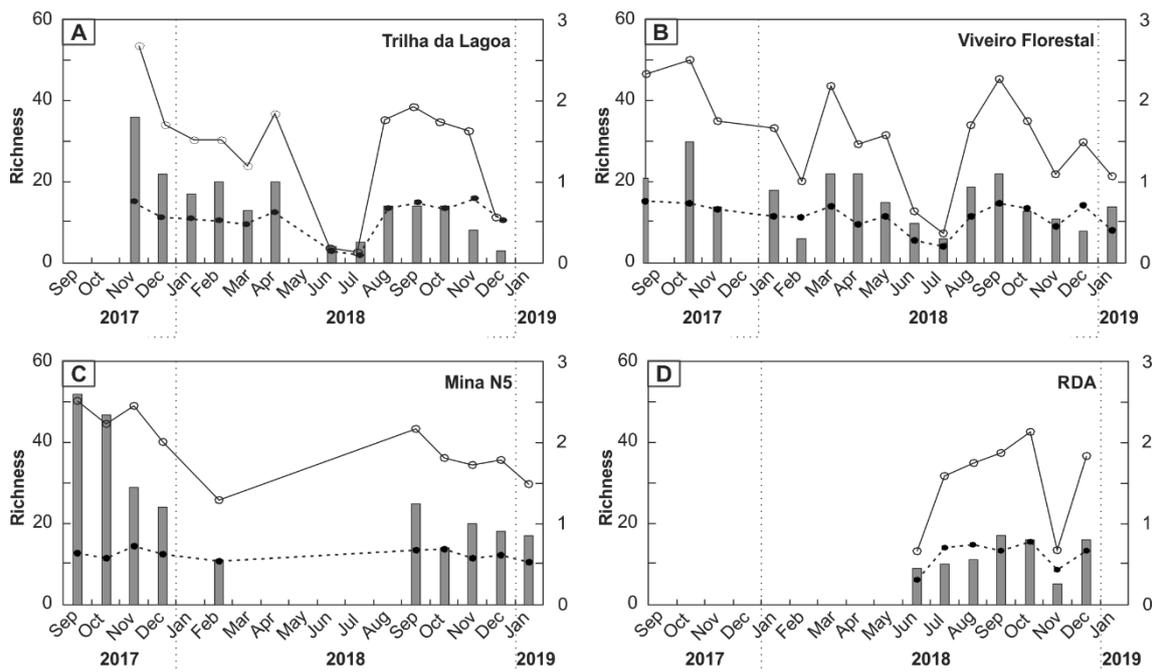
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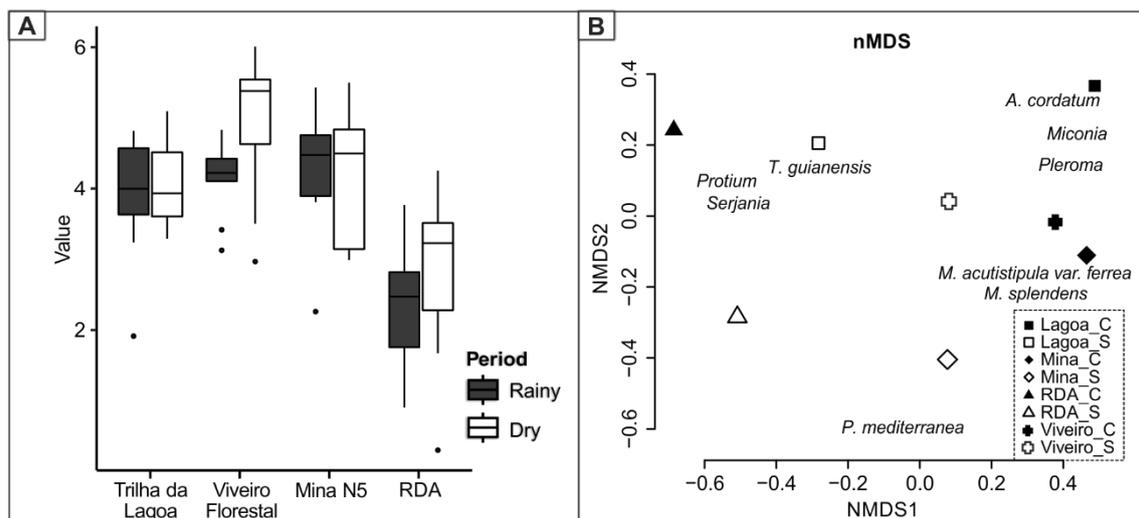


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661 **Figure 4.** Richness (gray bars), Shannon-Weaver diversity (H' ; green/upper straight line
 662 with empty circles) and Pielou's evenness (J' ; red/lower dashed line with black circles)
 663 of the pollen data per sampling area: (A) Lagoa da Trilha, (B) Viveiro Florestal, (C) Mina
 664 N5 and (D) RDA areas.

