

# **Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes**

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# 1 Landscape structure shapes the diversity of beneficial insects in coffee producing 2 landscapes

3  
4 **Abstract.** The expansion of monocultures and the overuse of agrochemicals have resulted in the  
5 loss of beneficial insects and disruption of ecosystem services such as pollination and biological  
6 control in agricultural landscapes. Bees, wasps and flower flies were our model groups to  
7 investigate how landscape structure attributes affect alpha and beta diversity of different  
8 beneficial insect groups in Brazilian landscapes containing coffee crops. Species richness and  
9 abundance of wasps, and bee richness were positively correlated with forest cover at multiple  
10 spatial extents. Bee abundance, and species richness and abundance of flower flies did not  
11 respond to any landscape predictor. The community composition of wasps and bees in  
12 landscapes with low forest cover was composed of subsets of the communities located in  
13 forested landscapes, leading to species loss in structurally impoverished landscapes. High  
14 variations in landscape diversity and edge density between landscapes resulted in flower fly  
15 species replacement suggesting that pairs of landscapes with high and low diversity of habitat  
16 types and edge density harbor different species. Such results indicate that initiatives for the  
17 conservation of beneficial insects in the Atlantic Forest biodiversity hotspot must focus on forest  
18 conservation and restoration, because high levels of forest loss can result in the loss of wasp and  
19 bee species with potential negative consequences for the provision of pollination and pest control  
20 services in agroecosystems. Our findings can aid conservationists and policy makers to define  
21 priority actions for biodiversity conservation as well as the selection of appropriate spatial scales  
22 in landscape planning and management.

23  
24 **Keywords:** agroecosystems; biodiversity conservation; landscape structure; pollinators; natural  
25 enemies; tropical forest.

26  
27 **1. Introduction**  
28 Balancing sustainable food production and biodiversity conservation is one of the key global  
29 environmental challenges (Johnson et al., 2017). Agricultural intensification is considered one of

30 the main threats to biodiversity conservation (Butchart et al., 2010) and the main cause of the  
31 decline of natural enemies and pollinators (hereafter beneficial insects), which provide important  
32 ecosystem services to both natural and anthropogenic ecosystems (Klein et al., 2007; Geiger et  
33 al., 2010; Potts et al., 2010; Ollerton, 2017; Grab et al., 2018). Ecosystem services provided by  
34 beneficial insects afford approximately US\$ 71.3 billion (2018 dollars, considering inflation)  
35 annually in the United States (Losey and Vaughan, 2006). Animal pollination services are  
36 responsible for 30% of global food production (Klein et al., 2007) contributing US\$235–577  
37 billion to global crop output (Potts et al., 2016), whereas biological control of crop pests has  
38 been valued at US\$619/ha (2018 dollars) globally (Costanza et al., 1997).

39 Agricultural intensification encompasses the overuse of agrochemicals and the conversion of  
40 natural and semi-natural habitats (e.g., grasslands, forests, hedgerows, abandoned pastures) into  
41 expansive monocultures – a process known as landscape simplification (Meehan et al., 2011).  
42 Pesticide applications heighten both mortality rates and sublethal effects on insect physiology  
43 and behavior such as foraging, fecundity, sex ratio, and learning performance (Stapel et al.,  
44 2000; Desneux et al., 2007; Geiger et al., 2010). Landscape simplification negatively affects the  
45 capacity of a landscape to provide spatio-temporal insurance through landscape complementation  
46 and supplementation (Ouin et al., 2004; Tscharntke et al., 2012; Fahrig, 2017). According to  
47 Tscharntke et al. (2012), landscape complementation means that organisms must forage in  
48 different habitats to gather spatially separated resources that are necessary to fulfill their needs.  
49 For landscape supplementation, landscapes provide organisms with supplemental non-crop and  
50 managed habitats with high concentrations of the same type of required resources.

51 Landscape simplification reduces the amount and diversity of land cover types (compositional  
52 heterogeneity) including natural and semi-natural habitats (hereafter non-crop habitats) that play

53 a key role for the maintenance of biodiversity in farmland, particularly invertebrates (Landis et  
54 al., 2000; Bianchi et al., 2006). Non-crop habitats are less affected by pesticides and provide  
55 refuge and resources for beneficial insects, especially during disturbances in crops such as  
56 pesticide application, tillage and harvest operations (Altieri, 1999; Landis et al., 2000; Bianchi et  
57 al., 2006; Tscharntke et al., 2012). Moreover, non-crop habitats support high plant diversity, thus  
58 providing diverse and continuously available food resources from floral resources (Danner et al.,  
59 2016) to alternative preys (Landis et al., 2008). Landscape simplification also alters the spatial  
60 arrangement of crop and non-crop habitats in the landscape (configurational heterogeneity)  
61 resulting in low connectivity and spill-over opportunities between complementary habitats  
62 (Tscharntke et al., 2012; Gámez-Virúés et al., 2015). Therefore, habitat loss and fragmentation  
63 reduce compositional and configurational landscape heterogeneity leading to the biotic  
64 homogenization, species loss and deterioration of ecosystem services (Tscharntke et al., 2012;  
65 Gámez-Virúés et al., 2015).

66 The land sharing/land sparing dichotomy has stimulated debate on how to attenuate agricultural  
67 intensification in order to conciliate food production and conservation, but sharing/sparing  
68 strategies are not mutually exclusive and should work synergistically to avoid undesirable  
69 consequences for biodiversity (Fischer et al., 2013; Kremen, 2015). Only a combination of large  
70 protected areas (land sparing) surrounded by agroecological wildlife-friendly matrix (land  
71 sharing) can improve landscape heterogeneity resulting in high recolonization rates and recovery  
72 of degraded ecosystem functioning (Tscharntke et al., 2012; Kremen, 2015).

73 Studies from temperate and tropical regions indicate that agricultural landscapes with high  
74 compositional and configurational heterogeneity can support greater diversity of beneficial  
75 insects than do simpler landscapes dominated by monocultures (Meyer et al., 2009; Mandelik et



76 al., 2012; Kennedy et al., 2013; González et al., 2015, 2016; Kratschmer et al., 2018). However,  
77 only a few studies have been conducted in the Neotropics, such as Brazilian agricultural  
78 landscapes (Moreira et al., 2015; Sartuni et al., 2016; Boscolo et al., 2017; Medeiros et al., 2018;  
79 Hipólito et al., 2018; Aristizabal and Metzger, 2019). Furthermore, most studies related to the  
80 effects of landscape simplification on biodiversity have focused on alpha diversity, whereas beta  
81 diversity has received much less attention (Mori et al., 2018).

82 According to Baselga (2010) beta diversity quantifies the differences among biological  
83 communities and reflects two different phenomena: spatial species turnover and nestedness,  
84 which represent the replacement and loss of species between communities, respectively. Beta  
85 diversity is an essential approach to elucidate processes involved with changes in community  
86 composition due to natural and anthropogenic disturbances such as biological invasions (Socolar  
87 et al., 2016; Silva and Hernández, 2018) and agricultural intensification (Gabriel et al., 2006;  
88 Karp et al., 2012). Local-field scale studies (alpha diversity) identify only a subset of diversity,  
89 whereas beta diversity is a useful tool to quantify all components of diversity at multiple spatial  
90 scales (Gabriel et al., 2006). Integrating alpha and beta diversity could accommodate multiple  
91 ecosystem services at the landscape level (Frei et al., 2018; Rodríguez-Loinaz et al., 2014) and  
92 can aid decision makers and conservationists in selecting appropriate indicators and spatial scales  
93 for species conservation (Clough et al., 2007).

94 We aimed to understand how compositional and configurational landscape heterogeneity  
95 influences the diversity of beneficial insects in Brazilian coffee farms. Specifically, we tested  
96 whether alpha and beta diversity of beneficial insects change with forest cover and landscape  
97 diversity (compositional heterogeneity) and edge density (configurational heterogeneity). We  
98 used wasps (Insecta: Hymenoptera: Vespidae), bees (Insecta: Hymenoptera: Apoidea) and flower

99 flies (Insecta: Diptera: Syrphidae) as a model of different groups of beneficial insects. Bees,  
100 wasps and flower flies provide important pollination services in natural and agroecosystems  
101 (Allen-Wardell et al., 1998; Potts et al., 2016; Inouye et al., 2015; Ollerton, 2017; Lucas et al.,  
102 2017, 2018) including coffee plantations (Roubik, 2002; Ricketts et al., 2004; Klein et al., 2003,  
103 2008; Vergara and Badano, 2009; Saturni et al., 2016; Hipólito et al., 2018). Moreover, bees,  
104 wasps and flower flies have been used as bioindicators to assess the loss of biodiversity and the  
105 efficiency of restoration and conservation policies (Sommaggio, 1999; Tschardt et al., 2005;  
106 Ricarte et al., 2011; Sommaggio and Burgio, 2014), and many wasp and flower fly species are  
107 important agents of biological control of pests in several agroecosystems (Richter, 2000; Rojo et  
108 al., 2003; Schmidt et al., 2004; Nelson et al., 2012; Eckberg et al., 2015).

109 We expected that forest cover, landscape diversity and edge density regulate community  
110 composition of beneficial insects such that communities located in coffee monocultural  
111 landscapes support subsets of species-rich communities in more heterogeneous landscapes. We  
112 also expected that low levels of compositional and configurational heterogeneity result in  
113 community homogenization with a few crop-associated species replacing most species. Atlantic  
114 Forest is the dominant non-crop habitat in the study region and provides undisturbed nesting  
115 habitats for wasps (Souza et al., 2010, 2014, 2015) and bees (Samejima et al., 2004; Siqueira et  
116 al., 2012), and specific larval micro habitats for several flower fly species (Medeiros et al.,  
117 2018). Bees, wasps and flower flies can be found in both crop and non-crop habitats;  
118 consequently, high landscape diversity and edge density may improve the capacity of landscapes  
119 to provide multiple resources for beneficial insects via landscape complementation and  
120 supplementation. We provide novel information on the effects of landscape composition and  
121 configuration on the diversity of pollinator and natural enemy insects in Brazilian farmland.

