

SILVER JONAS ALVES FARFAN

Agrônomo, Mestre em agronomia

**A MELIPONICULTURA COMO INDUTORA DE PROCESSOS DE RESILIÊNCIA
SOCIOECOLÓGICA EM AGROECOSSISTEMAS CAMPONESES NA BAIXADA
MARANHENSE**

Tese apresentada ao Curso de Doutorado do Programa de Pós-Graduação em Agroecologia da Universidade Estadual do Maranhão, para a obtenção do título de Doutor em Agroecologia.

Orientadora: Prof. Dra. Danielle Camargo
Celentano Augusto

Coorientador: Prof. Dr. Guillaume Rousseau

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Capítulo III

The effect of landscape composition on stingless bee (*Melipona fasciculata*) honey productivity in a wetland ecosystem of Eastern Amazon, Brazil

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A colmeia: nossa história com as abelhas

Bee Wilson, 2005

1 **The effect of landscape composition on stingless bee (*Melipona fasciculata*) honey**
2 **productivity in a wetland ecosystem of Eastern Amazon, Brazil**

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9 Silver Jonas Alves Farfan^{1,2*}, Danielle Celentano¹, Celso Henrique Leite Silva Junior^{1,3},
10 Marcus Vinicius de Freitas Silveira³, Raymony Tayllon Alves Serra¹, Jhonatan Andres
11 Munoz Gutierrez¹, Harryson Corrêa Barros⁴, Monique Hellen Martins Ribeiro⁵, Ortrud
12 Monika Barth Schatzmayr⁶, Rogério Marcos de Oliveira⁷, Luis Manuel Hernández García¹,
13 Guillaume Xavier Rousseau^{1,8}

14
15 ¹ Post-Graduate Program in Agroecology, Laboratory of Ecological Restoration
16 (LARECO), State University of Maranhão (UEMA). Cidade Universitária Paulo VI, Av.
17 Lourenço Vieira da Silva, nº 1000, Jd. São Cristovão. 65055-310, São Luís/MA, Brazil.

18
19 ² Technological Vocational Center (CVT Agroecology), Federal Institute of Sertão
20 Pernambucano (IFSertãoPE), PE-647, Km 22, PISNC N - 4, Zona Rural, Cx. Postal 277
21 CEP 56302-970, Petrolina/PE, Brazil.

22
23 ³ Post-Graduate Program in Remote Sensing, Tropical Ecosystem and Environmental
24 Science Laboratory (TREES), National Institute for Space Research / Instituto Nacional de
25 Pesquisas Espaciais (INPE). Av. dos Astronautas, 1758 - Jardim da Granja, 12227-010,
26 São José dos Campos/SP, Brazil.

27
28 ⁴ Laboratory for the Study of Bees (LEA), Federal University of Maranhão (UFMA). Av.
29 dos Portugueses, nº 1966 - Vila Bacanga, 65080-805, São Luís /MA, Brazil.

30
31 ⁵ State University of Maranhão (UEMA), Campus of Lago da Pedra, Lago da Pedra/MA,
32 Brazil.

33
34 ⁶ Laboratory for Viral Morphogenesis and Morphology of the Oswaldo Cruz Institute,
35 Fiocruz. Oswaldo Cruz Foundation, Instituto Oswaldo Cruz. Avenida Brasil, nº 4365,
36 Manguinhos, 21040-900 - Rio de Janeiro/ RJ, Brazil.

37
38 ⁷ Federal Institute for Education, Science and Technology of Bahia (IFBAIANO). Rua da
39 Gratidão, nº 232, Piatã. 41650-195-Salvador/BA, Brazil.

40
41 ⁸ Network for Biodiversity and Biotechnology of Legal Amazon (Bionorte). State
42 University of Maranhão. Cidade Universitária Paulo VI, Av. Lourenço Vieira da Silva, nº
43 1000, Jd. São Cristovão. 65055-310, São Luís/MA. Brazil.

44
45 * Correspondent author (silverjonasf@gmail.com)

46 **Abstract**

47 Humanity depends on the processes and resources of natural ecosystems, such as natural
48 grassland fields and forests. These ecosystems depend on pollinators, especially bees, to
49 ensure crossbreeding and plant productivity. Faced with deforestation and the fragmentation
50 of forest remnants, meliponiculture plays an important role in biodiversity conservation,
51 ecological restoration and generating income for family farmers. Little is known about the
52 effect of landscape on the productivity of native tiúba bees (*Melipona fasciculata*) in the
53 Baixada Maranhense Environmental Protection Area (APA) in the Brazilian Amazon. This
54 study aimed to evaluate the landscape effect on *M. fasciculata* honey productivity in APA.
55 We selected 34 stingless beekeepers, mapped and classified landscapes within a 2,000 m
56 radius around the meliponaries, measured honey productivity, and identified the pollen types
57 in each meliponary. We analyzed productivity as a function of mapping the landscape and
58 associated beekeeping. Our results have found that honeys from forest landscapes have
59 greater richness and abundance of species, indicating more pollination services in these
60 landscapes, but have lower productivity. The highest honey productivity occurs in
61 landscapes with a greater percentage of natural grassland field and a composition dominated
62 by shrubs. Melissopalynology and geographical information from landscape mapping
63 provide a precise ecological dimensioning of *M. fasciculata* honey productivity in the APA,
64 which can guide conservation, management and restoration actions in this region, and
65 enhance the recognition of environmental services provided by stingless beekeepers.

66 **Key words:** Meliponiculture, melissopalynology, mapping, forest, natural grassland field

67

68 1 INTRODUCTION

69 In the Brazilian state of Maranhão, 75 % of the Amazon Biome has already been
70 deforested to provide space for the expansion of large-scale agriculture and cattle ranching
71 (Celentano et al., 2017), which compromises the provision of essential ecosystem services
72 such as pollination due to reduced habitats and pollinators (Pioker-Hara et al., 2014).
73 Furthermore, among the Brazilian states, Maranhão is considered one of the poorest and
74 most vulnerable to climate change disasters (Almeida et al., 2016). Thus, the establishment
75 of state policies become crucial for forest conservation and restoration (Celentano et al.,
76 2017), as well as the promotion of low-impact economic activities that value
77 sociobiodiversity, such as the raising of native bees (Ribeiro et al., 2019).

78 Deforestation reduces the abundance and richness of pollinators, leading to reduced
79 gene flow and putting the entire plant community at risk, especially allogamous plants that
80 depend on pollinators to maintain heterozygosity (Sujii et al., 2021). This compromises the
81 maintenance of ecosystems, especially their ability to adapt to landscape and climate changes
82 (Waddell et al., 2020).

83 In Brazil, the native bees represent 40 % of pollinators (Kerr et al., 2001) while
84 environmental degradation alters their nesting, foraging and pollination behavior (Roubik,
85 2006). The bees are disappearing from natural landscapes due to the loss and fragmentation
86 of habitats, to the expansion of large-scale agriculture and to the indiscriminate use of
87 pesticides (Myerscough et al., 2017). This trend has drastic ecological, social and economic
88 impacts, given that the productivity of cultivated plants also depends on pollinators
89 (Brançalion et al., 2016).

90 In Maranhão the native stingless bee ‘tiuba’ (*Melipona fasciculata* Smith, 1854) is
91 traditionally the principal bee raised in an Environmental Protection Area (APA from
92 Portuguese *Área de Proteção Ambiental*) of the *Baixada Maranhense*, in the Amazon
93 Biome, and has economic importance in the generation of income by family farmers
94 (Venturieri et al., 2018). This bee prefers diversified sources of nectar and pollen from native
95 species available at the landscape level (Sponsler and Johnson, 2015). The greater variety of
96 flavors, colors and aromas found in the honey from the native bees is a function of the high
97 diversity of the plants they visit (Roubik, 2006), which gives that honey high medicinal and
98 culinary value (de Oliveira Alves, 2013).

99 These honeys contain higher content of water, sucrose and minerals than those of
100 *Apis mellifera* L., while the ash content and colors vary as a function of the botanical origin

101 (González-Miret et al., 2005). The floral origin of honey can be estimated using
102 melissopalynology, which reveals the richness of plants visited during the production period,
103 in addition to providing important information about plant diversity in the landscape
104 (Fernandes et al., 2020).

105 The raising of native bees (meliponiculture), conservation and restoration of
106 landscapes are synergistic processes (win-win); just as bees benefit from the amount and
107 diversity of pollen in the landscape, the landscape benefits from the pollination process
108 (Härtel and Steffan-Dewenter, 2014). However, the mechanism behind this interaction and
109 the effect of the landscape on honey productivity have remained poorly elucidated (Sponsler
110 and Johnson, 2015). Understanding the role of meliponiculture in maintaining this process,
111 and knowing these relationships are fundamental for encouraging policies and incentives for
112 sustainable productive activities.

113 The diversified context of the APA – with landscapes formed by agroecosystems of
114 small properties, forest remnants, areas in natural regeneration, floodplains and natural
115 grassland fields – configures a natural laboratory for studying the relationship between
116 landscape and honey productivity. We tested the hypothesis that *M. fasciculata* honey
117 productivity responds positively to old growth forest cover. In this context, our objective
118 was to identify how honey production varies as a function of different landscape
119 configurations. For this: 1) we measured the productivity of *M. fasciculata* honey; 2) we
120 mapped land use and land cover (LULC) in landscapes of meliponaries; 3) we identified the
121 pollen types in the honey samples; and 4) we modeled productivity as a function of
122 landscapes and floral origin.