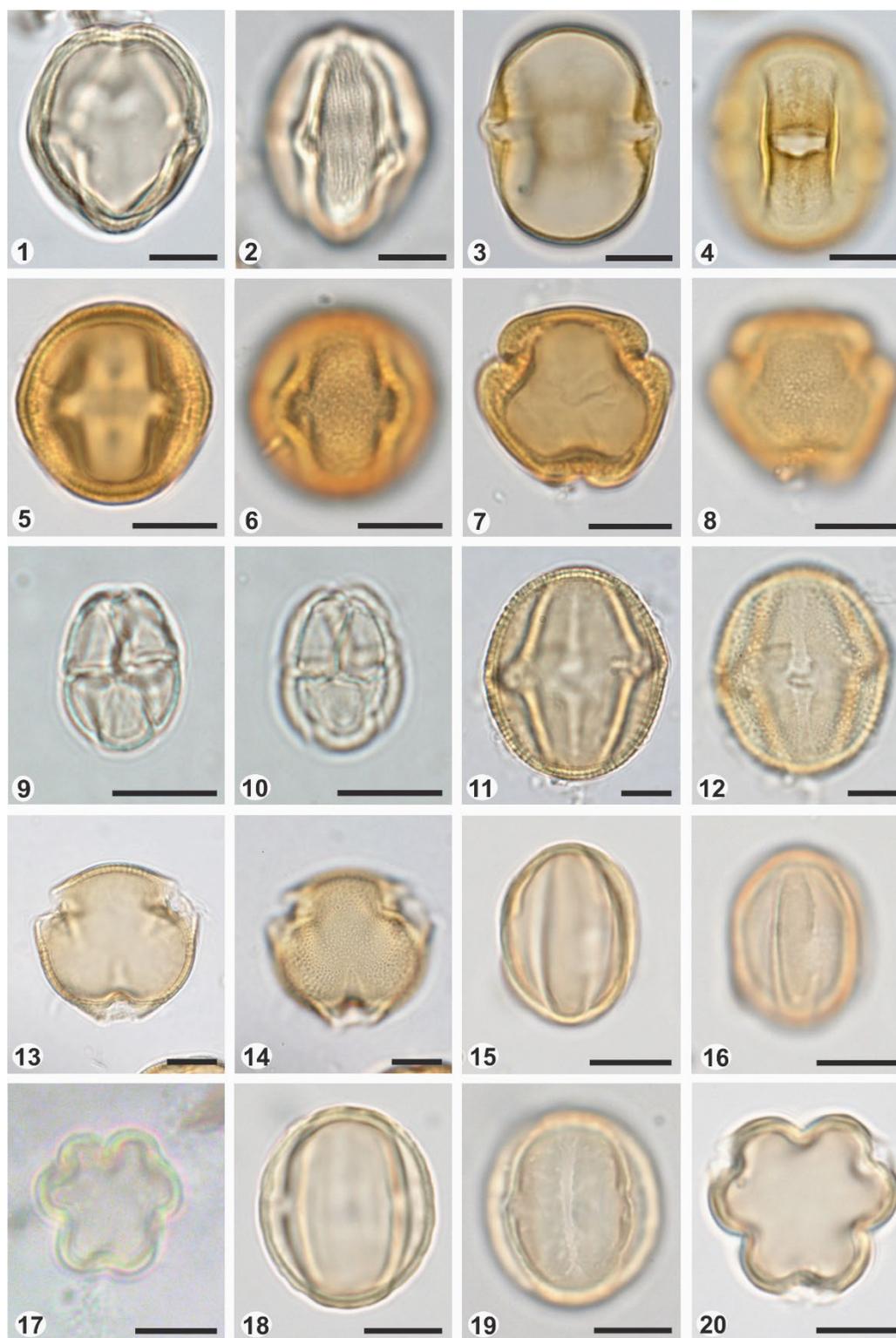
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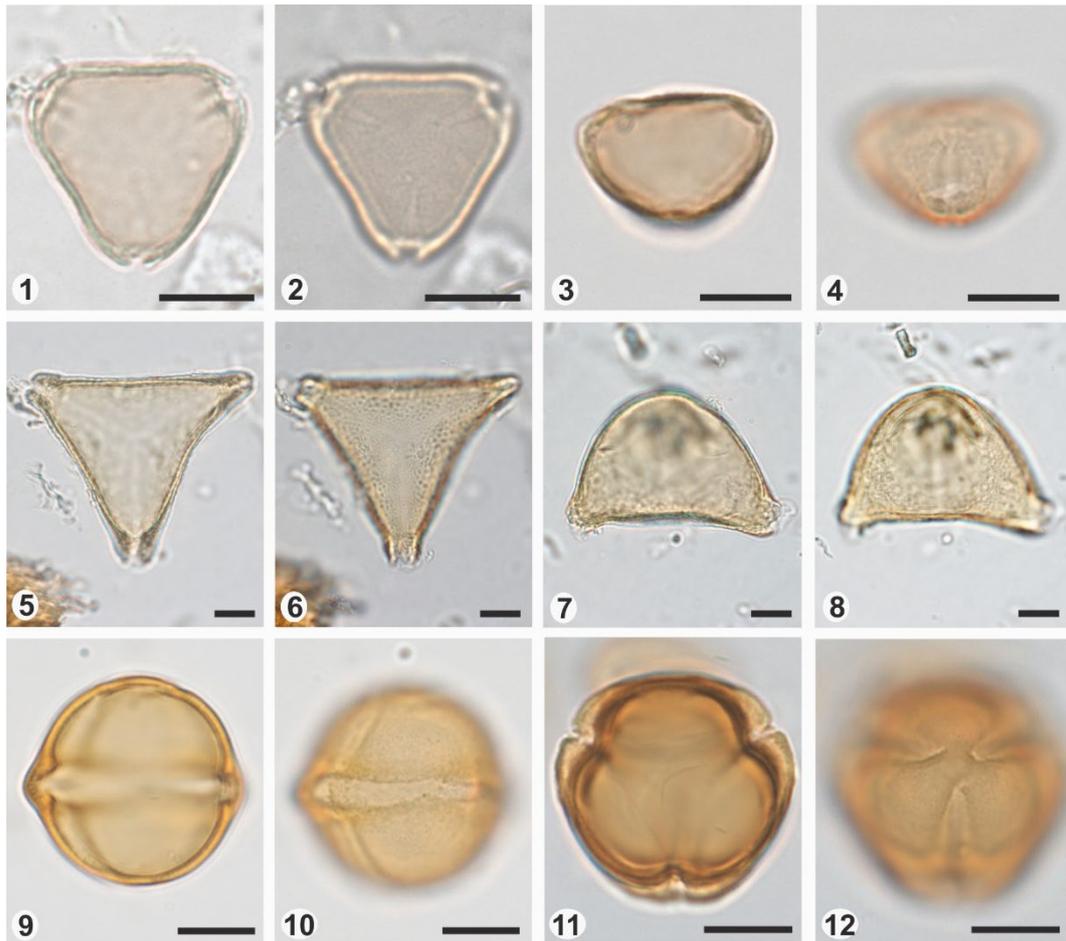
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668 **Figure 5.** (A) Boxplot of pairwise samples in rainy and dry period. (B) Result of Non-
 669 Metric Multidimensional Scaling using honey samples in two distinct periods (dark gray:
 670 rainy period; white: dry period). Named pollen taxa used in the analysis are included.