122

## 123 **2. Material and Methods**

### 124 *2.1. Study Area*

125 The study was conducted in 16 coffee producing landscapes near the border of the states of São  
126 Paulo and Minas Gerais in southeastern Brazil (Fig. 1). Landscape area was defined by a buffer  
127 of 1 km around the centroid of each sampling area, a subjectively determined location along the  
128 interface between forest and coffee habitats. Previous studies conducted in Brazil have indicated  
129 that the 1 km radius is suitable to encompass the dispersal range sizes of most bee, wasp and  
130 flower fly species (Santos et al., 2000; da Cruz et al., 2006; Saturni et al., 2016; Silva et al.,  
131 2017; Medeiros et al., 2018).

132 The study region experiences a subtropical highland climate (Köppen climate classification,  
133 Cwb) characterized by rainy summers and dry winters with an average annual rainfall and  
134 temperature of 1,478 mm and 19.9 °C, respectively (Cipriani et al., 2011; Barros et al., 2012).

135 The study region encompasses fragments of Atlantic Forest, pasture and eucalyptus stands  
136 immersed in a matrix of sun-coffee monocultures that are conventionally managed based on  
137 agrochemical usage (fertilizers, insecticides, fungicides and herbicides). The Atlantic Forest  
138 originally extended from northeastern to southwestern Brazil and into Argentina and Paraguay,  
139 mainly along the coast (Muylaert et al., 2018), but only 26% remains in Brazil (Rezende et al.,  
140 2018). The northern part of the study region has a hilly terrain where coffee is cultivated without  
141 mechanization by small and medium-scale farmers, whereas high levels of mechanization are  
142 employed in flat areas in the south where coffee is cultivated by medium and large-scale farmers.  
143 The original vegetation of the study region is seasonal semideciduous forest, which is considered  
144 one of the most threatened ecosystem types of the Atlantic Forest hotspot (Ribeiro et al., 2009).

145 Most forest remnants in the study region are small and isolated fragments composed of  
146 secondary vegetation due to intensive logging in past decades (local farmers, personal  
147 communication).

148

## 149 *2.2. Insect Surveys*

150 We sampled wasps (Hymenoptera: Vespidae: Polistinae and Eumeninae), bees (Hymenoptera:  
151 Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) and flower flies  
152 (Diptera: Cyclorrhapha: Syrphidae) in three distinct habitats centrally located in each landscape:  
153 interior of the coffee plantation, interior of the adjacent forest remnant and at the coffee-forest  
154 edge – hereafter coffee, forest and edge habitats. In each habitat we set up one Malaise trap  
155 (Townes model) and three baited traps along a linear transect parallel to the habitat edge to  
156 capture beneficial insects (a total of three transects per landscape). Transects within the interior  
157 of forest and coffee habitats were 100 m away from any edge. The four traps were 50 m apart  
158 along each transect. Baited traps consisted of 2 L PET (Polyethylene Terephthalate) bottles hung  
159 from branches approximately 1.3 m above the ground with four circular 4 cm diameter holes cut  
160 midway and filled with 300 ml of orange juice (Locher et al., 2014) and 0.4 ml of propylene  
161 glycol. Traps remained open for seven consecutive days per month for 13 months from June  
162 2016 to June 2017. Captured insects were preserved in 70% ethanol and identified to the lowest  
163 taxonomic level possible using available identification keys for each of the three insect groups  
164 (see Supplementary material).

165

## 166 *2.3. Insect Diversity*

167 We aggregated all individuals collected in the three habitats (coffee, forest, edge) per landscape  
168 to calculate alpha and beta diversity at the landscape level, as coffee and forest are the dominant  
169 crop and non-crop habitats in the study region. Among the sampled landscapes the average area  
170 and median proportion of area covered with coffee and forest combined were 72.3 % and 78.3  
171 %, respectively. Alpha diversity was characterized by the species richness and abundance of  
172 each insect group within each of the 16 landscapes.

173 We used Sorensen's dissimilarity index ( $\beta_{sor}$ ) to estimate total beta diversity, which we  
174 partitioned into two components: turnover and nested. The Simpson dissimilarity index ( $\beta_{sim}$ )  
175 was used to calculate the turnover component, while the difference between  $\beta_{sor}$  and  $\beta_{sim}$   
176 estimated the nested component ( $\beta_{nes}$ ) of beta diversity. Turnover and nested components,  
177 which refer to species replacement and the loss of species between landscapes respectively,  
178 reveal the processes involved in community assembly (Baselga, 2010). Total beta diversity and  
179 its components were calculated in the R software version 3.3.2 (R Core Team, 2014) using the  
180 presence-absence community matrix as input in the function *beta.pair* from the *betapart* package  
181 (Baselga and Orme, 2012).

182

#### 183 *2.4. Explanatory Variables*

184 For the landscape variables, we built land use maps for each landscape using high-resolution  
185 images from ArcGIS basemap imagery, Digital Globe satellites 2013–2015, ~ 1 m resolution at a  
186 1:5,000 scale. We mapped 10 land use types: abandoned crops, abandoned pastures, arable field,  
187 built up area, coffee, eucalyptus, forest, pasture, water body and wetland (Fig. 1c). We conducted  
188 extensive ground verification in order to guarantee high accuracy levels of the land use maps that  
189 were used to calculate the landscape explanatory variables: forest cover and landscape diversity

190 (compositional heterogeneity) and edge density (configurational heterogeneity) at four spatial  
191 extents (250, 500, 750 and 1000 m radii). Landscape variables were calculated using ArcGIS  
192 10.3 with Patch Analyst (Rempel et al., 2012) and V-LATE (LARG, 2006) extensions. To  
193 estimate landscape diversity, we used the Shannon diversity index, which considers both the  
194 richness of land use (number of land cover types) and the proportional area of each land cover  
195 type (McGarigal, 2015). Edge density is the sum of the lengths (m) of all true edge segments  
196 (boundaries between different land cover types) in the landscape, divided by the total landscape  
197 area (McGarigal, 2015). We also recorded the cumulative number of applications of  
198 agrochemical usage (insecticides, herbicides, fungicides and fertilizers) in the 16 sampled coffee  
199 plantations during the 13 months of insect surveys. Agrochemical usage information was  
200 obtained by periodic interviews with farmers.

201

## 202 *2.5. Statistical Analyses*

203 We used generalized linear mixed models (GLMMs) to determine the effect of landscape  
204 structure on alpha diversity of the three insect groups at four spatial extents. The abundance and  
205 species richness of each insect group were fitted with Poisson error structure. The variable  
206 “agrochemical usage” was included in the GLMM models as a random effect, in order to take  
207 into account a possible influence of local crop management. For each dependent variable and  
208 spatial extent, we analyzed four competing models (Table 1) including a null model composed  
209 only of an intercept indicating no variation among landscapes. We used Akaike Information  
210 Criterion (AIC; Burnham and Anderson, 1998) with the small sample correction (AICc; Hurvich  
211 and Tsai, 1989) to rank and identify the best fitting models; AICc weight (wAICc) and AICc  
212 delta ( $\Delta$ AICc) were used as criteria to rank the models (Burnham and Anderson, 2002). We only

213 considered models as plausible if they had p-values  $< 0.05$  (model fit),  $wAICc \geq 0.1$  and  $\Delta AICc$   
214  $\leq 2.5$ . All analyses were performed in R version 3.3.2 using the *bbmle* package (Bolker, 2010)  
215 for model selection.

216 To test the effect of explanatory variables and spatial extents on beta diversity (total, turnover  
217 and nested) we conducted a multiple regression on the distance matrix, a multiple regression  
218 used to model multivariate response data (Lichstein, 2007) with 9,999 permutations (Anderson,  
219 2017). Only explanatory variables with p-values lower than 0.05 were considered to have a  
220 significant relative contribution. To test whether agrochemical usage affected beta diversity we  
221 applied a redundancy analysis, which indicated that only the turnover component for wasps was  
222 influenced by this variable ( $R^2 = 0.87$ ,  $p = 0.01$ ). We used the residuals of this analysis in the  
223 multiple regressions as a way to exclude the influence of agrochemical usage on beta diversity  
224 components. We used multiple regressions to calculate the relative contribution of each beta  
225 diversity component by dividing each component by total beta diversity (Sorensen index). We  
226 also calculated the difference in each landscape variable for each pair of landscapes to evaluate  
227 the influence of landscape variables on alpha diversity, and on total, nested and turnover beta  
228 diversity (Medeiros et al., 2018). All analyses were conducted using the function *adonis* of the  
229 *vegan* package (Oksanen et al., 2007).

230

### 231 **3. Results**

232 We recorded a total of 265 species among the 27,035 specimens sampled for this study: 13,658  
233 wasps (Vespidae: Polistinae and Eumeninae) classified in 86 species and 26 genera; 8,393 bees  
234 in 116 species and 73 genera (Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and  
235 Megachilidae); and 4,984 flower flies (Syrphidae) in 63 species and 20 genera in the 16  
236 landscapes (Suppl. Material). Species richness varied from 19 to 44 species per landscape for

237 wasps; 18 to 51 for bees and 12 to 26 for flower flies, and abundance varied from 167 to 1,709  
238 specimens for wasps; 203 to 784 for bees and 112 to 659 for flower flies. There were two  
239 dominant species per group: *Agelaia multipicta* (Haliday, 1836) and *Agelaia vicina* (de Saussure,  
240 1854) (23.2% and 26.3% of wasp records respectively) (Fig. 2); *Apis mellifera* Linnaeus, 1758  
241 and *Trigona spinipes* (Fabricius, 1793) (25.5% and 31.2% of bee records) (Fig. 3); and  
242 *Toxomerus watsoni* (Curran, 1930) and *Dioprosopa clavata* (Fabricius, 1794) (25.6% and 38.6%  
243 of flower fly records) (Fig. 4).

244 Landscape explanatory variables differed considerably along the 16 landscapes. Within the  
245 radius of 1,000 m forest cover varied from 2.8 to 59.3 %, landscape diversity from 1.05 to 1.86  
246 and edge density from 127 to 246. Agrochemical usage varied from 2 to 13 applications per  
247 coffee plantation / year.