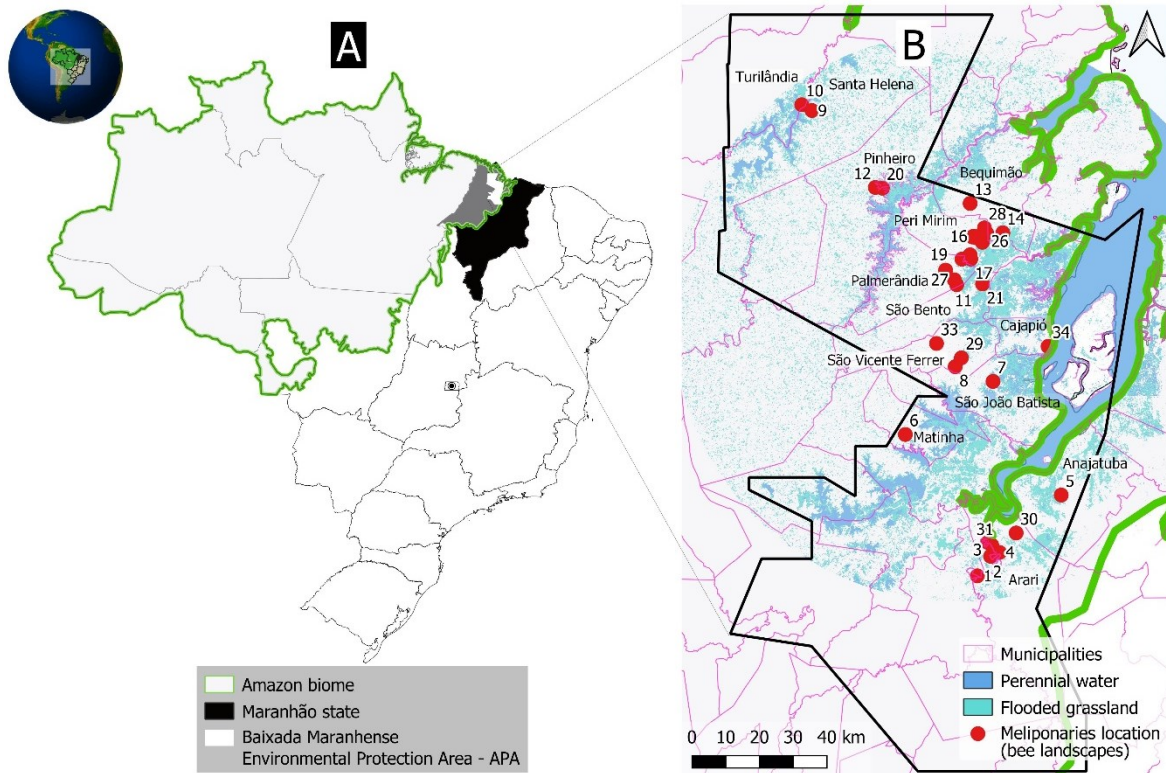
123

124 **2 METHODOLOGY**

125 **2.1 Study area**

126 The study was carried out between the years 2017 and 2021 in 13 municipalities of
127 an Environmental Protection Area (APA) in the state of Maranhão, Brazil: Anajatuba, Arari,
128 Matinha, Cajapió, São João Batista, São Vicente Ferrer, São Bento, Palmerândia, Peri
129 Mirim, Bequimão, Pinheiro, Santa Helena and Turilândia (Figure 1A). This APA is a
130 sustainable use conservation unit created in 1991 and designated as Sítio Ramsar in 2000
131 (site number: 1,020), which contains 17,750 km² (Figure 1B). The estimated population is
132 387 thousand inhabitants; the economy is based on the extraction of babassu (*Attalea*
133 *speciosa*), artisanal fishing and family farming (Ramsar, 2000). The study area is located in

134 the Amazon Biome with palm vegetation, the location of the largest lacustrine complex in
 135 the Northeast, floodplains and a part of the mangrove belt. According to the Koppen climate
 136 classification, the climate is tropical including Am, Aw and As, with an average temperature
 137 of 25 °C and annual rainfall between 1,600 and 2,000 mm, concentrated mainly between
 138 January and June (Alvares et al., 2013). The soils come from alluvial fluvial-marine
 139 geological formations with low natural fertility, fragile structure and limited drainage
 140 (Martin et al., 1980).



141 Figure 1. (a) Location of the study area in the Baixada Maranhense Environmental Protected Area
 142 (APA), Maranhão state, eastern Amazon, Brazil, and (b) the 34 sampling units (bee landscapes)
 143 enumerated (id) in the APA.

144

145 2.2 Experimental design

146 Thirty-four *M. fasciculata* beekeepers were selected to participate in this research
 147 through the 'snowball' sampling methodology (Albuquerque et al., 2014) where visits to the
 148 beekeepers residences were initiated by a key informant who indicated other beekeepers, a
 149 process that was reiterated until the sampling size was achieved. From the group of 47
 150 beekeepers visited, we excluded those with less than 12 boxes of bees or with productivity
 151 lower than 260 mL \cdot year⁻¹. We included beekeepers who used standardized or rustic-type
 152 boxes (without standard measures), beekeepers in urban, peri-urban and rural locations, and
 153 excluded those who raised bees in hollow tree trunks.

154 The research was authorized by the environmental agency of the state of Maranhão
155 (Sema A08/2019) and by the appropriate federal agency (Sisbio 68238/2019). All selected
156 beekeepers agreed to participate in the research and signed an informed consent form, which
157 was registered with the research ethics committee (CAAE: 84113418.3.0000.5554/2018) as
158 required by law. We carried out semi-structured interviews, which lasted about 30 minutes
159 each, to ascertain the social profile of beekeepers and the details of beehive management:
160 gender, age, number of years in beekeeping, name and number of beekeepers in the network
161 of contacts and number of boxes.

162

163 **2.3 Honey productivity**

164 To measure honey productivity ($ml.bx^{-1}$) three bee boxes from each meliponary were
165 randomly selected and reserved among those in the production phase – as it was previously
166 arranged with each beekeeper. We collected the samples in November 2019, respecting the
167 usual harvest schedule, containing the entire annual accumulation of pollen (December 2018
168 – November 2019) to account for a broad measure of the set of resource-providing
169 melittophilous plants. The sampling methodology allowed to control the temporal and spatial
170 variation in the species flowering, whose concentration occurs in the dry season between
171 July and December (de Oliveira Alves, 2013). For the harvest, a portable electric vacuum
172 suction pump (Aspiramax MA520-60) was employed, according to a hygiene protocol and
173 utilizing sterilized containers to avoid contamination between samples and the environment.
174 The total honey content of each box harvested was collected and measured, and the
175 meliponary yield was estimated as the mean production of the three boxes. We measured the
176 internal volume of the three harvested boxes and averaged the volume of the boxes. We
177 standardized the productivity value to minimize the effect of the variation in the volume of
178 boxes between meliponaries as follows: the average value of productivity (\bar{p}) of each
179 meliponary (ml) was divided by the average internal volume of the boxes from each
180 meliponary ($volbx$) and multiplied by the average volume of the total number of boxes in the
181 study ($16.84cm^3$), as described in the following calculation: $\bar{p} = ml/volbx \times 16.84$.

182

183 **2.4 Mapping the bee landscape**

184 We considered the landscape of the bee (sampling unit) as the circular area around
185 each of the 34 meliponaries within a radius of 2,000 m (an area equivalent to 1,256 hectares).
186 The radius was determined based on the flight of the bee *M. fasciculata* (Nunes-Silva et al.,

187 2020; Borges et al., 2020), controlling the spatial variation of plant flowering in the different
188 landscapes. We collected data from 2018 on land use and land cover (LULC) data from the
189 mapping carried out by the MapBiomass project (Souza et al., 2020). MapBiomass performs
190 the annual classification of the LULC of Brazilian biomes based on satellite images from the
191 Landsat satellite, with a spatial resolution of 30 m. We defined 12 classes in the studied
192 landscapes: mature forest, secondary vegetation subdivided into three classes (1-15 years,
193 16-25 years, 26-33 years) (Silva Junior et al., 2020), water, mangrove, urban area, pasture,
194 agriculture, natural grassland field, floodplain and mosaic. The classification 'mosaic'
195 includes shifting cultivation, sandy formations, small pastures and villages (Capanema et al.,
196 2019). From the LULC classification of each bee landscape, we calculated two metrics for
197 each class: area percentage ($\% = \text{class area} / \text{total area} \times 100$) and patch density ($\text{pd} = \text{number}$
198 $\text{of patches} / \text{area}$). These metrics were calculated using the landscape metrics package in the
199 software R. (Hesselbarth et al., 2019; R Core Team, 2020).

200 Complementarily, we calculated five landscape entropy measures (joint, marginal,
201 conditional, mutual, relative mutual information) (Nowosad and Stepinski, 2019) and
202 systematized climate variables with CHIRPS data (annual rainfall, annual rainy days, mean
203 rainfall per day) (Katsanos et al., 2016) and geographic metrics (long, long², long³, lat,
204 lat×long, lat×long², lat², long×lat², lat³) (Borcard et al., 2011).

205

206 **2.5 Floral origin with Melissopalynology**

207 For the melissopalynological analysis of each of the 34 meliponaries, we took a
208 subsample of 15 mL of honey harvested and homogenized from each box separately (see
209 item 2.3); this subsample was kept cooled until the moment of preparation of the slides by
210 acetolysis (Melhem et al., 2003). One slide was prepared from each box of bees studied, 3
211 boxes × 34 meliponaries = 102 slides (102 samples).

212 The slides were subjected to qualitative and quantitative analysis through microscopy
213 to determine the richness of species and the relative frequency of abundance among all
214 meliponaries with a minimal count of 500 pollen grains per sample. Although this count with
215 a predefined minimum value has as its main objective to determine the participation of
216 botanical species in the floral origin, it was adopted herein to estimate the abundance of
217 pollen in the samples.

218 The taxonomic identification of the species was determined according to the
219 specialized literature (Carreira et al., 1996; Carreira and Barth, 2003; Albuquerque et al.,

220 2013), and the classification system adopted for the botanical family level was APG IV
221 (Chase et al., 2016). The same samples were prepared in parallel without acetolysis to
222 analyze contaminants visible under a microscope (Barth, 2004).

223 We classified each pollen type identified by life form (tree, palm, shrub, herb, vine,
224 aquatic herb), floral resource (nectar, pollen, unidentified), origin (native to Brazil or exotic),
225 and preferential habitat (wetland, grassland, forest, savannah, anthropogenic) (“RCPol –
226 Rede de Catálogos Polínicos Online,” 2020). The origin of honey from each meliponary was
227 classified as: monofloral (when there is a dominant pollen type with presence of more than
228 45%) or heterofloral (when there is a set of types with more than 9% presence and the
229 absence of a dominant type), taking into account only the nectariferous species (Ribeiro et
230 al., 2019). The set of pollen types with low frequency (less than 9%) was considered in
231 calculations of richness, relative abundance and modeling.

232

233 **2.6 Data analysis**

234 **2.6.1 Preparation of matrices**

235 To evaluate the effect of landscape and floral origin on honey productivity, we set up
236 six data matrices. A: LULC, subdivided into A1: percentage of coverage of classes (%), A2:
237 density of patches by class (pd), B: profile and management of the beekeepers, C: richness
238 and abundance of pollen types by meliponary, D: counts of botanical species, E: life form of
239 species identified by meliponary (richness and abundance), F: entropy, climate and
240 geographic metrics.

241 The honey productivity values had an asymmetric distribution and were transformed
242 with the natural logarithmic function before the linear regression calculation to obtain
243 normalization of the residuals and homogeneity of the variance of the models used.

244 All mapping data (LULC) were tested for normality and heteroscedasticity with the
245 Shapiro-Wilk and Breusch-Pagan tests. The mapping variables did not have multinormality
246 (Mardia’s test $p < 0.05$) and 35.7% of the variables have more than 50% of zeros; thus, no
247 transformations were performed, only the standardization of each variable in z values (each
248 original value was subtracted from the mean and divided by the standard deviation of the
249 respective variable) (Borcard et al., 2011). We evaluated the variance and the number of
250 zeros, and eliminated the very rare variables and those with a variance close to zero
251 (Marchant, 2002): mangrove(%), agriculture(%), mangrove(pd), mature forest(pd),
252 urban(pd), agriculture(pd), mosaic(pd), floodplain(pd) and; multicollinearity: secondary

253 vegetation 26-33 years(%). Thus, 15 landscape variables remained, nine of which were
254 measures of area percentage (A1: secondary vegetation 1-15 years, secondary vegetation 16-
255 25 years, mature forest, permanent water, urban area, pasture, mosaic, natural grassland
256 field, floodplain) and six measures of patch density (A2: secondary vegetation 1-15 years,
257 secondary vegetation 16-25 years, mature forest, permanent water, pasture, natural grassland
258 field).