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672 **Plate 1.** Optical microscopy photomicrographs of the most abundant and frequent pollen
 673 types identified in this study. *Tapirira guianensis* (1, 2); *Protium* (3, 4), *Aparisthium*
 674 *cordatum* (5, 6) and *Alchornea* (7, 8), *Mimosa acutistipula* var. *ferrea* (9, 10) and
 675 *Periandra mediterranea* (11, 14), *Miconia* (17, 18) and *Pleroma carajasense* (19, 20).
 676 Scale bars: 10 μ m.



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678 **Plate 2.** Optical microscopy photomicrographs of the most abundant and frequent pollen
679 types identified in this study. *Myrcia splendens* (1, 4), *Serjania* (5, 6) and *Solanum*
680 *crinitum* (9, 12). Scale bars: 10 μ m.

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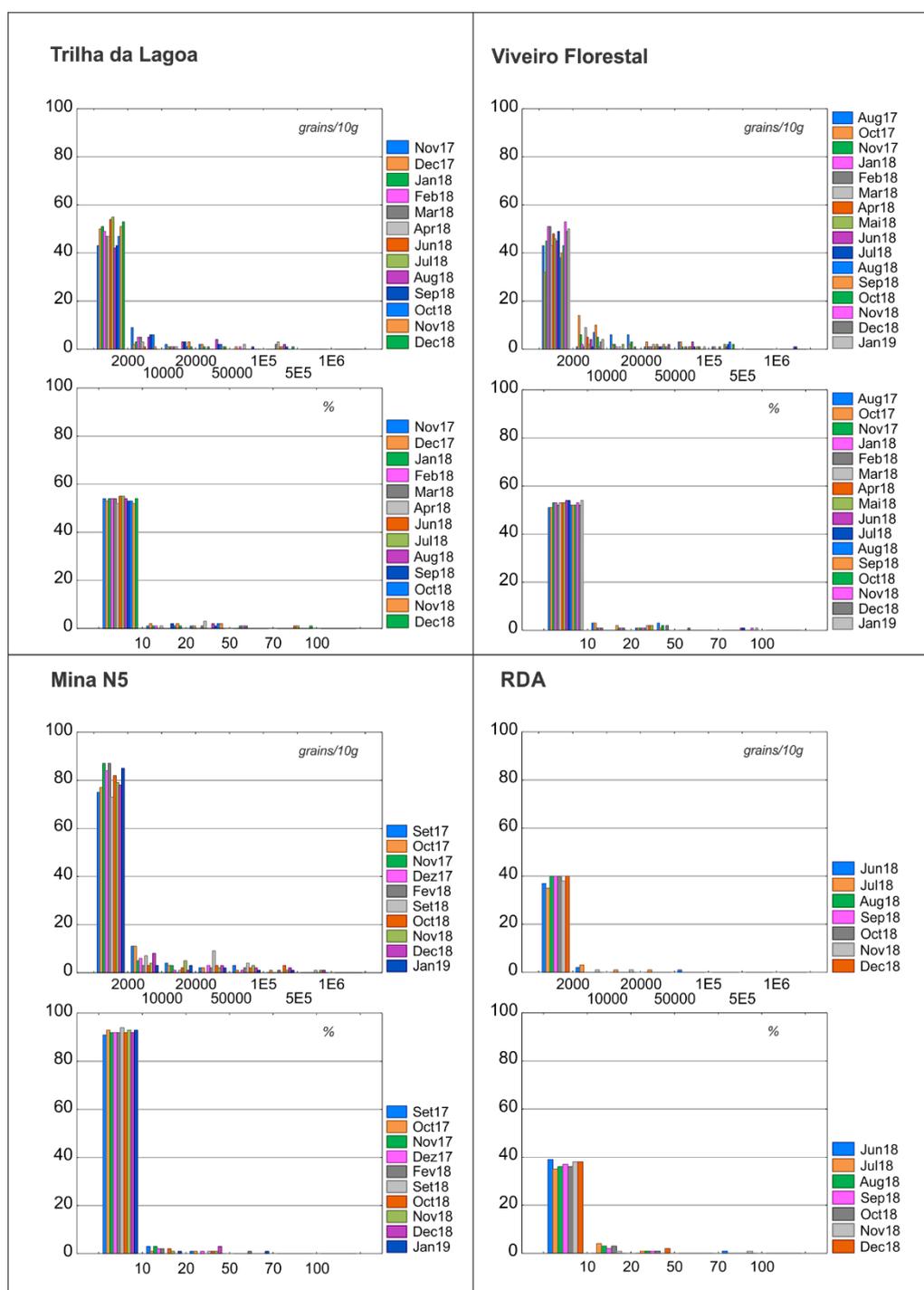
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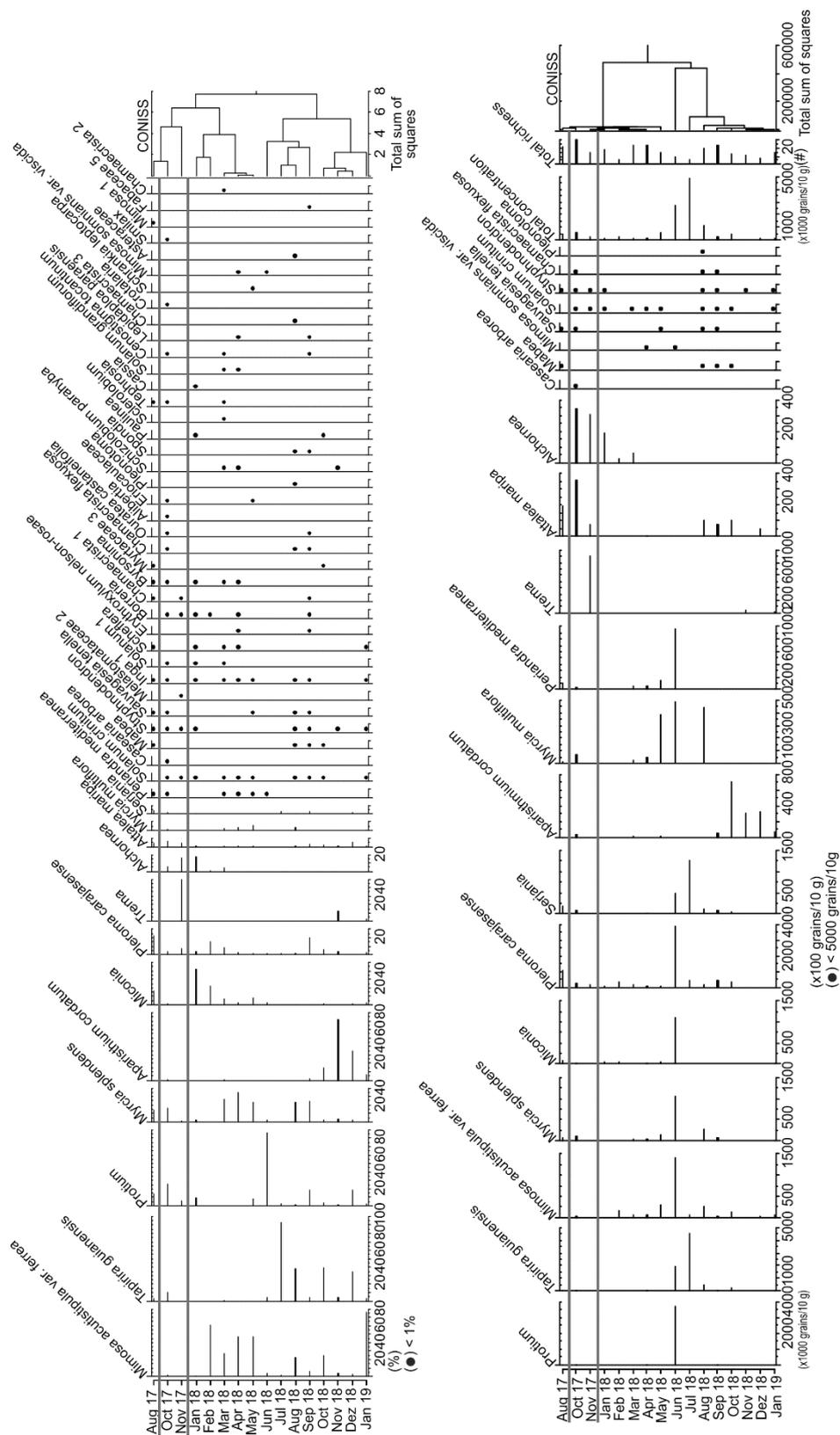
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690 Supplemental online material