248 Species richness and abundance of wasps and bee species richness were positively correlated  
249 with forest cover at all spatial extents (Table 2; Fig. 5). Bee abundance and species richness and  
250 abundance of flower flies were not explained by any of the explanatory variables at any of the  
251 extents that we considered.

252 Similarly to the alpha diversity, beta diversity, specifically the nested component of bees and  
253 wasps was influenced by forest cover at all spatial extents (Table 3; Fig. 6), wherein low forest  
254 cover resulted in species loss. The turnover component of beta diversity of flower flies was  
255 explained by landscape diversity at 250 m and edge density at all spatial extents (Table 3; Fig. 6)  
256 suggesting that high variation in landscape diversity and edge density between landscapes  
257 resulted in species replacement. In contrast, the turnover component of bees and wasp, as well as  
258 nested component of flies were not explained by any predictor.

259



## 260 **4. Discussion**

261 Our hypotheses that low levels of forest cover, landscape diversity and edge density lead to both  
262 species loss and community homogenization was supported for bees, wasps and flower flies.  
263 However, these insect groups were not equally affected by compositional and configurational  
264 landscape heterogeneity suggesting that bees, wasps and flower flies perceive landscape structure  
265 differently. Moreover, beta diversity revealed important landscape effects on flower flies that  
266 were not detected by alpha diversity highlighting the relevance of a beta diversity approach to  
267 better understand the effects of landscape structure on community composition of beneficial  
268 insects in farmland.

269

### 270 *4.1. Alpha Diversity: Responses of Beneficial Insects to Landscape Context*

271 Species richness of wasps and bees, and wasp abundance increased with increasing forest cover  
272 at multiple spatial extents, while bee abundance and flower fly richness and abundance were not  
273 explained by any of the explanatory variables at any spatial extends considered.

274 Wasps and bees forage in multiple agroecosystems including coffee plantations, where wasps  
275 provide important pest control services (Pereira et al., 2007; Androcioli et al., 2018) and bees act  
276 as major pollinators (Roubik, 2002). However, coffee monocultures present short mass-  
277 flowering periods and are constantly submitted to pesticide applications resulting in high  
278 mortality rates and sub-lethal effects (Stapel et al., 2000; Desneux et al., 2007; Geiger et al.,  
279 2010). In our study region, wasp nests found within coffee plantations or on human-built  
280 structures are usually removed to avoid stings. In contrast, Atlantic Forest remnants support high  
281 plant diversity (Murray-Smith et al., 2009) and act as an important perennial source of floral  
282 resources for beneficial insects including bees (Ramalho, 2004) and flower flies (de Sousa et al.,  
283 2014). Atlantic Forest remnants are also relatively stable and provide nesting substrates and

284 undisturbed nesting sites for wasps (Souza et al., 2010, 2014, 2015) and bees (Siqueira et al.,  
285 2012) compared to the intensive crop management and nest removal within coffee plantations.  
286 Therefore, the long-term persistence of bees and wasps in coffee producing landscapes seems to  
287 depend on forest remnants with suitable nesting sites and floral resources that are critical for nest  
288 survival, dispersal and reproductive division of bee and wasp colonies (Seppä et al., 2002;  
289 Siqueira et al., 2012). In the same study region, Saturni et al. (2016) found that forest cover  
290 positively affected richness, abundance and diversity of bees, which were responsible for an  
291 increase in coffee fruit set of 28%. Therefore, forest conservation and restoration are not only  
292 important for conserving biodiversity, but also for agriculture and ecosystem services.

293 Flower fly communities encompass a variety of larval functional groups (e.g., predator,  
294 endoparasitoids, phytophagous, mycophagous, saprophagous) with specific habitat and food  
295 requirements that are not found in an agricultural matrix (Sommaggio, 1999; Sommaggio and  
296 Burgio, 2007; Jauker et al., 2009). Therefore, we expected that flower flies would also depend on  
297 forest cover to find a high diversity of larval micro habitats; however, alpha diversity did not  
298 respond as expected. Similar results were obtained by Lucas et al. (2017), where the diversity of  
299 the plant community had no significant influence on the diversity or abundance of flower fly  
300 communities. The absence of effects of landscape variables on flower fly alpha diversity may be  
301 related to the fact that adult flower flies do not collect pollen and nectar for their offspring but for  
302 their own resources of carbohydrates, lipids and proteins (in contrast to wasps and bees that need  
303 to return to their nests repeatedly for foraging) and can move linearly into the landscape (Kleijn  
304 and van Langevelde, 2006; Jauker et al., 2009). Lucas et al. (2017) also concluded that flower  
305 abundance has a key influence on Syrphidae abundance and species richness, with increases in  
306 flower fly abundance and species richness with increases in flower resources (also increasing the

307 feeding opportunities for adult flower flies). Moreover, the flower type present in the habitat,  
308 with varying nectar production or symmetry, might affect pollinators' abundance and richness  
309 (Lucas et al., 2017).

310

#### 311 *4.2. Beta Diversity*

312 Wasps and bees were affected by forest cover such that communities located in landscapes with  
313 low forest cover were composed of subsets of the communities located in forested landscapes.  
314 These findings suggest that forest cover moderates dissimilarity of local communities of these  
315 beneficial insect groups, revealing species loss when forest cover is reduced within agricultural  
316 impoverished landscapes. The diversity of both bees and wasps is positively related to flower  
317 diversity (Tylianakis et al., 2006); therefore, coffee monocultural landscapes with low  
318 availability and diversity of floral resources fail to provide resources required by most wasp and  
319 bee species resulting in local extinctions and the potential disruption of pollination and pest  
320 control services within the agricultural matrix. Thus, non-crop habitats like forest remnants act as  
321 key environments for the long-term maintenance of high pollinator and natural enemy diversity  
322 in farmland (Mandelik, 2012; González et al., 2015), providing complementary and constant  
323 supply of multiple resources that are available for short periods in crops (Tschardt et al.,  
324 2012).

325 Although the alpha diversity of flower flies was not affected by any predictor, the turnover  
326 component of beta diversity was influenced by both compositional (landscape diversity) and  
327 configurational (edge density) landscape heterogeneity. Landscape heterogeneity is a key driver  
328 of flower flies communities (Andersson et al., 2013; Haenke et al., 2014; Larrieu et al., 2015;  
329 Villa et al., 2016), wherein species spillover between different crop and non-crop habitats to find

330 a greater variety of resources. High variations in landscape diversity and edge density between  
331 landscapes resulted in species replacement suggesting that pairs of landscapes with high and low  
332 diversity of habitat types and edge density harbor different flower fly species. In the study  
333 region, low landscape diversity and edge density mean that the landscape is mainly composed of  
334 coffee monocultures and forest remnants, while high diverse landscapes can be composed of 10  
335 different crop and non-crop habitat types. Our findings suggest that there are two distinct flower  
336 fly community groups within the regional species pool which rely on different elements of  
337 landscape to access landscape complementation and supplementation. One community group  
338 relies on distinct habitat types and edge environments in high heterogeneous landscapes to gather  
339 all resources necessary to fulfill their needs. The other group seems to thrive in more  
340 homogeneous coffee-forest dominated landscapes, where species probably find a constant supply  
341 of floral resources and specific larval microhabitats within Atlantic Forest remnants (Souza et al.,  
342 2014; Medeiros et al., 2018).

343

#### 344 *4.3. Insect Conservation in Farmland*

345 We suggest that initiatives for the conservation of beneficial insects in the Atlantic Forest  
346 biodiversity hotspot must focus on forest conservation and restoration since high levels of forest  
347 loss lead to the loss of wasp and bee species with potential negative consequences for the  
348 provision of pest control and pollination services in agroecosystems. From the point of view of  
349 ecosystem services, the influence of landscape heterogeneity indicates that conservation  
350 initiatives should include not only forest conservation and restoration, but also agroecological  
351 initiatives to retain crop pollination and biological control, such as sown flower strips at crop  
352 edges (Haenke et al., 2009; Campbell et al., 2017), diversified crop rotations (Bommarco et al.,

2013) and conversion to organic systems (Kremen et al., 2002). Agroecological management and crop diversification make crops more friendly environments for beneficial insects, whereas forest provides multiple resources that are not available in the crop matrix from larval microhabitats for flower flies (Speight and Castella, 2015) to undisturbed nesting sites for wasps and bees (Morato and Martins, 2006). The synergic adoption of these actions can promote both an increase in ecosystem services and the conservation of greater insect diversity including threatened species (Kleijn et al., 2015) as well as forest and crop-associated species.

Despite the growing knowledge of ecosystem services in farmlands, research on how landscape structure and crop management affect biodiversity and associated ecosystem services is still in their infancy in the Neotropical region. Future studies should focus on understanding how organisms at multi-taxon levels and associated ecosystem services are affected by environmental changes at multiple spatio-temporal extents. Beta diversity detected important landscape effects on flower fly communities that were not captured by alpha diversity highlighting the importance of considering differences between communities and their drivers to better understand how landscape structure affects biodiversity. We also highlight that stakeholders' (e.g., farmers and regional planners) demands and perceptions are crucial to understanding interactions between biophysical and socio-economic systems and better integrating concepts of biodiversity and ecosystems services in policy and decision-making (Albert et al., 2014; Palacios-Agundez et al., 2014). Such information derived from real-world case studies is needed for the synergistic implementation of sustainable agricultural practices and biodiversity conservation initiatives as well as the selection of appropriate spatial scales in landscape planning and management.