259

260 **2.6.2 Modeling the effects of landscapes on productivity**

261 To model the landscape effect (LULC) on honey productivity, we applied a
262 redundancy analysis (RDA) using matrices A1 and A2 as explanatory variables for honey
263 productivity and profile and management variables (matrix B) as covariates to remove their
264 effects (Borcard et al., 2011; Jaffé et al., 2015). RDA is a multivariate analysis method that
265 consists of performing a multiple linear regression between the explanatory variables of an
266 X matrix with each response variable of a Y matrix and then performing a Principal
267 Component Analysis (PCA) on the adjusted values of the Y matrix (Borcard et al., 2011).
268 The analysis was performed by the package Vegan v.2.5-7 (Oksanen et al., 2020). We made
269 a direct selection of variables using the Ordistep function from the Vegan package with each
270 of the matrices A1 and A2 separately as explanatory variables and grouped to obtain the best
271 final model (Borcard et al., 2011). To control the collinearity between the variables in the
272 final model, we ensured that all selected variables had a variance inflation factor (VIF) below
273 10 and, at the end, we partitioned the variation of A1 and A2 (Borcard et al., 2011).

274 Furthermore, we performed a multiple linear regression with the same variables as
275 the final RDA model to evaluate the linear coefficients of each variable and to verify whether
276 the linear regression assumptions (normality of the distribution and constant variance of the
277 residuals) had been achieved, with the packages Stats v.4.0.5 and lmttest v.0.9-38. The
278 transformations and modeling were performed with functions from the package Vegan and
279 Stats (Oksanen et al., 2020). The same script was performed with the F matrix, but the
280 models were not significant ($p > 0.05$) and the results will not be presented.

281 We organized the set of landscapes according to the honey productivity gradient,
282 indicating the high and low honey productivity meliponaries according to the categories: low
283 (up to the first quartile), medium (between the first and third quartiles) and high (above the
284 third quartile) to obtain a visual description of the effects of landscape variables.

285

286 **2.6.3 Modeling the effects of floral origin on productivity**

287 We analyzed honey productivity as a function of pollen analysis variables. The
288 relationship between productivity and, richness and abundance (matrix C) was determined
289 through independent linear regressions. For the counts of identified botanical species (matrix
290 D), we applied the Hellinger transformation that is recommended for abundance data
291 (Borcard et al., 2011) and the relationship with productivity followed the same steps
292 described for the mapping analysis to obtain a final independent model, whereas a second
293 model was obtained by repeating the analysis after omitting some species selected in the first
294 because they were very rare (Marchant, 2002). The relationship between productivity and
295 life forms (matrix E) followed the same steps as the multivariate analysis; and with the
296 selected variables, we calculated independent linear regressions, since there was no
297 significant multiple model ($p > 0.05$).

298

299 **3 RESULTS**

300 **3.1 Profile of beekeepers and honey productivity**

301 In the Baixada Maranhense APA, the meliponaries were established mainly in the
302 rural area (76.5%) and to a lesser extent in the urban area (23.5%). The backyard of the
303 houses was the preferred place in 88% of the cases. Those responsible for this activity were
304 mostly men (75%) with an average age of 56 years (± 13.24), working in this activity for
305 18.3 years (± 14). The size of their contact network varied from 1 to 40 people (18.3 ± 11.1),
306 and allowed us to estimate the existence of 150 *Melipona* beekeepers in the APA, which
307 means that the 34 sampled represent 23% of the universe. Respondents had between 12 and
308 320 tiuba bee boxes (79 ± 73), boxes whose internal volume varied from 10 to 25cm³ (16.8
309 ± 3.6). Meliponiculture was not the main activity of the interviewees, but rather was part of
310 the family's set of activities. The honey productivity in meliponaries ranged from 260.0 to
311 4,794.8mL.bx⁻¹ (1.302 ± 928.7); the low productivity category ranged from 260.0 to
312 513.8mL.bx⁻¹ and high from 1,788.4 to 4,794.8mL.bx⁻¹.

313

314 **3.2 Bee landscape**

315 The following classes occurred in all 34 landscapes: secondary vegetation 26 to 33
316 years old which is the most representative class with a cover gradient ranging from 2.4 to
317 72% (34.8 ± 19.6); secondary vegetation varying from 16 to 25 years, ranging from 3.6 to
318 32.2% (15.5 ± 6.2); secondary vegetation between 1 to 15 years ranging from 0.4 to 9% (2.3

319 ± 2.1); floodplain ranging from 1.3 to 52.4% (14.6 ± 14.0) and permanent water from 0.1 to
320 31.6% (8.1 ± 8.3). Other important classes were: pasture that occurred in 29 landscapes
321 ranging from 0 to 50% (10.8 ± 11.9); natural grassland field occurring in 27 landscapes and
322 ranging from 0 to 41.7% (7.2 ± 11.5); mosaic found in 29 landscapes ranging from 0 to 9%
323 (2.0 ± 2.6) and mature forest occurring in 10 landscapes and varying from 0 to 10% ($0.5 \pm$
324 1.8).

325

326 **3.3 Landscape effects on honey productivity**

327 When the LULC variables were modeled separately (matrices A1 and A2), the
328 percentage of classes ($R^2 = 0.36$, $p = 0.036$) and the patch density ($R^2 = 0.08$, $p = 0.050$)
329 resulted in lower explanatory values than when considering the 15 variables together ($R^2 =$
330 0.63 , $p = 0.001$) (Table 1). The profile and management covariates were significant, after
331 discounting their effects; the landscape explained almost half of the variance of honey
332 production in the final additive model ($R^2 = 0.44$, $p = 0.001$); six variables were selected:
333 three with a positive effect (% natural grassland field, % permanent water and natural
334 grassland field patch density) and three with a negative effect (% mosaic; % mature forest
335 and pasture patch density). The construction of the multiple linear model with the same
336 variables selected in the RDA revealed a significant model ($p < 0.0001$) that fulfills the
337 assumptions of the regression. When partitioned, the variances of the final additive model,
338 matrix A1 and matrix A2, have respective explanatory powers of 0.561 ($p < 0.0001$) and
339 0.245 ($p < 0.0001$) with no interaction effect between them. In general, the RDA and multiple
340 linear regression coefficients are coherent (Table 2).

341 The landscape variables selected in the modeling and their effect on productivity can
342 be visualized when organized according to the productivity gradient, using the categories of
343 meliponaries with low and high honey productivity (Figure 2). In line with the modeling,
344 there is a greater predominance of native field coverage and density of native field patches
345 in the landscapes among meliponaries with high productivity (at the top of the figure), as
346 well as the permanent water class. The higher frequency of landscapes with low productivity
347 meliponaries (at the bottom of the figure) contain higher forest cover and greater presence
348 of mosaic and pasture patches.

349 Table 1. Redundancy analysis (RDA) sequence to test landscape effects (Land use and Land Cover) on *Melipona fasciculata* honey productivity (Y) in the
 350 Baixada Maranhense Environmental Protected Area (APA), Maranhão state, eastern Amazon, Brazil, in 2019.

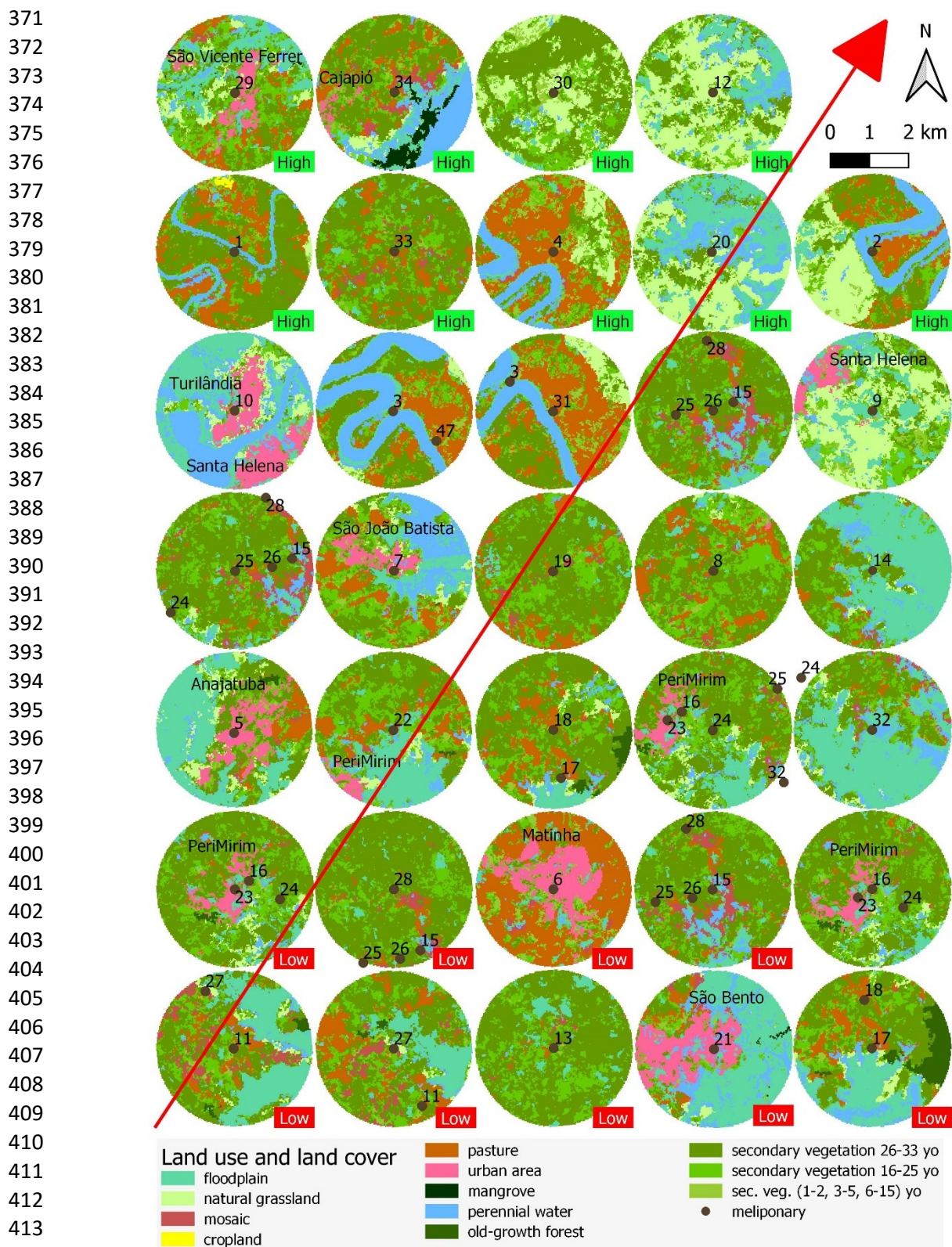
Step	LULC	Model [‡]	p	R ² adj.
Original independent models	A1 (%)	Y ~ sf15+sf25+old forest+water+urban+pasture+mosaic+natural grassland+floodplain	0.002	0.36
	A2 (pd)	Y ~ sf15pd+sf25pd+sf33pd+waterpd+pasture pd+ natural grassland pd	0.050	0.08
	A1 (%) + A2 (pd)	Y ~ sf15+sf25+old forest+water+urban+pasture+mosaic+ natural grassland + floodplain + Sf15pd+ sf25pd+sf33pd+waterpd+pasturepd+ natural grassland pd	0.001	0.63
Covariable - management		Y ~ age+b-time+network+n-box+vol	0.047	0.17
Additive model	All	Y ~ A1 (%) + A2 (pd) – management (network+n-box)		
Final additive model		Y ~ native grassland(%) + water(%) + native grassland(pd) + mosaic(%) + old forest(%) + pasture(pd)	0.001	0.44

351 [‡]sf15 is secondary forest 1-15 year(%); sf25 is secondary forest 16-25 year(%); sf33 is secondary forest 26-33 year(%); old forest is old-growth forest(%); water
 352 is perennial water(%); urban is urban area; pasture is pasture; mosaic is shifting agriculture; sandy formations; small pastures and villages; natural grassland is
 353 natural grassland fields; floodplain is flooded grassland; pd is density patches; age is age of beekeeper; b-time is time that raises bees; network is size of the
 354 network; n-box is number of beehives; vol is average volume of boxes; R² adj. is r square adjusted; p is significance level.