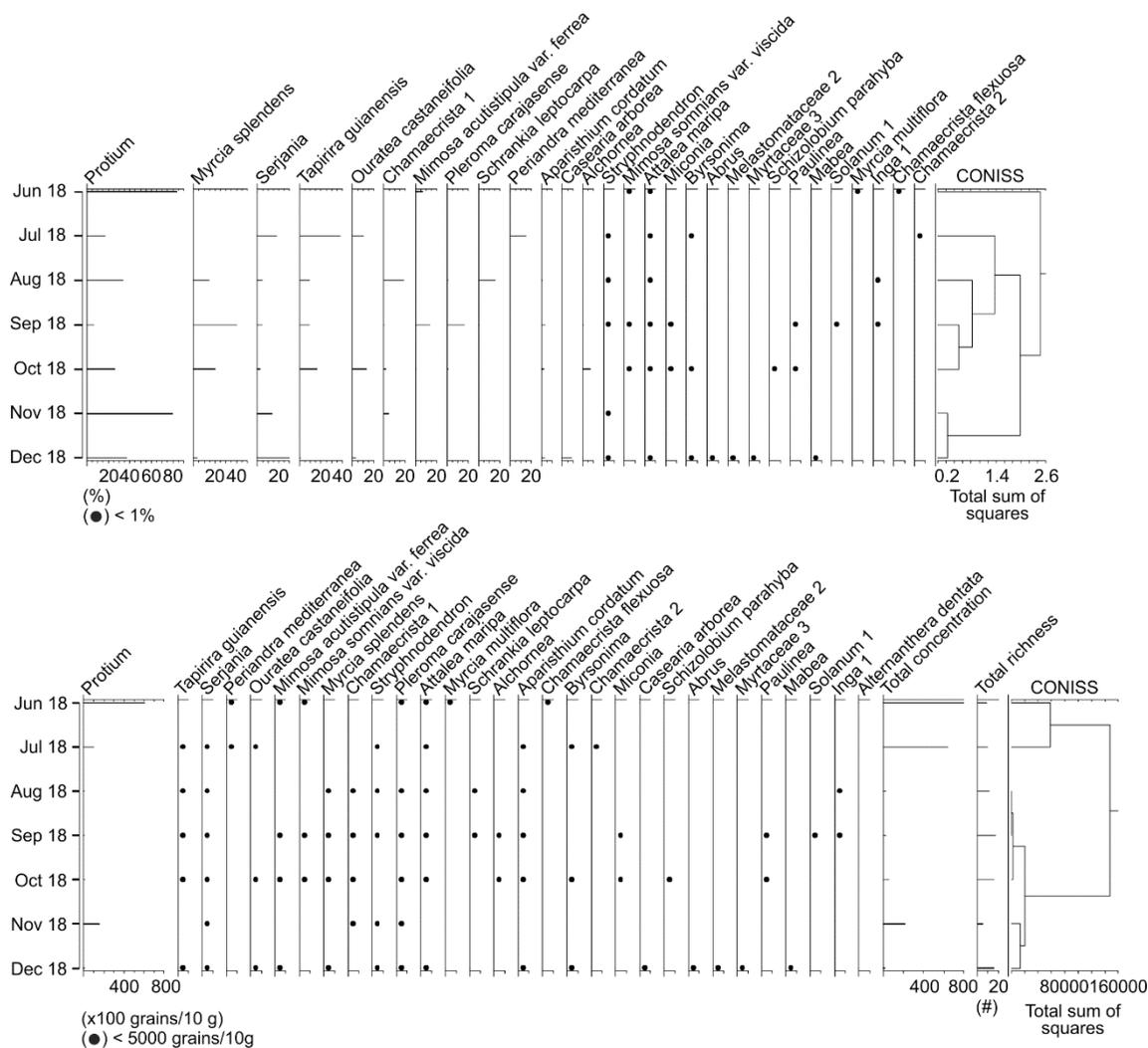
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692 **Supplementary Figure S1.** Number of observations per (1) groups of pollen
 693 concentration (grains/10g; Maurizio, 1975): Group I (<20,000), Group II (20,000–
 694 100,000), Group III (100,000–500,000), Group IV (500,000–1,000,000) and Group V
 695 (>1,000,000); and per (2) distribution frequency of the pollen types (percent-%; Feller-
 696 Demalsy et al., 1987): very frequent (>50), frequent (20–50), infrequent (10–20) and rare
 697 (<10).



Supplementary Figure S3. Percentage and concentration pollen diagram illustrating the pollen content of the honey samples from Viveiro Florestal area. Gray lines indicate gaps in the honey sampling.

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710 **Supplementary Figure S5.** Percentage and concentration pollen diagram illustrating the
 711 pollen content of the honey samples from RDA area.

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722 **Supplementary Table S1.** Main plant species observed in the natural and anthropized

723 areas where the studied apiaries were installed. Humid Evergreen Tropical Forest (HETF),

724 Seasonally Dry Forest (SDF). XLSfile 1

725

726 **Supplementary Table S2.** Occurrence per area and distribution frequency of the pollen

727 types (Feller-Demalsy et al., 1987): very frequent (>50%), frequent (freq.: 20–50%),

728 infrequent (infreq.: 10–20%) and rare (<10%); and groups of pollen concentration

729 (Maurizio, 1975): Group I (<20,000), Group II (20,000–100,000), Group III (100,000–

730 500,000), Group IV (500,000–1,000,000) and Group V (>1,000,000). XLSfile 2