374

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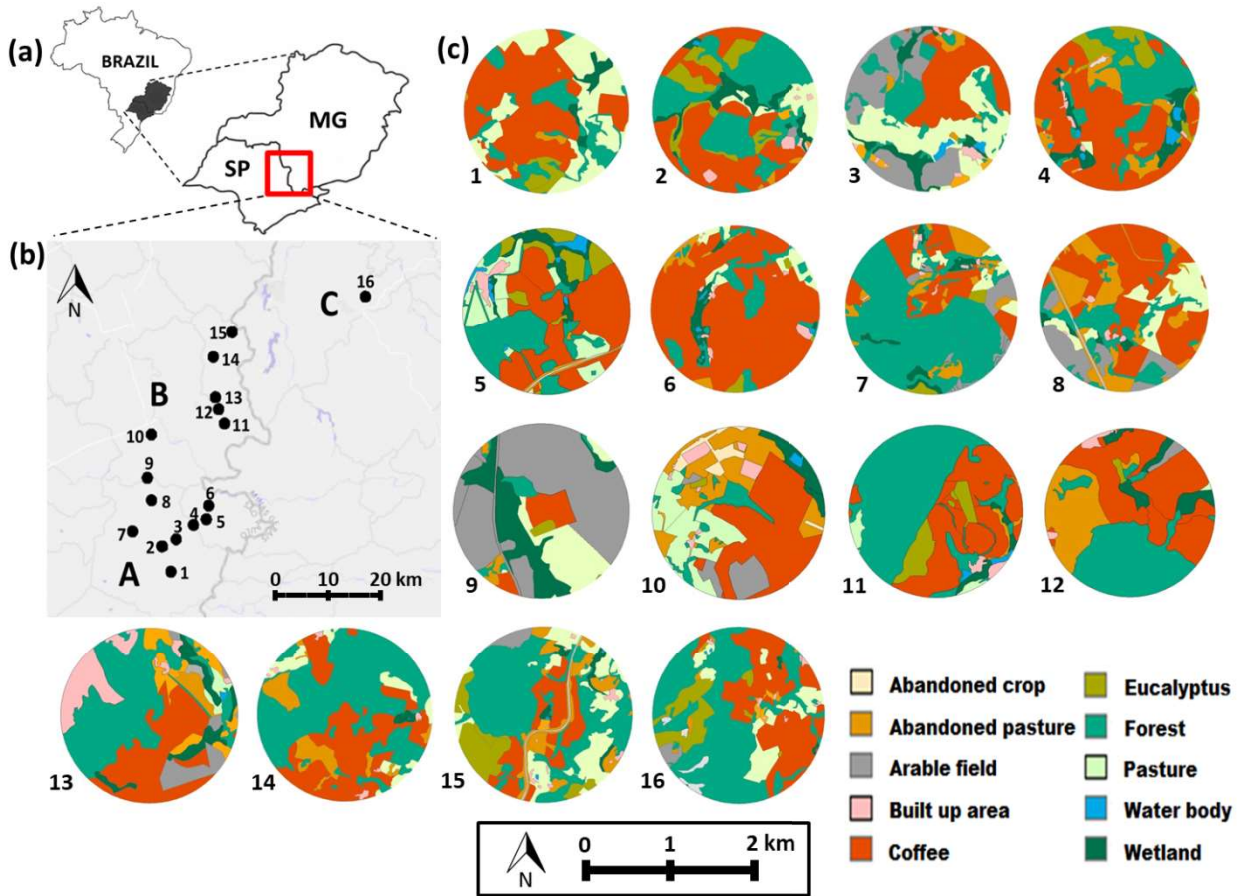
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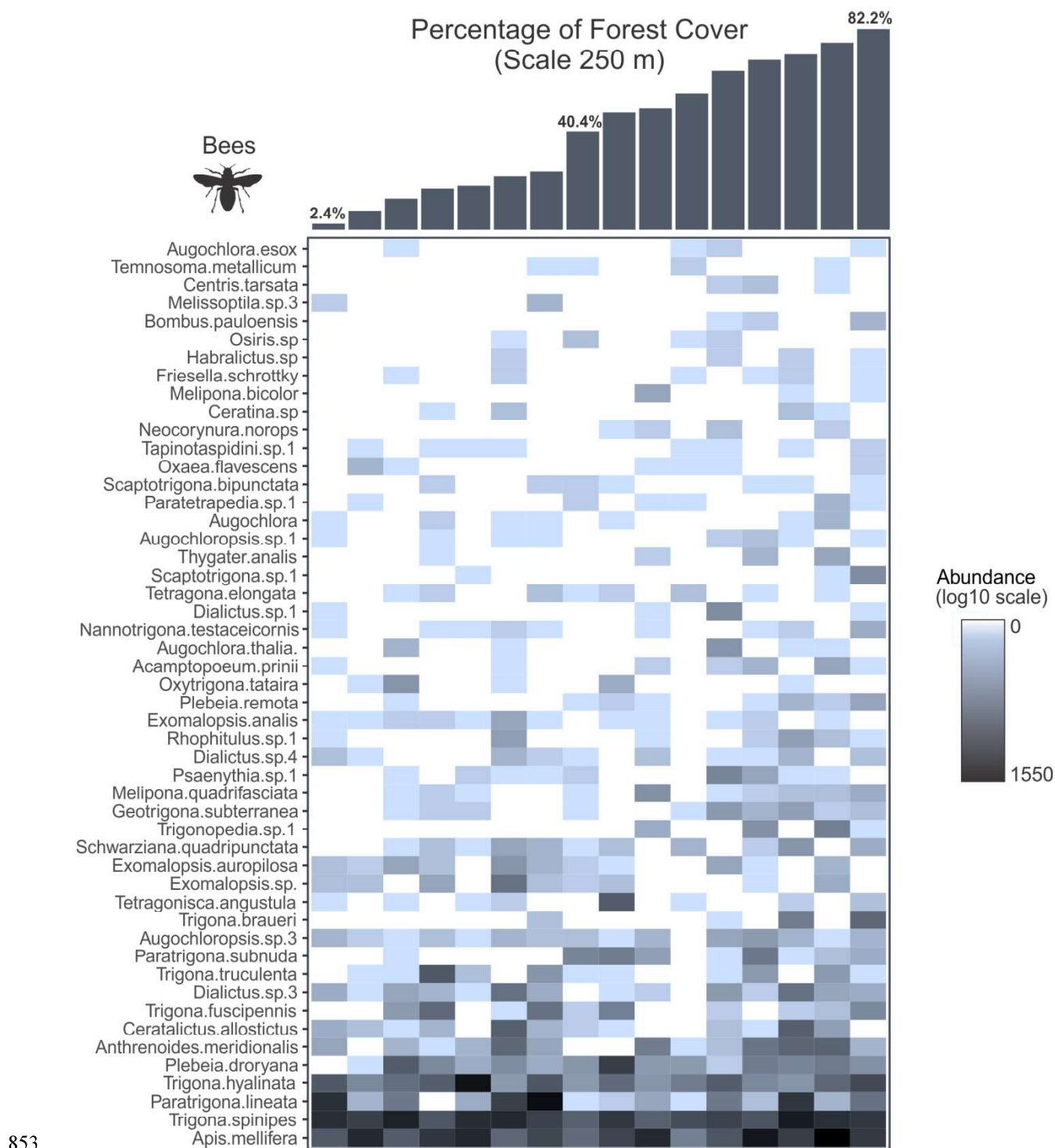
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841 **Fig. 1.** Location of study sites in southeastern Brazil: a) Minas Gerais (MG) and São Paulo (SP)  
 842 states in southeastern Brazil and the study region along the border of SP and MG, b) the sampled  
 843 landscapes (black points) within the study region and c) land use maps of the studied landscape.  
 844 In b) letters A, B and C represent the locations of the following cities: A = Espírito Santo do  
 845 Pinhal, B = São João da Boa Vista, and C = Poços de Caldas. The dark gray line in b) represents  
 846 the border between MG and SP. The land use maps in c) are 1 km radius and show the gradient  
 847 of forest cover from 2.8 % (landscape 9) to 59.3% (landscape 7).

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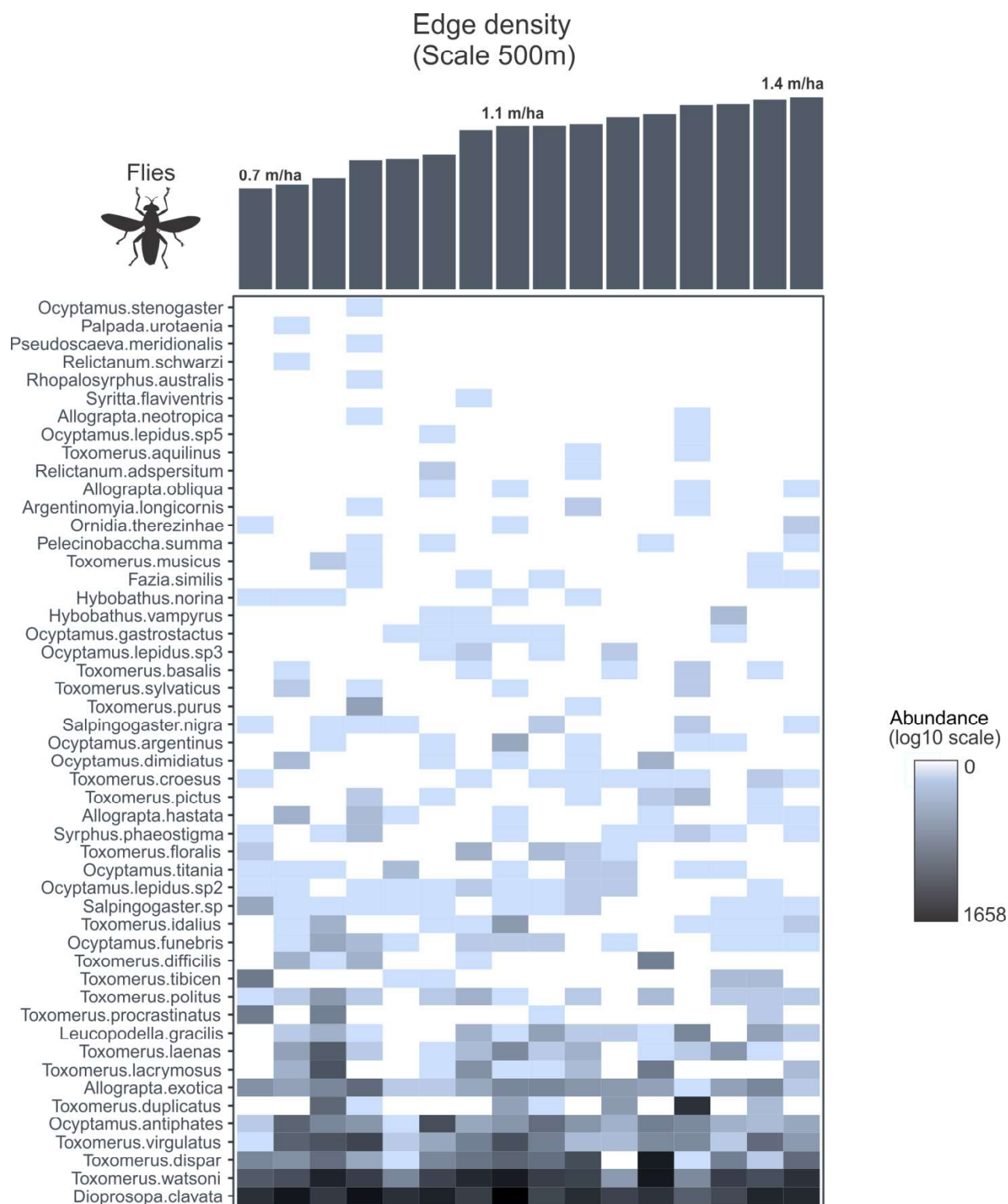