356 Table 2. Analysis of variance of the final additive model to test on *Melipona fasciculata* honey productivity, in the Baixada Maranhense Environmental Protected
 357 Area (APA), Maranhão state, eastern Amazon, Brazil, in 2019.

explanatory variable: landscape / covariable: management [‡]	Df	F	p	score rda	coef lm
natural grassland (%)	1	29.12	0.001	0.690	0.494
perennial water (%)	1	9.033	0.005	0.380	0.230
native grassland (pd)	1	5.460	0.027	0.358	0.233
mosaic (%)	1	4.172	0.050	-0.388	-0.195
old-growth forest (%)	1	7.460	0.010	-0.355	-0.240
pasture (pd)	1	8.532	0.006	-0.244	0.556
residual	27				
network	1	4.499	0.042	0.724	0.245
n-box	1	4.575	0.046	-0.710	-0.239
residual	31				

369 [‡]network is size of the network, n-box is number of beehives. pd is density of patches, df is degrees of freedom, F is Fischer test, score rda is biplot scores for
 370 constraining variables, coef lm is multiple linear regression coefficients; p is significance level.



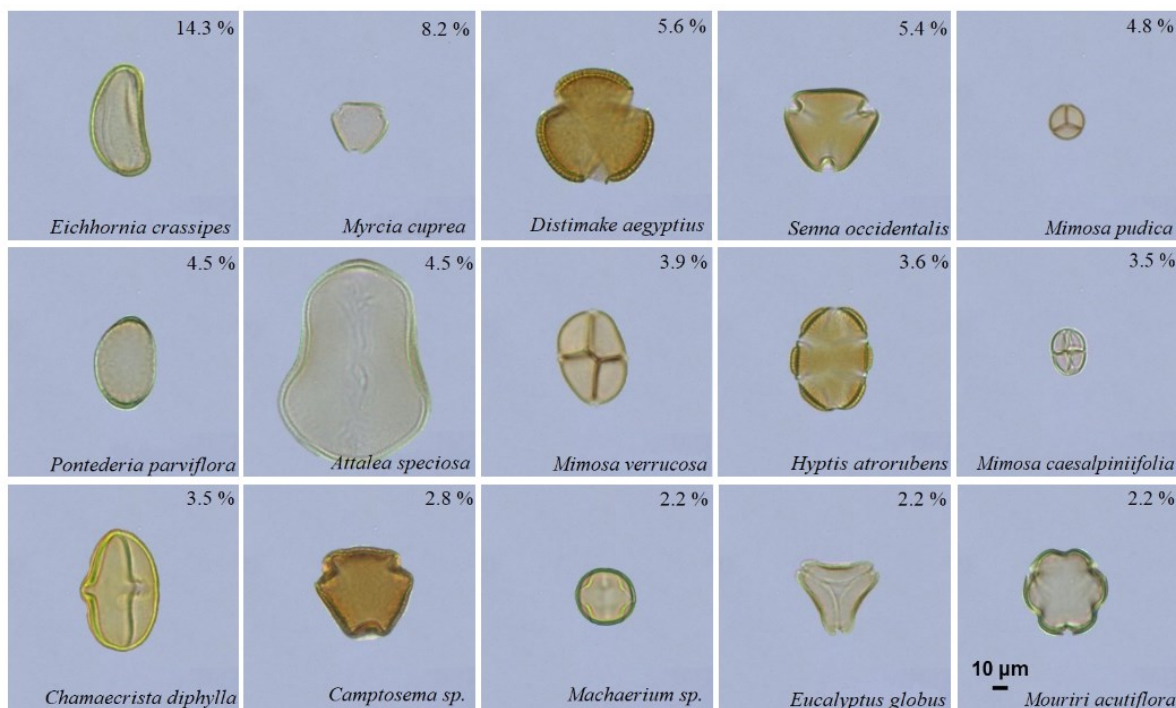
414 Figure 2. Composition of the bee landscape (*Melipona fasciculata*) in 34 meliponary
 415 arranged in a productivity gradient, sampling unit (id) refer to the meliponary in the center
 416 of the bee landscape, indication of low and high honey productivity, cities (urban area) are
 417 identified, in APA of Baixada Maranhense, state of Maranhão, Brazil, in 2018.

418 3.4 Floral origin of honey

419 The pollen present in the analyzed honeys was classified into 77 pollen types
420 belonging to 23 botanical families, of which 50 were identified at the species level, 26 at the
421 genus level and one only to the family level (see Table 4 in SM), with the majority of plants
422 (84.2%) being native, 28.5% arboreal, 28.5% shrubs, 15.6% herbaceous, 14.2% vines,
423 0.05% palms and 0.03% aquatic plants. As for the floral origin, 19 honey samples were
424 classified as heterofloral and 15 as monofloral. Cultivated plants (*Eucalyptus globulus*
425 Labill, *Psidium guajava* L.) were representative in honey samples from three sites only (6,
426 19, and 33), in the other honey samples (93.1%) the floral origin is composed of native plants
427 (details in Table 5 in SM).

428 The floral origin of honeys from 29 meliponaries (83%) is explained by 15 plant
429 species with greater relative abundance (Figure 3), they are: *Eichhornia crassipes* Mart.
430 (Solms), *Myrcia cuprea* (O. Berg) Kiaersk., *Senna occidentalis* (L.) Link, *Distimake*
431 *aegyptius* (L.) A.R. Simões & Staples, *Mimosa pudica* L., *Pontederia parviflora* Alexander,
432 *Attalea speciosa* Mart. ex Spreng, *Mimosa verrucosa* Benth, *Mimosa caesalpinifolia* Benth,
433 *Hyptis atrorubens* Poit, *Chamaecrista diphylla* (L.) Greene, *Machaerium* sp., *Camptosema*
434 sp., *Eucalyptus globulus* Labill. and *Mouriri acutiflora* Naudin. The description of these
435 plants and their frequencies in the 34 landscapes studied are displayed in Table 6 (SM).

436



437 Figure 3. Microphotographs (40x objective; 10 micrometer scale) of the fifteen main pollens,
 438 in relative abundance, observed in the pollen slide of honey samples from the bee *Melipona*
 439 *fasciculata* of meliponaries of 13 municipalities of the Baixada Maranhense APA, in eastern
 440 Brazilian Amazon. 2019.

441

442 The identification and counting of contaminants in honeys, performed in samples
 443 without acetolysis, detected the absence of contaminants or foreign elements, and the
 444 presence of common elements with the following frequency in the set of 34 honeys:
 445 vegetable tissue (53.8%), yeast (23%), Bryophyte spore (9.6%), insect organ: paw or antenna
 446 (3.8%) plant part: root (3.8%), monolet fern spore (2%), algae (2%) and Lycophyte (2%).

447

448 3.5 Relationships between floral origin and honey productivity

449 The mean richness of species registered in the slide of honeys from the meliponaries
 450 was 17.4 (\pm 3.5) species, varying from 11 to 26 species while the average abundance of
 451 grains counted by honeys was 774 (\pm 161.5) grains and ranged from 421 to 1,223 grains.
 452 Honey productivity had a negative relationship with species richness ($r = -0.36$ Pearson, p
 453 $= 0.032$) and with pollen abundance ($r = -0.39$ Pearson, $p = 0.019$).

454 Honey productivity was positively correlated with shrub richness ($r = 0.37$ Pearson,
 455 $R^2 = 0.11$, $p = 0.029$) and negatively correlated with palm abundance (Kendall' tau = -0.33,
 456 $R^2 = 0.18$, $p = 0.008$) present in bees' landscapes (see Table 3). There was no relationship
 457 between tree species and productivity.

458 In the modeling of productivity as a function of botanical species, eight species that
 459 account for honey productivity ($R^2 = 0.86$; $p < 0.0001$) were selected in model '1'. However,
 460 among the eight species, *Cenostigma bracteosum* (Tul.) Gagnon & G.P.Lewis is rare and
 461 only occurred in one sample from the meliponary with the greatest productivity (id = 12)
 462 with two grains, whereas *Ipomoea carnea* Jacq. only occurred in two meliponaries (id: 2 and
 463 23), with three grains in each. In model '2' we omitted *C. bracteosum* and *I. carnea* and the
 464 modeling selected three species (one different from model 1: *Mimosa caesalpinifolia*
 465 Benth), which account for more than half of the variance of honey productivity ($R^2 = 0.54$;
 466 $p < 0.0001$).

467 The species set (considering models 1 and 2) contained nine native botanical species
 468 grouped into six families (Table 3). The main botanical family is Fabaceae (44.4%). The life
 469 forms of this species set were: shrubs (44.4%), trees (33.3%), palms (11.1%), and herbs
 470 (11.1%). As to the floral resources of these species for the bees, all were nectariferous and
 471 polliniferous species; two were highly polliniferous.

472

473 Table 3. Coefficients of independent model obtained with RDA and multiple linear model of honey
 474 yield (Y) of *Melipona fasciculata* as a function of 77 species, obtained by melissopalynology in
 475 eastern Brazilian Amazon, Brazil. Model 2 omitted rare species.

Yield	explanatory variables: botanical species [‡]	family	score rda / coef lm	
			model 1	model 2
	<i>Cenostigma bracteosum</i> Tul., N/P, shrub, savanna	Fabaceae	0.394 / 7.159	omitted
	<i>Tibouchina aspera</i> Aubl., N/P, tree, savanna	Melastomataceae	0.388 / 0.478	0.506 / 0.004
	<i>Ipomoea carnea</i> Jacq., N/P, shrub, anthropic	Convolvulaceae	0.258 / 3.791	omitted
Y ~	<i>Neptunia plena</i> (L.) Benth, N/P, herb, wetland	Fabaceae	-0.621 / -1.111	-0.723 / -0.023
	<i>Anacardium occidentale</i> L., N/P, tree, savanna	Anacardiaceae	-0.507 / -2.635	-
	<i>Attalea speciosa</i> Mart. ex Spreng, N/P*, palm, anthropic	Arecaceae	-0.423 / -1.063	-
	<i>Psychotria carthagenensis</i> Jacq., N/P, shrub, wetland	Rubiaceae	-0.149 / -2.547	-
	<i>Plathymenia sp.</i> , N/P, tree, savanna	Fabaceae	-0.003 / -1.334	-
	<i>Mimosa caesalpinifolia</i> Benth, N/P*, shrub, savanna	Fabaceae	-	0.245 / 0.009
		R² adj.	0.86	0.54
		p	<0,0001	<0,0001

476 [‡] Botanical species; resources for bees (N - nectariferous, P - polliniferous, P* - too much pollen);
 477 life form; habitat; R² adj. is r square adjusted; p is significance level, score rda is biplot scores for
 478 constraining variables, coef lm is multiple linear regression coefficients.

479

480 4 Discussion

481 The Amazon is the largest and most biodiverse Brazilian biome, but has the lowest
 482 number of laws and public policies related to pollinators (Hipólito et al., 2021), while in
 483 recent years deforestation, forest fragmentation and land use change have intensified (Silva
 484 Junior et al., 2020). Although there are several studies on the effect of landscape on the

485 production of *Apis mellifera* honey (Sponsler and Johnson, 2015; Donkersley, 2019),
486 detailed studies on the landscapes and productivity of stingless honeybees are scarce (Jaffé
487 et al., 2015). The Environmental Preservation Area (APA) of Baixada Maranhense is a
488 natural laboratory for elucidating how the landscape influences the honey productivity of *M.*
489 *fasciculata*.

490 *M. fasciculata* is a tropical bee, endemic in the north, northeast, and center of Brazil,
491 in the Amazon and Cerrado biomes (Camargo and Pedro, 2013). It has a life expectancy
492 varying between 25 and 105 days and starts foraging around 25–33 days after emergence.
493 Climatic and floristic characteristics of the region determine behavior and foraging activity
494 (Kerr et al., 1996; Vit et al., 2013; Gostinski et al., 2018). In a study using radio-frequency
495 identification tags (Oliveira et al., 2021) identified that most of the *M. fasciculata* bees (65%)
496 drifted to another hive nearby (not necessarily associated with orientation mistakes) and that
497 factors such as temperature, humidity, and solar irradiation influenced the rates of drifting
498 behavior and affected foraging activity. Authors also identified that *M. Fasciculata* forages
499 during the entire day, but prefer the morning (peak activity per colony at 9:00 am). Indeed,
500 the species is very susceptible to climatic variation and small fluctuations can impact their
501 lifespan and implicate extranidal activities (Oliveira et al., 2021). In our study, climate
502 variables were not significant to explain honey productivity, probably because of a small
503 variation between sites. However, in the context of climate change, it is fundamental to
504 understand the impact of climatic variables on stingless bee behavior and extranidal activity.

505 Meliponiculture in the APA has a familial character, is conducted by people with
506 advanced age, many years engaged in the activity and an important network of contacts. The
507 beekeeper's experience indicated by the network of contacts, the number of boxes and
508 handling helped to account for the variation in productivity (Jaffé et al., 2015). However, the
509 honey productivity of the studied meliponaries is low and of greater variability ($1,302 \pm$
510 $928.7 \text{ ml} \cdot \text{bx}^{-1}$) when compared to the average productivity of 2,430 ml in a similar ecosystem
511 in the state of Pará (Venturieri et al., 2003).

512 Our analyses revealed that the variation in honey productivity is related to the
513 configuration of the landscapes around the meliponaries, the floral origin and the profile and
514 management of the beekeepers. These factors also affect the food and medicinal quality of
515 honey (de Oliveira Alves, 2013), which will be revealed in future physicochemical and
516 sensory analyses. The analysis of honey contaminants indicated only natural elements of the
517 working ecosystem of the bees and the absence of foreign bodies, which validates our

518 samples, the sampling method, and values the APA beekeepers for their management and
519 hygiene (Barth, 2004).

520

521 **4.1 Landscapes related to greater honey productivity**

522 In the APA, the highest honey productivity is associated with landscapes with greater
523 coverage of natural grassland fields and permanent water, and with associated species.
524 However, the identification of the floral origin by melissopalynology indicated that these
525 honeys have lower richness and abundance of pollen, which suggests an abundant nectar
526 supply in these landscapes.

527 The natural grassland field is a very old and stable non-forest ecosystem that, in the
528 geomorphological evolution of the Baixada Maranhense, was formed between 9,000 and
529 5,000 years ago (Lima et al., 2020). Areas of natural grassland field are similar to areas in
530 early succession, they are open, have high solar radiation, great richness and abundance of
531 herbaceous, shrub and grassland species with much flowering (Kohler et al., 2008;
532 Neumüller et al., 2020), which guarantees a high nectariferous potential and honey
533 production for *M. fasciculata*. Our results confirm that high honey productivity is positively
534 related to shrubs and some trees. However, there are very few botanical records on the APA
535 natural grassland field vegetation (Pinheiro, 2020) to correlate to our data. Therefore, further
536 research should assess the floristic aspect and phytosociology related to this ecosystem.
537 Studies on landscape structure indicate that the most efficient pollination and foraging
538 services occur where there are hedges, alleys, strips or forest corridors interspersed with
539 open fields, because they facilitate formation of the “cognitive map”, communication and
540 social flight guidance of the bees due to the three-dimensional structure of the landscape, as
541 opposed to the absence of these structures (Donkersley, 2019; Kheradmand and Nieh, 2019).

542 The positive effect of permanent water is due on the one hand to the water essential
543 resource, which ensures greater productivity of local ecosystems, as well as the presence of
544 nectariferous aquatic plants, especially *Eichhornia crassipes*, the most abundant species in
545 the set of analyses and the primary one in 30% of the analyzed honeys (Table 5 in SM). Also,
546 the availability of permanent water in the Amazonian dry period favors honey productivity
547 (de Oliveira Alves, 2013).

548

549

550

551 **4.2 Landscapes related to lower honey productivity**

552 The lower honey productivity in the APA is associated with landscapes possessing
553 greater coverage of mature forest, pastures and mosaic. Although these landscape classes
554 have a negative effect on honey productivity, which leads us to reject our original hypothesis,
555 these honeys contain greater abundance and richness of pollen, with up to 26 species. These
556 data suggest a higher frequency of pollen foraging and a greater contribution of these
557 meliponaries in ecosystem services of pollination and maintenance of gene flows, especially
558 in fragmented forest areas, compensating for the restriction of seed dispersal due to distance
559 (Sujii et al., 2021). Furthermore, in mature tropical forests present the possibility of complex
560 and diversified webs and greater competition for resources with other species of native bees
561 (Vit et al., 2013).

562 The negative relationship with pastures and mosaic, land cover that includes shifting
563 agriculture and small pastures (Capanema et al., 2019), is most likely related to the dynamics
564 of fire use in the landscape (Junior et al., 2016; Peralta et al., 2017), where culturally fire is
565 used for pasture clearing and slash-and-burn practice (Júnior et al., 2008). The fire and
566 smoke from forest fires trigger signals proportional to the size of the danger to the hive that
567 is transmitted among bees; in the short term they interfere with the olfactory sense in general
568 and in the long term hamper foraging and harm the plant-bee relationship (Cho et al., 2021).

569 The botanical species with the greatest negative effect on honey productivity is
570 *Attalea speciosa* (babassu), a highly polliniferous palm, typical of the palm forest, and very
571 abundant in anthropized environments. *A. speciosa* is not a good supplier of nectar, but it is
572 home to wild *M. fasciculata* nests and other native insects (Anderson et al., 1988). Babassu
573 has high social and economic importance in the region led by women babassu palm breakers,
574 the largest traditional forest products extractive group in Brazil (Porro et al., 2011).

575

576 **4.3 Relations between floral origin and honey productivity**

577 The diversity of land-use classes and landscape configuration of the APA reveal a
578 plasticity in the behavior of *M. fasciculata* and may indicate a range of tolerance, or an effort
579 to adapt to forest fragmentation (Lichtenberg et al., 2017). The richness of botanical species
580 identified in this study highlights the strong local adaptation of this bee species, which
581 depending on the situation may adopt generalist (Ribeiro et al., 2019) or specialist (Antonini
582 et al., 2006) behavior. The ecological appearance hypothesis (Feeny, 1976) explains that
583 animal foraging takes place preferentially in the most “apparent” and easy-to-find plants,

584 which can result in a specialization of foraging depending on the abundance and ease of
585 finding floral resources. In all the studied meliponaries, the sampling methodology
586 controlled the temporal and spatial foraging frequency variation of different landscapes and
587 flora compositions as it evaluated the annual accumulation of pollen and nectar in a
588 determined area - reflecting on honey productivity and floral origin.

589 Our study provides an important dimensioning of pollination ecosystem services
590 associated with meliponiculture in the APA, and confirms the synergy between this activity,
591 conservation and restoration of landscapes in this region. We identified a set of 77 botanical
592 species (84% native) associated with *M. fasciculata*, distributed in landscapes with different
593 configurations of land use and land cover. In practice, these results indicate a complex
594 relationship of interdependence between people, hives, waters and ecosystems, where the
595 benefits of nature for people are multiple, and the families that raise their bees are equally
596 important for nature (Spangenberg et al., 2014). The work of Melipona beekeepers for the
597 conservation of biodiversity in the APA must be valued and recognized, as an economic and
598 sociocultural activity based on local nature, which guarantees ecological management that
599 is very important for future generations.

600

601 **5. Conclusion**

602 Landscape composition has an important effect on the honey productivity of the
603 stingless bee *Melipona fasciculata* in the APA of Baixada Maranhense, in the Eastern
604 Amazon. In landscapes with higher percentage and density of natural grassland field patches,
605 percentage of permanent water and a specific composition of native shrub botanical species
606 is where there is greater honey productivity, but lower species richness and pollen abundance
607 in honey. Meliponaries in landscapes with greater mature forest cover present lower honey
608 productivity, but have honeys with greater richness and abundance of native species,
609 indicating more pollination ecosystem services in these landscapes.

610

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612

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621

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829 **The effect of landscape composition on stingless bee (*Melipona fasciculata*) honey**
 830 **productivity in a wetland ecosystem of Eastern Amazonia, Brazil**

831

832 **Supplementary Material - SM**

833 Table 4. Pollen types (77) identified in *Melipona fasciculata* honeybee samples by plant species in
 834 the 34 studied landscapes of APA Baixada Maranhense, in eastern Brazilian Amazon, Brazil, in 2019.