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854 **Fig. 3.** Abundance of the 50 most abundant bee species in coffee producing landscapes across

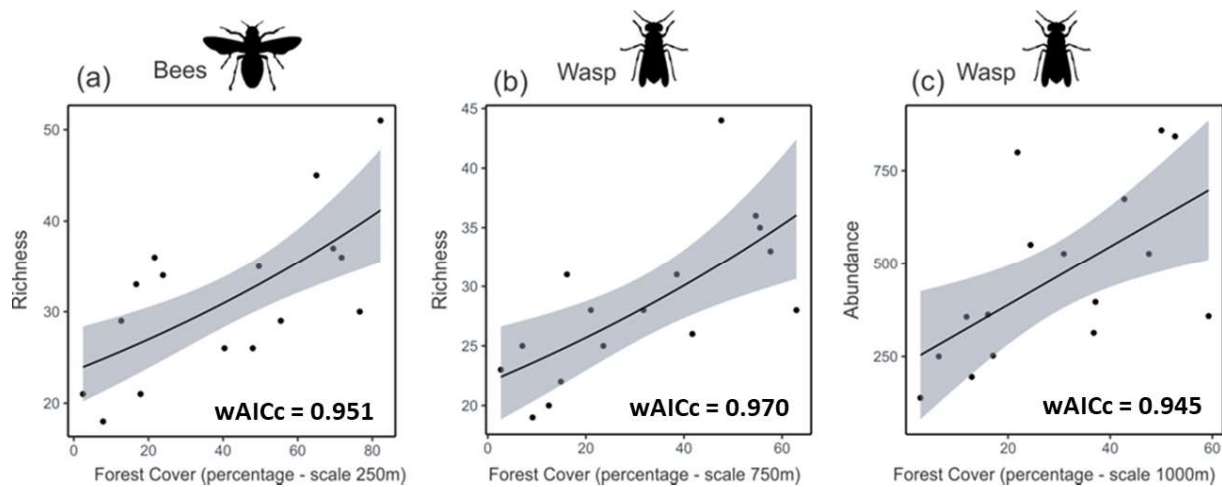
855 the gradient of forest cover at the 250 m scale. Species were sorted by abundance, which was

856 log-transformed to improve visualization.



857 **Fig. 4.** Abundance of the 50 most abundant flower fly species in coffee producing landscapes  
858 across the gradient of edge density at the 500 m scale. Species were sorted by abundance, which  
859 was log-transformed to improve visualization.  
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863 **Fig. 5.** The best-supported models and spatial scales (the highest wAICc value) of the  
864 relationship with forest cover for species richness of bees (a) and wasps (b), and abundance of  
865 wasps (c) in southeastern Brazil. Wasps and bees had similar responses at all spatial extents.

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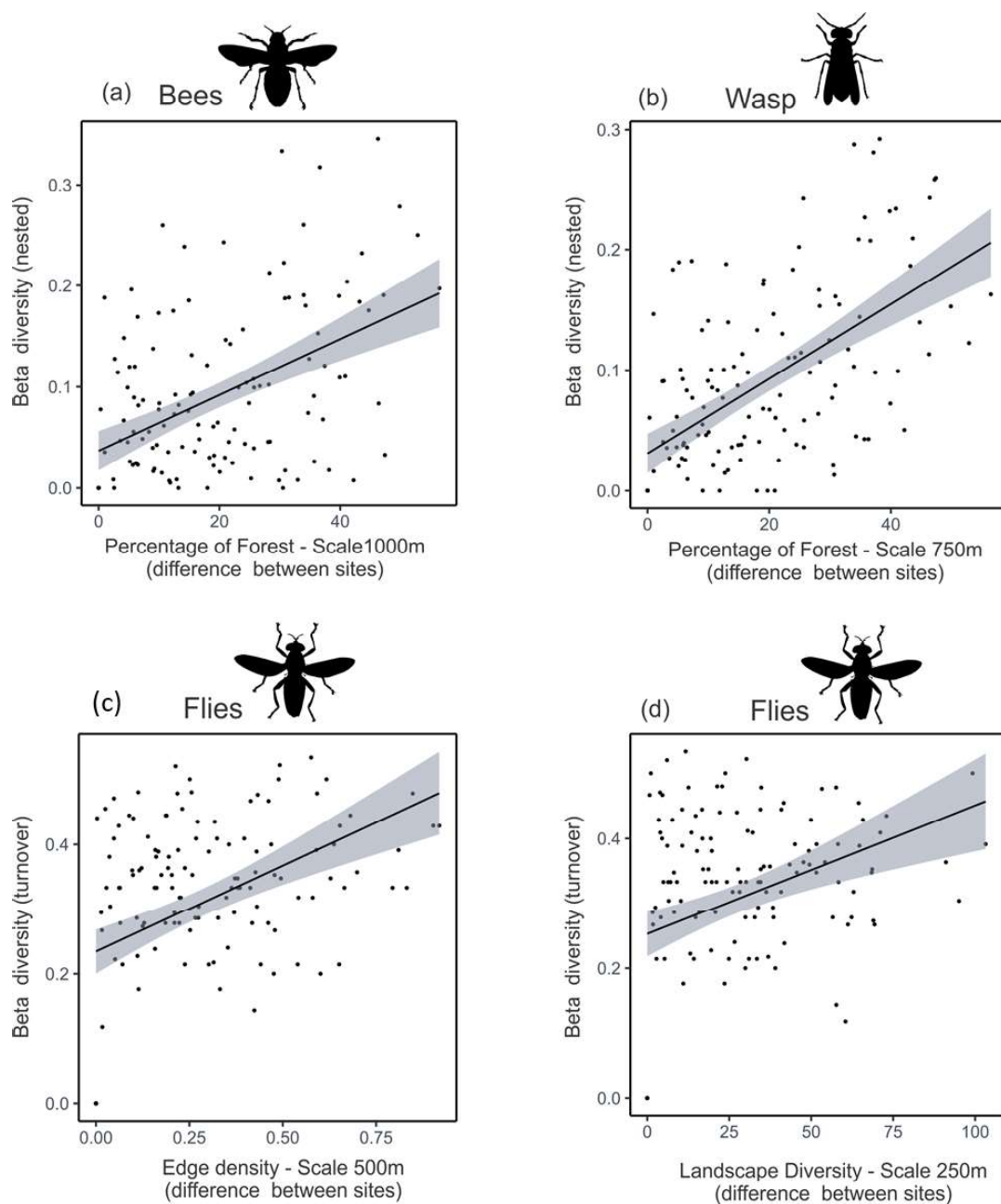
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879 **Fig. 6.** The best-supported models and spatial scales for the nested component of beta  
 880 diversity of bees (a) and wasps (b) versus the differences in forest cover (%) between  
 881 paired landscapes and the turnover component of beta diversity of flower flies (c and  
 882 d) versus the differences in edge density and landscape diversity between paired  
 883 landscapes. Similar results were observed at all spatial extents.

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885 **Table 1**

886 Competing models used to explain patterns of each insect group in coffee producing  
 887 landscapes in southeastern Brazil. Y indicates species richness and abundance of each  
 888 focal group (bees, wasps and flower flies).

Models	Fixed effects
Forest cover	Y ~ % Forest cover
Landscape diversity	Y ~ Shannon diversity index
Edge density	Y ~ Edge density index
Null	Y ~ 1

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909 **Table 2**

910 Plausible models to explain species richness and abundance of wasps, bees and flower flies  
 911 within coffee producing landscapes in southeastern Brazil. wAICc = weight of evidence of the  
 912 models. All selected models have  $\Delta\text{AICc} = 0.0$ . Asterisks indicate the level of significance of the  
 913 models (model fit). (+) indicates positive correlation between response variables and forest cover  
 914 at all four spatial scales.

Taxon	Response variable	Model	Spatial extents (meters)			
			250	500	750	1000
			wAICc	wAICc	wAICc	wAICc
Wasp	Richness	Forest cover (+)	0.937***	0.957***	0.970***	0.961***
	Abundance	Forest cover (+)	0.460***	0.813**	0.770**	0.945**
Bee	Richness	Forest cover (+)	0.951***	0.938***	0.815***	0.890***
	Abundance	Null	-	-	-	-
Flower flies	Richness	Null	-	-	-	-
	Abundance	Null	-	-	-	-

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\*\* P&lt; 0.01; \*\*\* P&lt; 0.001

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922 **Table 3**

923 Coefficients of determination ( $R^2$ ) of the permutation test statistics of each explanatory  
 924 variable and residuals of the redundancy analysis for explaining beta diversity  
 925 components (Nested and Turnover) of wasps, bees and flower flies within coffee  
 926 producing landscapes in southeastern Brazil.

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<b>Taxon</b>	<b>Component</b>	<b>Spatial extents</b>	<b>Forest cover</b>	<b>Edge density</b>	<b>Landscape diversity</b>
<b>Bees</b>	Nested	250	12.44 / 0.45*	-	-
		500	10.29 / 0.42*	-	-
		750	11.50 / 0.45*	-	-
		1000	11/50 / 0.48*	-	-
<b>Wasp</b>	Nested	250	15.85 / 0.51***	-	-
		500	16.15 / 0.49**	-	-
		750	16.83 / 0.55***	-	-
		1000	14.76 / 0.53**	-	-
<b>Flower flies</b>	Turnover	250	-	2.38 / 0.11*	1.99 / 0.14**
		500	-	2.17 / 0.16**	-
		750	-	2.13 / 0.13*	-
		1000	-	2.13 / 0.13*	-

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\* P&lt; 0.05; \*\* P&lt; 0.01; \*\*\* P&lt; 0.001

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939 Supplementary material

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941 List of bee, wasp and flower fly species recorded in 16 coffee producing landscapes in  
 942 southeastern Brazil. Bee family level classification follows Silveira et al., (2002), whereas genus-  
 943 and species-level taxonomy follows Moure et al., (2012), complemented by Almeida (2008). In  
 944 order to identify bees, the following literature was used: Camargo and Moure (1994, 1996),  
 945 Silveira et al., (2002), Michener (2007), Silveira et al., (2002), Almeida (2008), Aguiar and Melo  
 946 (2011), Nemésio and Ferrari (2011), Camargo and Moure (1994, 1996), Ferrari and Silveira  
 947 (2015), Freitas and Silveira (2017), Nemésio and Ferrari (2011). For the identification of  
 948 Polistinae, we used Andena and Carpenter (2012), Richards (1978) and Santos-Junior et al.,  
 949 (2015). And for the identification of Eumeninae, Bohart and Stange (1965), Giordani Soika  
 950 (1990), Willink and Roigk-Alsina (1998), Carpenter and Garcete-Barrett (2002) and Grandinete  
 951 et al., (2015) were used. For the identifications of flower flies, we used Thompson (1999) and  
 952 Mengual et al., (2018) in order to identify the specimens at generic level, and Hull (1949),  
 953 Thompson (1981, 2006), Borges and Couri (2009), Carvalho-Filho and Esposito (2009), and  
 954 Miranda et al., (2014) for the identification of flower fly species of different genera.

WASP SPECIES	N	REFERENCES
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<i>Agelaia multipicta</i> (Haliday, 1836)	3170	Brachygastra Perty, 1833, and description of a new species
<i>Agelaia pallipes</i> (Olivier, 1792)	1731	(Hymenoptera; Vespidae: Epiponini). Am. Mus. Novit. 3753, 1-38.
<i>Agelaia vicina</i> (de Saussure, 1854)	3589	
<i>Alphamenes campanulatus</i> (Fabricius, 1804)	2	Bohart, R.M., Stange, L.A., 1965. A revision of the genus
<i>Alphamenes</i> sp.	4	Zethus Fabricius in the Western Hemisphere (Hymenoptera: Eumenidae). University of California Press, California.
<i>Apoica pallens</i> (Fabricius, 1804)	98	
<i>Brachygastra augusti</i> (de Saussure, 1854)	2	Carpenter, J.M., Garcete-Barrett, B.R., 2002. A key to the
<i>Brachygastra lecheguana</i> (Latreille, 1824)	101	Neotropical genera of Eumeninae (Hymenoptera: Vespidae). Bol. Mus. Nac. Hist. Nat. Parag. 14, 52-73.
<i>Brachygastra mouleae</i> Richards, 1978	2	
<i>Cyphomenes anisitsii</i> (Bréthes, 1906)	1	
<i>Hypalastoroides</i> sp.	1	
<i>Hypancistrocerus</i> sp.1	13	
<i>Hypancistrocerus</i> sp.2	2	
<i>Metapolybia cingulata</i> (Fabricius, 1804)	3	
<i>Mischocyttarus cassununga</i> (von Ihering, 1903)	16	
<i>Mischocyttarus cearensis</i> Richards, 1978	13	
<i>Mischocyttarus drewseni</i> de Saussure, 1857	25	
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	87	Giordani Soika, A., 1990. Revisione degli Eumenidi neotropicale appartenenti ai generi Pachymenes Sauss.,
<i>Mischocyttarus socialis</i> (de Saussure, 1854)	8	
<i>Mischocyttarus</i> sp.1	2	

<i>Mischocyttarus</i> sp.2	6	Santamenes n. gen.,
<i>Mischocyttarus</i> sp.3	1	Brachymenes G.S., Stenosigma
<i>Mischocyttarus</i> sp.4	1	G.S. e Gamma Zav.
<i>Monobia</i> sp.	1	(Hymenoptera). Bolletino dela
<i>Montezumia ferruginea</i> de Saussure, 1852	2	Museo Civico de Storia Naturale
<i>Montezumia petiolata</i> de Saussure, 1855	1	di Venezia. 39, 71-172.
<i>Montezumia</i> sp	1	Grandinete, Y.C., Hermes, M.G.,
<i>Omicron gondwanianum</i> Giordani Soika, 1978	1	Carpenter, J.M., 2015.
<i>Omicron graculum</i> (Zavattari, 1912)	1	Systematics and phylogeny of the
<i>Omicron microscopicum</i> (de Saussure, 1852)	1	neotropical Pachymenes de
<i>Omicron opifex</i> (Brèthes, 1909)	1	Saussure and Santamenes
<i>Omicron ruficolle</i> (Zavattari, 1912)	1	Giordani Soika (Hymenoptera,
<i>Omicron</i> sp.1	3	Vespidae, Eumeninae). Syst.
<i>Omicron</i> sp.2	1	Entomol.40, 365-384.
<i>Omicron</i> sp.3	1	Richards, O.W., 1978. The social
<i>Omicron tuberculatum</i> (Fox, 1899)	15	wasps of the Americas excluding
<i>Pachodynerus guadulpensis</i> (de Saussure, 1853)	12	the Vespinae. British Museum of
<i>Pachodynerus nasidens</i> (Latreille, 1817)	1	Natural History, London.
<i>Pachodynerus serrulatus</i> Brèthes, 1920	1	Santos-Junior, J.N., Silveira,
<i>Pachymenes ater</i> de Saussure, 1852	28	O.T., Carpenter, J.M., 2015.
<i>Pachymenes bipartitus</i> (Fox, 1899)	2	Phylogeny of Protopolybia
<i>Pachymenes ghilianii</i> (Spinola, 1851)	10	Ducke, 1905 and taxonomic
<i>Pachymenes laeviventris</i> (Fox, 1899)	2	revision of the Protopolybia
<i>Pachymenes olympicus</i> (Zavattari, 1912)	3	exigua species-group
<i>Pachymenes sericeus</i> de Saussure, 1852	6	(Hymenoptera: Vespidae,
<i>Parancistrocerus</i> sp.1	1	Polistinae) with description of
<i>Parancistrocerus</i> sp.2	1	four new species. Zootaxa. 3956,
<i>Pirhosigma superficiale</i> (Fox, 1899)	6	151-182.
<i>Polistes billardieri</i> Fabricius, 1804	1	Willink, A., Roig-Alsina, A.,
<i>Polistes cinerescens</i> de Saussure, 1854	6	1998. Revision del genero
<i>Polistes erythrocephalus</i> Latreille, 1813	62	<i>Pachodynerus</i> Saussure
<i>Polistes lanio</i> (Fabricius, 1775)	6	(Hymenoptera: Vespidae,
<i>Polistes melanosoma</i> de Saussure, 1853	2	Eumeninae). Contrib. Am.
<i>Polistes pacificus</i> Fabricius, 1804	8	Entomol. Inst. 30, 1-117.
<i>Polistes simillimus</i> Zikán, 1851	60	
<i>Polistes</i> sp.1	1	
<i>Polistes subsericeus</i> de Saussure, 1854	4	
<i>Polistes versicolor</i> (Olivier, 1792)	259	
<i>Polybia bifasciata</i> de Saussure, 1854	13	
<i>Polybia chrysothotax</i> (Lichtenstein, 1796)	217	
<i>Polybia dimidiata</i> (Olivier, 1792)	31	
<i>Polybia fastidiosuscula</i> de Saussure, 1854	772	
<i>Polybia ignobilis</i> (Haliday, 1836)	501	

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<i>Polybia jurinei</i> de Saussure, 1854	183
<i>Polybia minarum</i> Ducke, 1906	60
<i>Polybia occidentalis</i> (Olivier, 1792)	755
<i>Polybia paulista</i> von Ihering, 1896	951
<i>Polybia punctate</i> du Buysson, 1908	377
<i>Polybia sericea</i> (Olivier, 1792)	236
<i>Protonectarina sylveirae</i> (de Saussure, 1854)	102
<i>Protopolybia exigua</i> (de Saussure, 1854)	4
<i>Protopolybia sedula</i> (de Saussure, 1854)	23
<i>Pseudodynerus griseus</i> (Fox, 1902)	1
<i>Pseudopolybia vespiceps</i> (de Saussure, 1863)	10
<i>Stenonartonia apicipennis</i> (Fox, 1902)	1
<i>Synoeca cyanea</i> (Fabricius, 1775)	14
<i>Zeta argillaceum</i> (Linnaeus, 1758)	5
<i>Zethus fuscus</i> (Perty, 1833)	1
<i>Zethus</i> sp.	2
<b>Total number of wasps recorded</b>	<b>13658</b>