Plant species	Resource [‡]	Life form	Origin	Habitat	P(%) [§]
MONOCOTS					
ARECACEAE					
<i>Attalea speciosa</i> Mart. ex Spreng	N/P*	palm	native	anthropic	4.426
<i>Euterpes</i> sp.	N/P*	palm	native	forest	0.500
<i>Mauritia flexuosa</i> L.	P*	palm	native	forest	0.060
<i>Syagrus</i> sp.	N/P*	palm	native	anthropic	0.078
CYPERACEAE					
<i>Cyperus luzulae</i> (L.) Rottb. ex Retz.	A	aq herb	native	anthropic	0.967
<i>Eriophorum vaginatum</i> L.	A	herb	exotic	wetland	0.493
POACEAE					
Poaceae	A	herb	-	grassland	0.015
PONTEDERIACEAE					
<i>Eichornia crassipes</i> Mart. (Solms)	N	aq herb	native	wetland	11.401
<i>Pontederia parviflora</i> Alexander	N	aq herb	native	wetland	4.583
EUDICOTS					
AMARANTHACEAE					
<i>Alternanthera brasiliana</i> (L.) Kuntze	N/P	herb	native	anthropic	2.183
<i>Amaranthus</i> sp.	N/P	herb	exotic	anthropic	0.007
ANACARDIACEAE					
<i>Anacardium occidentale</i> L.	N/P	tree	native	savanna	0.265
ASTERACEAE					
<i>Baccharis</i> sp.	N/P	shrub	native	anthropic	0.011
<i>Mikania cordifolia</i> (L.f) Willd.	N/P	vine	native	anthropic	0.146
<i>Vernonia polyanthes</i> (Spreng.) Less.	N	shrub	exotic	grassland	0.093
BEGONIACEAE					
<i>Begonia</i> sp.	P	herb	native	anthropic	0.034
BIGNONIACEAE					
<i>Adenocalymma</i> sp.	N/P	vine	native	savanna	0.045
<i>Arrabidaea</i> sp.	N/P	vine	native	anthropic	0.011
<i>Tabebuia</i> sp.	N	tree	native	anthropic	0.030
BURSERACEAE					
<i>Protium leptostachyum</i> Cuatrec.	N	tree	native	forest	1.101
CECROPIACEAE					
<i>Cecropia</i> sp.	P	tree	native	anthropic	0.220
CONVOLVULACEAE					
<i>Ipomoea carnea</i> Jacq.	N/P	shrub/vine	native	anthropic	0.022
<i>Distimake aegyptius</i> (L.) A.R. Simões & Staples	N/P	creeper	native	anthropic	5.534
<i>Merremia</i> sp.	N/P	vine	exotic	anthropic	0.713
DILLENIACEAE					
<i>Curatella</i> sp.	P	shrub	native	grassland	0.022
EUPHORBIACEAE					
<i>Croton heliotropiifolius</i> Kunth	N	shrub	native	savanna	0.026
<i>Sebastiania</i> sp.	N/P	shrub	native	grassland	0.187
FABACEAE					
<i>Anadenanthera macrocarpa</i> (Benth.)	P	tree	native	savanna	0.037
<i>Andira anthelmia</i> (Vell.) Benth.	N/P	tree	exotic	anthropic	1.896
<i>Bauhinia forficata</i> Link.	P	shrub	exotic	anthropic	0.011
<i>Bowdichia</i> sp.	P	shrub	native	savanna	1.956

<i>Cenostigma bracteosum</i> Tul. Gagnon & G.P.Lewis	N/P	shrub	native	savanna	0.007
<i>Camptosema</i> sp.	NA	vine	native	grassland	2.877
<i>Campsiandra</i> sp.	NA	tree	native	forest	0.224
<i>Centrosema pubescens</i> Benth.	N/P*	vine	native	grassland	0.896
<i>Coursetia</i> sp.	NA	shrub	native	savanna	0.007
<i>Chamaecrista diphylla</i> (L.) Greene	N/P*	herb	native	anthropic	3.512
<i>Crotalaria retusa</i> L.	N	shrub	exotic	anthropic	1.008
<i>Cynometra</i> sp.	NA	tree	native	forest	0.209
<i>Desmodium incanum</i> DC.	N/P	herb	exotic	anthropic	0.026
<i>Dicorynia</i> sp.	NA	tree	native	grassland	0.034
<i>Dioclea</i> sp.	NA	vine	native	anthropic	0.011
<i>Inga cayennensis</i> Sagot ex Benth	N/P*	tree	native	anthropic	0.019
<i>Machaerium</i> sp.	N	shrub	native	anthropic	2.788
<i>Martiodendron parviflorum</i> (Amshoff) R. Koeppen	NA	tree	native	forest	1.821
<i>Mimosa verrucosa</i> Benth	N/P*	shrub	native	forest	3.896
<i>Mimosa caesalpinifolia</i> Benth	N/P*	shrub	native	savanna	3.523
<i>Mimosa pudica</i> L.	P	Herb	native	anthropic	4.795
<i>Myrocarpus frondosus</i> Allem	P	tree	exotic	forest	1.034
<i>Neptunia plena</i> (L.) Benth	N/P	herb	native	wetland	1.956
<i>Newtonia</i> sp.	NA	tree	exotic	forest	0.019
<i>Piptadenia phyllostachya</i> Benth	N/P	tree	native	forest	0.011
<i>Plathymenia</i> sp.	N/P	tree	native	savanna	0.063
<i>Phyllocarpus</i> sp.	NA	tree	native	forest	0.011
<i>Schrankia leptocarpa</i> DC.	N/P	herb	native	anthropic	0.355
<i>Senna occidentalis</i> (L.)	N/P	shrub	native	anthropic	5.620
<i>Schizolobium amazonicum</i> Huber ex Ducke	N/P*	tree	native	anthropic	0.970
<i>Stryphnodendron adstringens</i> (Mart.) Coville	N/P	tree	native	savanna	1.564
<i>Stylosanthes</i> sp.	N/P*	herb	native	savanna	0.011
<i>Zollernia</i> sp.	N/P*	shrub	native	forest	0.015
LAMIACEAE					
<i>Hyptis atrorubens</i> Poit.	N	herb	native	anthropic	3.575
<i>Hyptis</i> sp.	N	herb	native	anthropic	0.821
MALPIGHIACEAE					
<i>Peixotoa jussieuana</i> A.Juss	NA	shrub	native	savanna	0.179
MELASTOMATAACEAE					
<i>Miconia alata</i> (Aubl.) DC	N/P	shrub	native	grassland	0.086
<i>Mouriri acutiflora</i> Naudin.	N/P	tree	native	forest	2.407
<i>Tibouchina aspera</i> Aubl.	N/P	tree	native	savanna	1.952
MYRTACEAE					
<i>Eugenia flavescens</i> DC.	N/P*	shrub	native	savanna	0.194
<i>Eucalyptus globulus</i> Labill.	N/P	tree	exotic	anthropic	2.228
<i>Myrcia cuprea</i> (O.Berg) Kiaersk	N/P	shrub	native	forest	8.121
<i>Psidium guajava</i> L.	N/P*	tree	native	anthropic	1.907
PASSIFLORACEAE					
<i>Passiflora glandulosa</i> Cav.	P	creeper	native	forest	0.007
RUBIACEAE					
<i>Borreria tenella</i> (Kunth) Cham & Schultde	N/P*	herb	native	grassland	0.202
<i>Borreria verticillata</i> (L.) G. Mey	N/P*	shrub	native	anthropic	1.720
<i>Psychotria carthagenensis</i> Jacq.	N/P	shrub	native	wetland	0.037
SAPINDACEAE					
<i>Paullinia pinnata</i> L.	N	vine	native	anthropic	0.179
<i>Serjania Lethalis</i> A.St.-Hil	N	vine	native	savanna	1.123
SOLANACEAE					
<i>Solanum paniculatum</i> L.	P	shrub	native	anthropic	0.907

835 ‡ Resources (N: nectariferous, P: polliniferous, *: excess pollen, NA: information not available, A:
836 anemophilous). † P (%): relative pollen frequency in the 102 studied bee boxes;

837 Table 5. Analysis of the floral origin in honey of *Melipona fasciculata* of 34 meliponaries (id) in APA of Baixada Maranhense, eastern Brazilian Amazon,
838 Brazil, in 2019. Pollen type 1, 2, 3, 4 specifies the main pollen of nectariferous species and its relative abundance.

id	Classification	Pollen type 1	Pollen type 2	Pollen type 3	Pollen type 4
13	Heterofloral	<i>Attalea speciosa</i> 37 %	<i>Hyptis atrorubens</i> 17 %	<i>Mouriri acutiflora</i> 10 %	<i>Protium leptostachium</i> 9 %
20	Heterofloral	<i>Tibouchina aspera</i> 33 %	<i>Mouriri acutiflora</i> 27 %	<i>Hyptis atrorubens</i> 24 %	<i>Protium leptostachium</i> 9 %
19	Heterofloral	<i>Mimosa pudica</i> 29 %	<i>Eucalyptus globulus</i> 23 %	<i>Andira anielmia</i> 18 %	<i>Hyptis sp.</i> 15 %
24	Heterofloral	<i>Eichhornia crassipes</i> 33 %	<i>Pontederia parviflora</i> 27 %	<i>Myrcia cuprea</i> 19 %	<i>Attalea speciosa</i> 13 %
23	Heterofloral	<i>Eichhornia crassipes</i> 30 %	<i>Alternanthera brasiliiana</i> 17 %	<i>Myrcia cuprea</i> 13 %	<i>Pontederia parviflora</i> 11 %
28	Heterofloral	<i>Camptosema sp.</i> 22 %	<i>Attalea speciosa</i> 22 %	<i>Stryphnodendron adstringens</i> 13 %	<i>Distimake aegyptius</i> 9 %
30	Heterofloral	<i>Centrosema pubescens</i> 42 %	<i>Distimake aegyptius</i> 19 %	<i>Mouriri acutiflora</i> 13 %	<i>Eichhornia crassipes</i> 12 %
22	Heterofloral	<i>Mimosa caesalpinifolia</i> 29 %	<i>Stryphnodendron adstringens</i> 19 %	<i>Neptunia plena</i> 17 %	
2	Heterofloral	<i>Distimake aegyptius</i> 32 %	<i>Myrcia cuprea</i> 20 %	<i>Mouriri acutiflora</i> 19 %	
4	Heterofloral	<i>Distimake aegyptius</i> 43 %	<i>Distimake sp.</i> 12 %	<i>Eugenia flavescens</i> 10 %	
5	Heterofloral	<i>Myrcia cuprea</i> 44 %	<i>Distimake aegyptius</i> 34 %	<i>Distimake sp.</i> 14 %	
8	Heterofloral	<i>Machaerium sp.</i> 47 %	<i>Myrcia cuprea</i> 27 %	<i>Hyptis atrorubens</i> 15 %	
6	Heterofloral	<i>Myrcia cuprea</i> 36 %	<i>Psidium guajava</i> 22 %	<i>Hyptis sp.</i> 13 %	
34	Heterofloral	<i>Distimake aegyptius</i> 44 %	<i>Myrcia cuprea</i> 34 %	<i>Machaerium sp.</i> 15 %	
33	Heterofloral	<i>Andira anthelmia</i> 32 %	<i>Psidium guajava</i> 28 %		
7	Heterofloral	<i>Myrcia cuprea</i> 45 %	<i>Distimake aegyptius</i> 31 %		
25	Heterofloral	<i>Eichhornia crassipes</i> 43 %	<i>Pontederia parviflora</i> 36 %		
27	Heterofloral	<i>Machaerium sp.</i> 28 %	<i>Serjania lethalis</i> 24 %		
29	Heterofloral	<i>Eichhornia crassipes</i> 36 %	<i>Alternanthera brasiliensis</i> 18 %		
1	Monofloral	<i>Machaerium sp.</i> 48 %			
3	Monofloral	<i>Peixotoa jussieuana</i> 48 %			
9	Monofloral	<i>Hyptis atrorubens</i> 79 %			
10	Monofloral	<i>Hyptis atrorubens</i> 55 %			
11	Monofloral	<i>Alternanthera brasiliiana</i> 48 %			
12	Monofloral	<i>Myrcia cuprea</i> 53 %			
14	Monofloral	<i>Eichhornia crassipes</i> 50 %			
15	Monofloral	<i>Eichhornia crassipes</i> 55 %			
16	Monofloral	<i>Eichhornia crassipes</i> 52 %			
17	Monofloral	<i>Eichhornia crassipes</i> 62 %			
18	Monofloral	<i>Eichhornia crassipes</i> 58 %			
21	Monofloral	<i>Distimake aegyptius</i> 65 %			
26	Monofloral	<i>Eichhornia crassipes</i> 50 %			
31	Monofloral	<i>Schizolobium amazonicum</i> 49 %			
32	Monofloral	<i>Pontederia parviflora</i> 51 %			

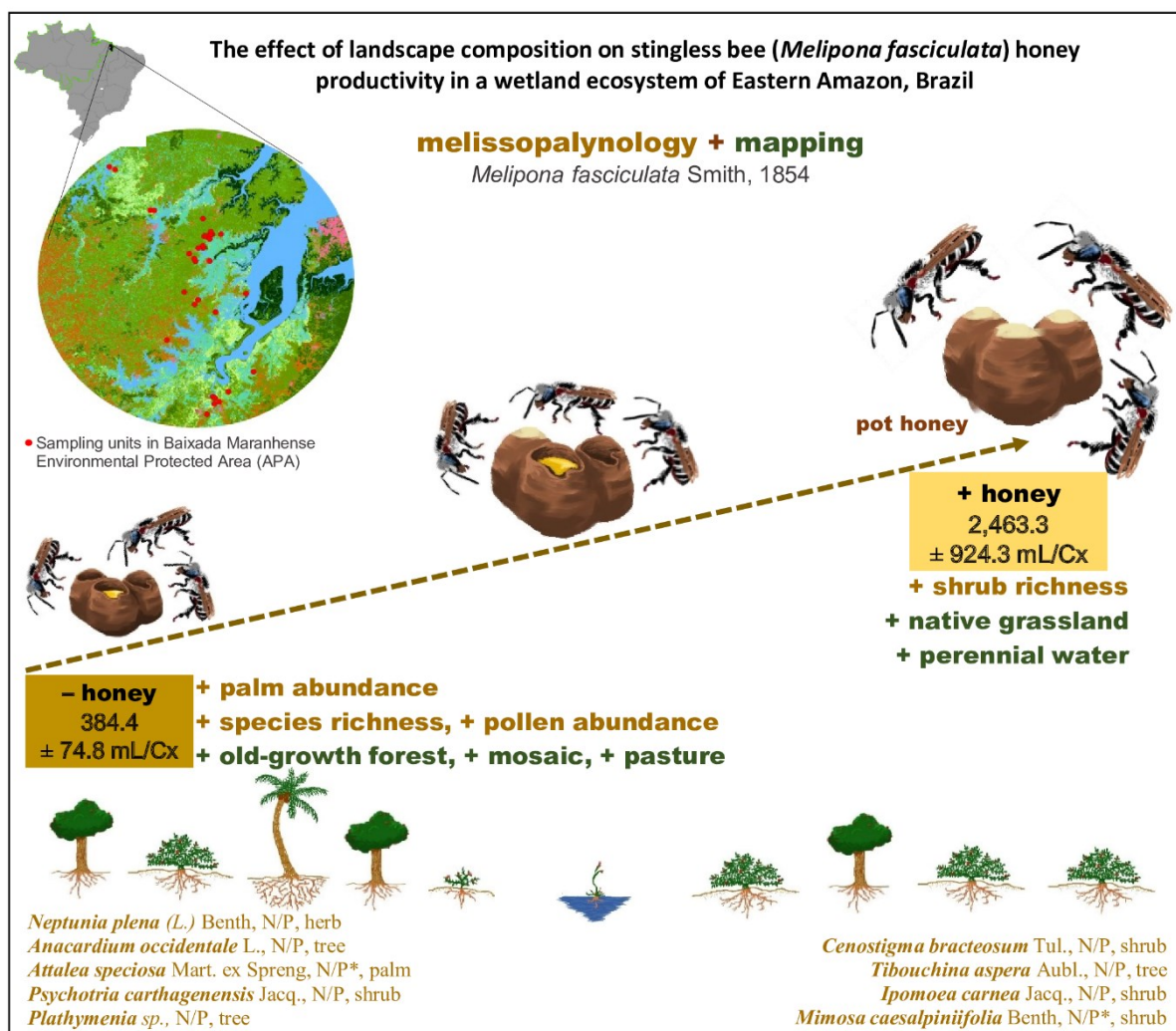
839 Table 6. Fifteen main botanical species and its occurrence (%) in the 34 meliponaries (id) in APA of Baixada Maranhense, eastern Brazilian Amazon, Brazil,
840 in 2019.

specie	occurrence, classification, number (id)	source of resources and habitat	specie	occurrence, classification, number (id)	source of resources and habitat
<i>Eichhornia crassipes</i> Mart. (Solms)	19 occurrences (56 %) ● Monofloral: 14, 15, 16, 17, 18, 26 ● Heterofloral: 23, 24, 25, 29 ● Low frequency: 2, 4, 7, 21, 22, 28, 30, 31, 32	nectariferous, aquatic, native, inhabits lakes, rivers and flooded fields.	<i>Mimosa verrucosa</i> Benth	20 occurrences (59 %) ● Alta frequência: 12, 14, 17, 18, 20, 32, 33 ● Low frequency: 1, 4, 9, 10, 11, 13, 16, 19, 21, 24, 25, 27, 34	very polyniferous and nectariferous, native, inhabits forest environment or wetlands.
<i>Myrcia cuprea</i> (O. Berg) Kiaersk	30 occurrences (88 %) ● Monofloral: 13 ● Heterofloral: 2, 5, 6, 7, 8, 23, 34 ● Low frequency: 1, 3, 4, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 22, 24, 25, 26, 27, 28, 29, 31, 32	nectariferous and polyniferous, shrub, native, inhabits forests or fields.	<i>Hyptis atrorubens</i> Poit	9 occurrences (26 %) ● Monofloral: 9, 10 ● Heterofloral: 8, 13, 20 ● Low frequency: 22, 27, 29, 33	nectariferous and polyniferous, shrub, native, inhabits forest or native grassland environment.
<i>Distimake aegyptius</i> (L.) A.R. Simões & Staples	21 occurrences (61 %) ● Monofloral: 21 ● Heterofloral: 2, 4, 5, 7, 30, 34 ● Low frequency : 6, 11, 13, 14, 16, 17, 18, 19, 20, 22, 24, 27, 28, 31	nectariferous and polyniferous, liana, native, inhabits anthropic or savannah environment.	<i>Chamaecrista diphylla</i> (L.) Greene	16 occurrences (47 %) ● Alta frequência: 1, 2, 4 ● Low frequency: 3, 6, 7, 9, 10, 11, 12, 13, 17, 28, 29, 31, 32	nectariferous and polyniferous, herb, native, inhabits anthropic environment or wetland.
<i>Senna occidentalis</i> (L.) Link	27 occurrences (79 %) ● Alta frequência: 1, 3, 5, 6, 7, 8, 10, 11, 20, 29, 31 ● Low frequency: 2, 9, 14, 15, 16, 17, 18, 19, 22, 23, 24, 26, 27, 30, 32, 33	it provides only pollen, which influences the physiology and survival of bees, shrub, native, from anthropogenic or savanna environment.	<i>Mimosa caesalpinifolia</i> Benth	21 occurrences (62 %) ● Monofloral: 0 ● Heterofloral: 2, 3, 4, 9, 18, 20, 22, 28, 31 ● Low frequency: 1, 6, 7, 10, 12, 13, 16, 19, 24, 25, 26, 30	nery poliniferous, shrub, native, inhabits savanna environment.
<i>Mimosa pudica</i> L.	30 occurrences (88 %) ● Monofloral: 0 ● Heterofloral: 19, 33 ● Low frequency: 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 21, 22, 23, 24, 25, 26, 27, 29, 30, 32, 34	polyniferous and nectariferous, herbaceous, native, inhabits anthropogenic or savannah environment.	<i>Camptosema</i> sp.	13 occurrences (38 %) ● Monofloral: 0 ● Heterofloral: 17, 28, 33, 34 ● Low frequency: 13, 15, 16, 22, 23, 24, 25, 26, 32	unknown floral resource, liana, native, inhabits native grassland.
<i>Pontederia parviflora</i> Alexander	15 occurrences (44 %) ● Monofloral: 32 ● Heterofloral: 24, 25 ● Low frequency: 4, 5, 8, 11, 14, 16, 17, 23, 26, 29, 30, 34	nectariferous, aquatic herb, native, inhabits anthropogenic or savannah environment.	<i>Mouriri acutiflora</i> Naudin	12 occurrences (35 %) ● Monofloral: 0 ● Heterofloral: 2, 13, 20 ● Low frequency: 1, 3, 9, 10, 11, 19, 30, 31, 33	nectariferous and polyniferous, tree, native, inhabits forest environment or wetland.
<i>Attalea speciosa</i> Mart. ex Spreng	27 occurrences (79 %) ● Monofloral: 13 ● Heterofloral: 28 ● Low frequency: 1, 2, 3, 4, 5, 6, 7, 8, 11, 12, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 30, 32	very polyniferous and nectariferous, palm tree, native, inhabits anthropogenic or savannah environment. Plant characteristic of Maranhão and APA.	<i>Machaerium</i> sp.	11 occurrences (32 %) ● Monofloral: 1 ● Heterofloral: 8, 27 ● Low frequency: 2, 5, 7, 13, 23, 24, 29, 31, 34	nectariferous and polyniferous, shrub, native, inhabits anthropic or savannah environment.
			<i>Eucalyptus globulus</i> Labill	23 occurrences (67 %) ● Monofloral: 0 ● Heterofloral: 19 ● Low frequency: 3, 5, 6, 7, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 21, 22, 27, 28, 29, 31, 32, 34	nectariferous and polyniferous, tree, exotic, inhabits anthropic environment.

* ● monofloral: > 45 %, ● heterofloral: plant composition 9 % - 45 %, ● low frequency: < 9 %, ● high frequency: > 9 %, (Barth, 2004).

APÊNDICE B - Figura resumo para revista Journal of Apicultural Research

Figura 4. Figura resumo para revista Journal of Apicultural Research, parte do artigo: o efeito da composição da paisagem na produtividade do mel de abelhas sem ferrão (*Melipona fasciculata*) em um ecossistema de zonas úmidas da Amazônia Oriental, Brasil.



N - nectariferous; P - polliferous; * - too much pollen; mosaic - includes shifting agriculture, sand formations, small pastures and villages.

APÊNDICE D - Figuras extras da execução da pesquisa

Figuras ilustrativas das atividades da pesquisa:

Figura 1. Alguns dos meliponicultores envolvidos na pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

Figura 2. Esquema de localização e mapeamento das paisagens utilizadas pelas abelhas na pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

Figura 3. Esquema de análise das variáveis do artigo sobre produtividade de mel de *Melipona fasciculata*. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

Figura 4. Esquema de análise das variáveis do artigo sobre características físico-química de mel de *Melipona fasciculata*. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

Figura 5. Diversos momentos da etapa de campo da pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

Figura 1. Alguns meliponicultores (as) envolvidos na pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.