<b>BEE SPECIES</b>	<b>N</b>	<b>REFERENCES</b>
<i>Acamptopoeum prinii</i> (Holmberg, 1884)	18	Aguiar, A.J.C., Melo, G.A.R., 2011. Revision and phylogeny of the bee genus <i>Paratetrapedia</i> Moure, with description of a new genus from the Andean Cordillera (Hymenoptera, Apidae, Tapinotaspidini). Zool J Linnean Soc. 162, 351–442.
<i>Alloscitetica</i> sp.1	3	
<i>Ancyloscelis</i> cf. <i>apiformis</i> (Fabricius, 1793)	1	Almeida, E.A.B., 2008. Revision of the Brazilian Species of <i>Pseudaugochlora</i> Michener 1954 (Hymenoptera: Halictidae: <i>Augochlorini</i> ). Zootaxa. 1679, 1–38.
<i>Anthrenoides</i> cf. <i>meridionalis</i> (Schrottky, 1906)	180	
<i>Apis mellifera</i> Linnaeus, 1758	2141	
<i>Arhysoceble</i> sp.1	1	
<i>Arhysoceble</i> sp.2	2	
<i>Augochlora</i>	14	
<i>Augochlora</i> ( <i>Augochlora</i> ) <i>esox</i> (Vachal, 1911)	6	
<i>Augochlora</i> ( <i>Augochlora</i> ) sp.2	5	
<i>Augochlora</i> ( <i>Augochlora</i> ) sp.3	2	
<i>Augochlora</i> ( <i>Oxystoglossella</i> ) cf. <i>thalia</i> Smith, 1879	16	
<i>Augochlorella</i> sp.1	2	Camargo, J.M.F., Moure, J.S., 1994. Meliponinae neotropicais: Os gêneros <i>Paratrigona</i> Schwarz, 1938 e <i>Aparatrigona</i> Moure, 1951 (Hymenoptera, Apidae). Arquivos de Zoologia. 32, 33–109.
<i>Augochloropsis</i> sp.1	12	
<i>Augochloropsis</i> sp.2	1	
<i>Augochloropsis</i> sp.3	58	
<i>Augochloropsis</i> sp.4	1	
<i>Bombus pauloensis</i> Friese, 1913	8	
<i>Caenohalictus</i> sp.1	2	
<i>Centris</i> ( <i>Hemisiella</i> ) sp.1	1	
<i>Centris</i> ( <i>Hemisiella</i> ) <i>tarsata</i> Smith, 1874	6	
<i>Centris</i> ( <i>Xanthemisia</i> ) sp.1	1	
<i>Centris</i> sp.1	1	Camargo, J.M.F., Moure, J.S., 1996. Meliponini neotropicais: O gênero <i>Geotrigona</i> Moure, 1943 (Apinae, Apidae, Hymenoptera), com especial referência a filogenia e biogeografia. Arquivos de Zoologia. 33, 95–
<i>Cephalotrigona capitata</i> (Smith, 1854)	5	

<i>Ceratalictus allostictus</i> Moure, 1950	109	161.
<i>Ceratina</i> sp.1	10	
<i>Coelioxys</i> sp.1	3	Ferrari, R.R., Silveira, F.A., 2015. The species of Colletinae (Hymenoptera: Colletidae) in the Brazilian state of Minas Gerais. <i>Zootaxa</i> . 3914, 245–274. <a href="http://dx.doi.org/10.11646/zootaxa.3914.3.2">http://dx.doi.org/10.11646/zootaxa.3914.3.2</a>
<i>Colletes rugicollis</i> Friese, 1900	1	
<i>Colletes</i> sp.1	1	
<i>Cyphomelissa diabolica</i> (Friese, 1900)	3	
<i>Diadasina</i> cf. <i>distincta</i> (Holmberg, 1903)	2	
<i>Dialictus</i> sp.1	15	
<i>Dialictus</i> sp.2	1	Freitas, F.V., Silveira, F.A., 2017. Synopsis of the bee genus <i>Thygater</i> Holmberg 1884 (Hymenoptera, Apidae) in the Brazilian state of Minas Gerais, with the description of a new species and a key to all Brazilian species. <i>Zootaxa</i> . 4238, 1–29.
<i>Dialictus</i> sp.3	103	
<i>Dialictus</i> sp.4	24	
<i>Dichranthidium</i> cf. <i>gregarium</i> (Schrottky, 1905)	3	
<i>Epicharis</i> ( <i>Cyphepicharis</i> ) <i>morio</i> Friese, 1924	1	
<i>Euglossa</i> ( <i>Glossura</i> ) <i>imperialis</i> Cockerell, 1922	1	
<i>Exaerete smaragdina</i> (Guérin, 1844)	1	
<i>Exomalopsis</i> ( <i>Exomalopsis</i> ) <i> analis</i> Spinola, 1853	23	Michener, C.D., 2007. <i>The Bees of the World</i> , second ed. John Hopkins University Press, Baltimore.
<i>Exomalopsis</i> ( <i>Exomalopsis</i> ) <i>auropilosa</i> Spinola, 1853	44	
<i>Exomalopsis</i> sp.	51	
<i>Friesella schrottky</i> (Friese, 1900)	9	
<i>Geotrigona subterranea</i> (Friese, 1901)	33	Moure, J.S., Urban, D., Melo, G.A.R., 2012. Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region - online version.
<i>Habralictus</i> sp.1	7	
<i>Hopliphora velutina</i> (Lepeletier & Serville, 1825)	1	
<i>Megachile</i> sp.1	4	
<i>Melipona</i> ( <i>Eomelipona</i> ) <i>bicolor</i> Lepeletier, 1836	10	Nemésio, A., Ferrari, R.R., 2011. Species of <i>Euglossa</i> ( <i>Glossura</i> ) and <i>E.</i> ( <i>Glossuropoda</i> ) (Hymenoptera: Apidae: Euglossina) occurring in the Amazon, including new records for Brazil. <i>Zootaxa</i> . 2885, 1–13.
<i>Melipona</i> ( <i>Melipona</i> ) <i>quadrifasciata</i> Lepeletier, 1836	33	
<i>Melissodes</i> sp.1	1	
<i>Melissoptila</i> cf. <i>minarum</i> (Bertoni & Schrottky, 1910)	2	
<i>Melissoptila</i> sp.1	2	
<i>Melissoptila</i> sp.2	2	
<i>Melissoptila</i> sp.3	6	Silveira, F.A., Melo, G.A.R., Almeida, E.A.B., 2002. <i>Abelhas Brasileiras: Sistemática e Identificação</i> . IDM, Belo Horizonte.
<i>Melitoma segmentaria</i> (Fabricius, 1804)	1	
<i>Mesocheira</i> sp.1	1	
<i>Mesoplia</i> cf. <i>rufipes</i> (Perty, 1833)	3	
<i>Monoeca</i> sp.1	1	
<i>Nannotrigona testaceicornis</i> (Lepeletier, 1836)	15	
<i>Neocorynura</i> cf. <i>norops</i> (Vachal, 1904)	10	
<i>Nomada</i> sp.1	1	
<i>Nomada</i> sp.2	1	
<i>Nomada</i> sp.3	2	
<i>Osiris</i> sp.1	8	
<i>Oxaea flavescens</i> Klug, 1807	11	
<i>Oxytrigona tataira</i> (Smith, 1863)	24	
<i>Paratetrapedia connexa</i> (Vachal, 1909)	0	

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<i>Paratetrapedia flaveola</i> Aguiar & Melo, 2011	1
<i>Paratetrapedia</i> sp.1	13
<i>Paratetrapedia</i> sp.2	3
<i>Paratetrapedia</i> sp.3	2
<i>Paratetrapedia</i> sp.4	2
<i>Paratrigona lineata</i> (Lepeletier, 1836)	704
<i>Paratrigona subnuda</i> Moure, 1947	89
<i>Paroxystoglossa</i> sp.1	1
<i>Partamona</i> sp.1	5
<i>Peponapis fervens</i> (Smith, 1879)	1
<i>Pereirapis</i> sp.1	1
<i>Plebeia droryana</i> (Friese, 1900)	300
<i>Plebeia remota</i> (Holmberg, 1903)	22
<i>Psaenythia</i> sp.1	28
<i>Pseudagapostemon (Pseudagapostemon) pissisi</i> (Vachal, 1903)	2
<i>Pseudaugochlora callaina</i> Almeida, 2008	3
<i>Pseudaugochlora graminea</i> (Fabricius, 1804)	1
<i>Pseudaugochlora indistincta</i> Almeida, 2008	5
<i>Ptiloglossa</i> sp.1	1
<i>Rhopitulus</i> sp.1	22
<i>Rhynocorynura</i> sp.	3
<i>Scaptotrigona cf. bipunctata</i> (Lepeletier, 1836)	16
<i>Scaptotrigona</i> sp.1	14
<i>Schwarziana quadripunctata</i> (Lepeletier, 1836)	46
<i>Sphecodes</i> sp.	3
<i>Tapinotaspidini</i> sp.1	12
<i>Tapinotaspoides serraticornis</i> (Friese, 1899)	5
<i>Temnosoma metallicum</i> Smith, 1853	6
<i>Tetragona elongata</i> (Lepeletier, 1828)	23
<i>Tetragonisca angustula</i> (Latreille, 1811)	52
<i>Tetrapedia</i> sp.1	2
<i>Thygater (Thygater) analis</i> (Lepeletier, 1841)	14
<i>Trichocerapis mirabilis</i> (Smith, 1865)	1
<i>Trigona braueri</i> Friese, 1900	74
<i>Trigona cf. fuscipennis</i> Friese, 1900	191
<i>Trigona hyalinata</i> (Lepeletier, 1836)	893
<i>Trigona spinipes</i> (Fabricius, 1793)	2616
<i>Trigona truculenta</i> Almeida, 1984	96
<i>Trigonisca intermedia</i> Moure, 1990	1
<i>Trigonopedia</i> sp.1	31
<i>Trigonopedia</i> sp.2	1
<i>Trophocleptria</i> sp.1	4
<i>Tropidopedia</i> sp.1	2

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<i>Tropidopedia</i> sp.2	1
<i>Xanthopedia</i> sp.1	2
<i>Xylocopa</i> ( <i>Neoxylocopa</i> ) <i>frontalis</i> (Olivier, 1789)	1
<i>Xylocopa</i> ( <i>Neoxylocopa</i> ) sp.1	2
<i>Xylocopa</i> ( <i>Schonnherria</i> ) <i>varians</i> Smith, 1874	3
<i>Xylocopa</i> sp.2	1
<b>Total number of bees recorded</b>	<b>8393</b>