Figura 2. Esquema de localização e mapeamento das paisagens da abelha utilizados na pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

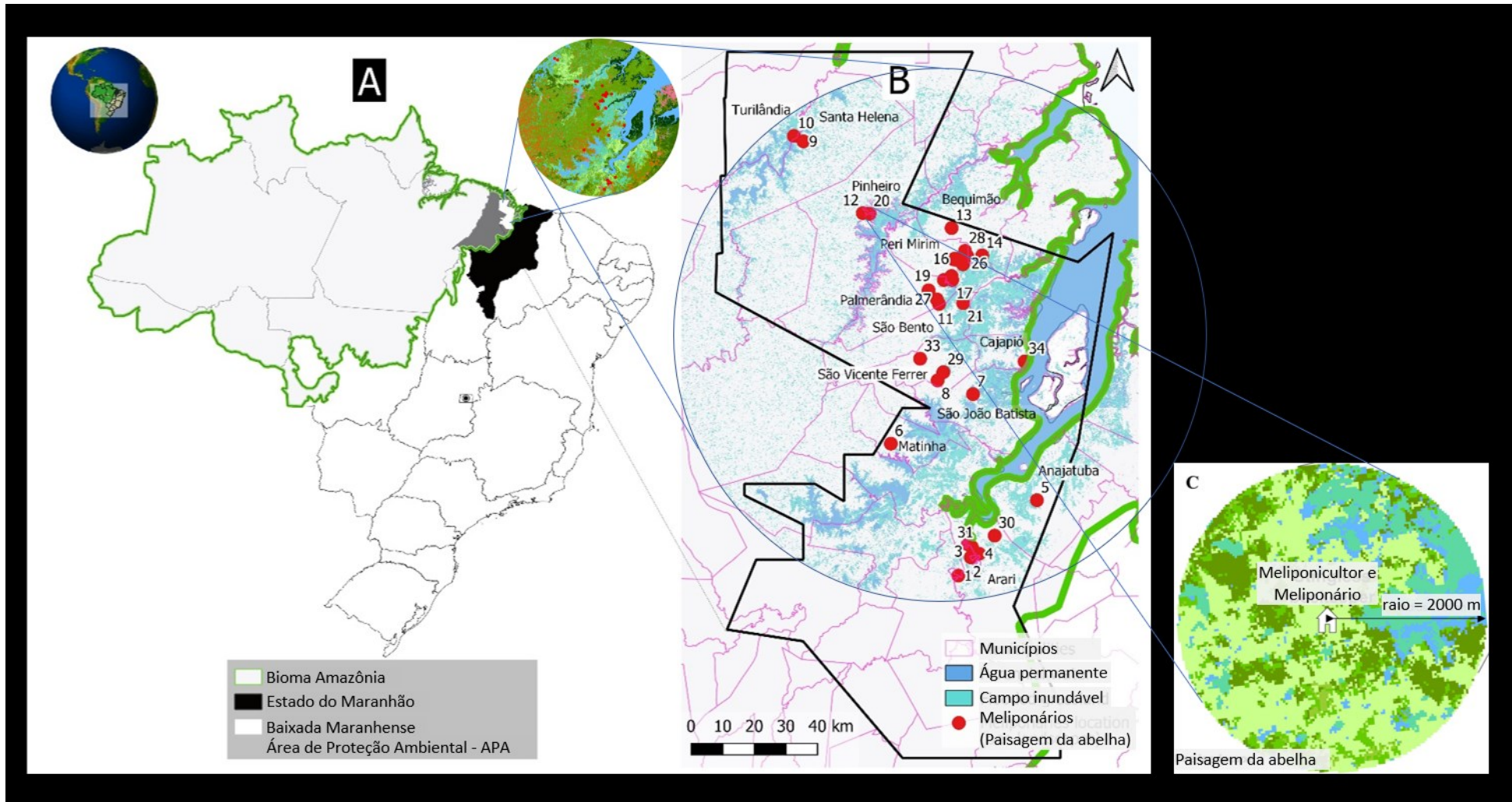


Figura 3. Esquema de análise das variáveis do artigo sobre produtividade de mel de *Melipona fasciculata*. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

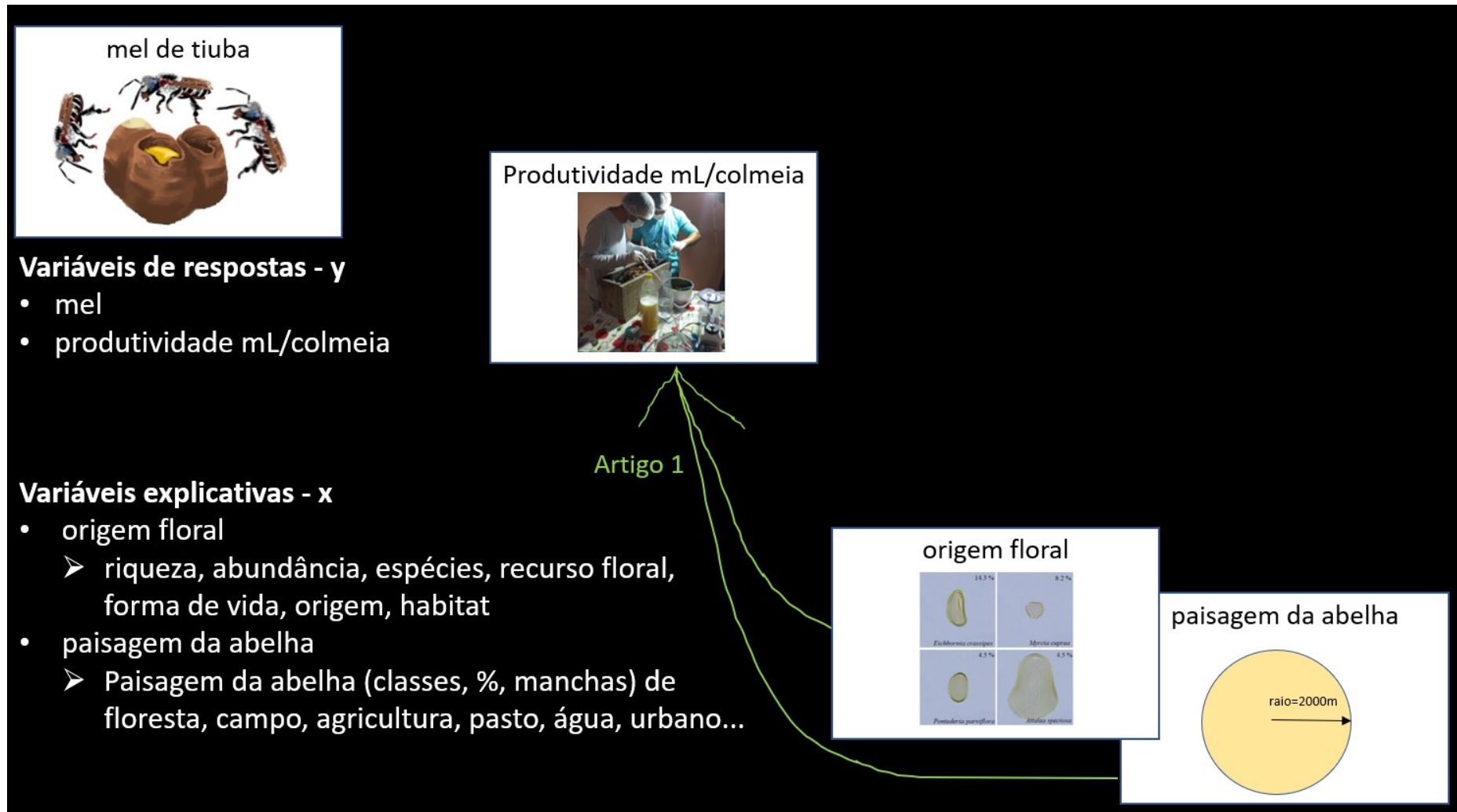


Figura 4. Esquema de análise das variáveis do artigo sobre características físico-química de mel de *Melipona fasciculata*. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018.

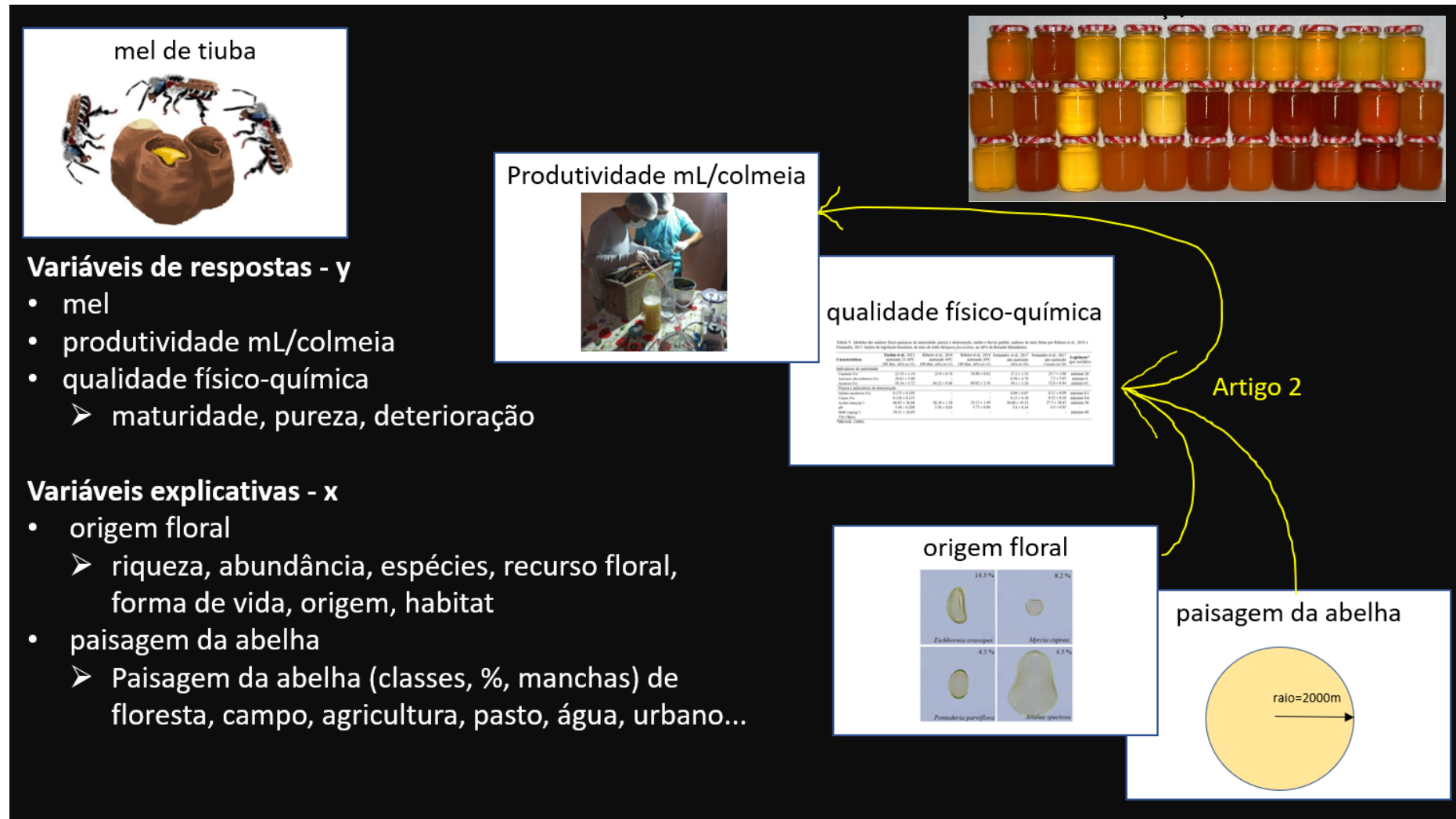


Figura 5. Diversos momentos da etapa de campo da pesquisa. APA da Baixada Maranhense, estado do Maranhão, Brasil, em 2018