<b>FLOWER FLY SPECIES</b>	<b>N</b>	<b>REFERENCES</b>
<i>Allograpta exotica</i> (Wiedemann, 1830)	131	Borges, Z.M., Couri, M.S., 2009. Revision of <i>Toxomerus</i>
<i>Allograpta hastata</i> Fluke, 1942	16	Macquart, 1855 (Diptera: Syrphidae) from Brazil with synonymic notes, identification key to the species and description of three new species. <i>Zootaxa</i> . 2179, 1–72.
<i>Allograpta neotropica</i> Curran, 1936	2	
<i>Allograpta obliqua</i> (Say, 1823)	5	
<i>Argentinomyia longicornis</i> (Walker, 1836)	4	
<i>Argentinomyia neotropica</i> (Curran, 1937)	1	
<i>Copestylum lanei</i> (Curran, 1936)	1	
<i>Copestylum</i> sp.1	1	Carvalho-Filho, F.S., Esposito, M.C., 2009. A review of the flower fly genus <i>Ornidia</i> Lepeletier & Serville (Diptera: Syrphidae) with the description of a new species from Brazil. <i>Zootaxa</i> , 2014, 59–64.
<i>Copestylum</i> sp.2	1	
<i>Dioprosopa clavata</i> (Fabricius, 1794)	1955	
<i>Fazia alta</i> (Curran, 1936)	1	
<i>Fazia similis</i> (Curran, 1925)	6	
<i>Hybobathus</i> cf. <i>norina</i> (Curran, 1941)	6	
<i>Hybobathus</i> cf. <i>vampyrus</i> (Hull, 1943)	5	Hull, F.M., 1949. The genus <i>Baccha</i> from the New World. <i>Entomol. Am.</i> 27, 89–291.
<i>Leucopodella bigoti</i> (Austen, 1893)	1	
<i>Leucopodella gracilis</i> (Williston, 1891)	45	
<i>Leucopodella</i> sp.1	1	
<i>Meromacrus nectarinoides</i> (Lynch Arribáizaga, 1892)	1	Mengual, X., Miranda, G.F.G., Thompson, F.C., 2018. Unraveling <i>Ocyptamus</i> and the <i>Baccha</i> legacy (Diptera: Syrphidae): redefinition of groups and new species descriptions. <i>Zootaxa</i> . 4461, 001–044.
<i>Mimocalla erebus</i> (Hull, 1943)	1	
<i>Ocyptamus</i> sp.1	1	
<i>Ocyptamus antiphates</i> (Walker, 1849)	223	
<i>Ocyptamus argentinus</i> (Curran, 1939)	11	
<i>Ocyptamus</i> cf. <i>titania</i> (Hull, 1943)	16	
<i>Ocyptamus dimidiatus</i> (Fabricius, 1781)	11	Miranda, G.F.G., Marshall, S.A., Skevington, J.H., 2014. Revision of the genus <i>Pelecinobaccha</i> Shannon, description of <i>Relictanum</i> gen. nov. and redescription of <i>Atylobaccha flukiella</i> (Curran, 1941). <i>Zootaxa</i> 3819 (1), 1–154.
<i>Ocyptamus funebris</i> Macquart, 1834	23	
<i>Ocyptamus gastrostactus</i> (Wiedemann, 1830)	6	
<i>Ocyptamus lepidus</i> -grp sp.1	1	
<i>Ocyptamus lepidus</i> -grp sp.2	15	
<i>Ocyptamus lepidus</i> -grp sp.3	6	
<i>Ocyptamus lepidus</i> -grp sp.4	1	
<i>Ocyptamus lepidus</i> -grp sp.5	2	Thompson, F.C., 1999. A key to the genera of the flower flies of the Neotropical Region including the descriptions of genera and species and a glossary of
<i>Ocyptamus lepidus</i> -grp sp.6	1	
<i>Ocyptamus stenogaster</i> -grp sp1	1	
<i>Ornidia therezinhae</i> Carvalho Filho & Esposito, 2009	5	

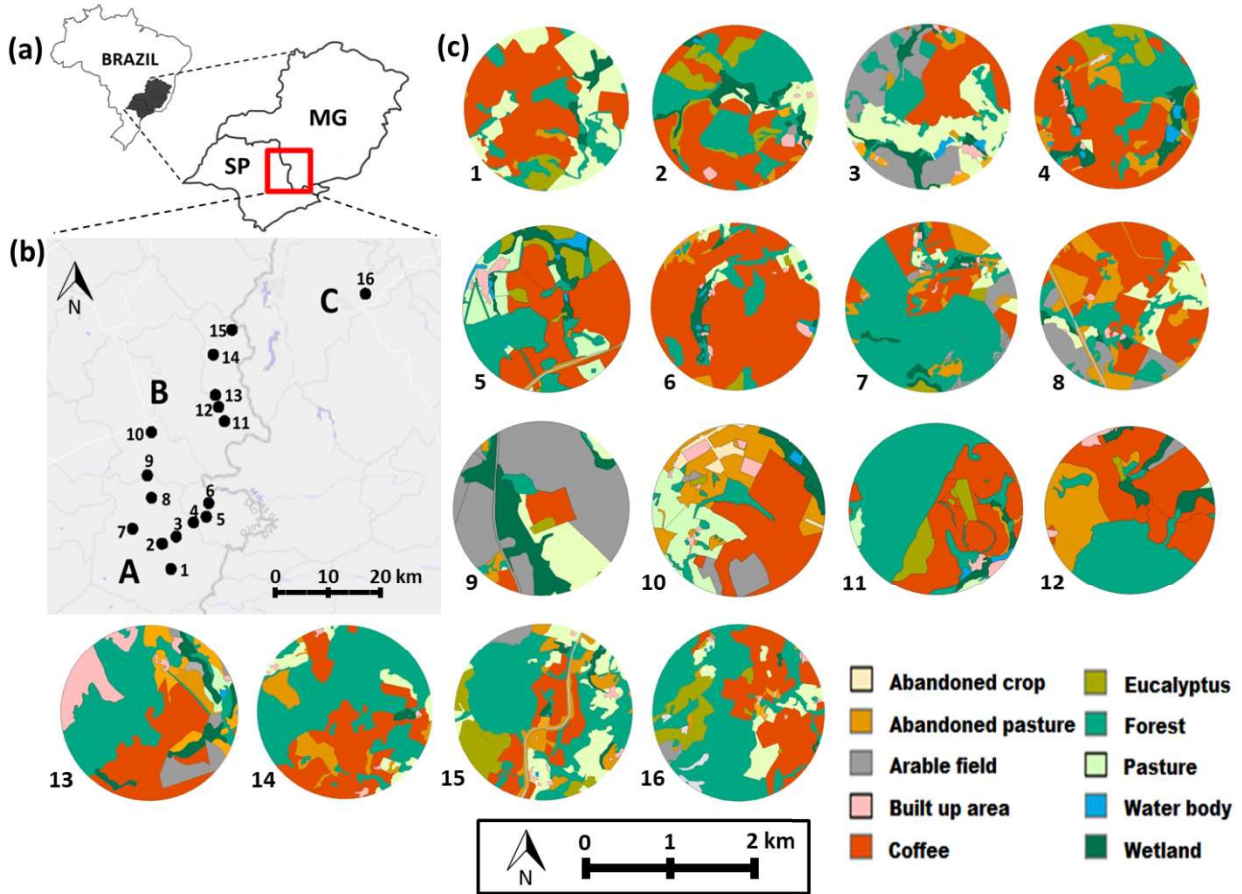
<i>Palpada urotaenia</i> (Curran, 1930)	1	taxonomic terms. Contr. Entomol. 3, 319–378.
<i>Pelecinobaccha summa</i> (Fluke, 1936)	4	
<i>Pseudoscaeva meridionalis</i> (Fluke, 1950)	1	Thompson, F.C., 2006. Primer Taller de Identificación Syrphidae del Neotrópico. Universidad del Valle, Cali.
<i>Relictanum adpersitum</i> Miranda in Miranda et al., 2014	3	
<i>Relictanum</i> aff. <i>schwarzi</i> (Curran, 1939)	1	
<i>Rhopalosyrphus australis</i> Thompson, 2003	1	Thompson, F.C., 1981. The flower flies of the West Indies (Diptera: Syrphidae). Proc. Entomol. Soc. Wash. 9, 1–200.
<i>Salpingogaster nigra</i> Schiner, 1868	10	
<i>Salpingogaster</i> sp.1	20	
<i>Syritta flaviventris</i> Macquart, 1842	1	
<i>Syrphus phaeostigma</i> Wiedemann, 1830	12	
<i>Toxomerus aquilinus</i> Sack, 1941	2	
<i>Toxomerus basalis</i> (Walker, 1836)	6	
<i>Toxomerus croesus</i> (Hull, 1940)	10	
<i>Toxomerus difficilis</i> (Curran, 1930)	23	
<i>Toxomerus dispar</i> (Fabricius, 1794)	396	
<i>Toxomerus duplicatus</i> (Wiedemann, 1830)	126	
<i>Toxomerus floralis</i> (Fabricius, 1798)	12	
<i>Toxomerus idalius</i> (Hull, 1951)	21	
<i>Toxomerus lacrymosus</i> (Bigot, 1884)	75	
<i>Toxomerus laenas</i> (Walker, 1852)	76	
<i>Toxomerus musicus</i> (Fabricius, 1805)	4	
<i>Toxomerus pictus</i> (Macquart, 1842)	10	
<i>Toxomerus politus</i> (Say, 1823)	35	
<i>Toxomerus procrastinatus</i> Metz, 2001	30	
<i>Toxomerus purus</i> (Curran, 1930)	7	
<i>Toxomerus sylvaticus</i> (Hull, 1943)	6	
<i>Toxomerus tibicen</i> (Wiedemann, 1830)	26	
<i>Toxomerus virgulatus</i> (Macquart, 1850)	281	
<i>Toxomerus watsoni</i> (Curran, 1930)	1277	
<b>Total number of flower flies recorded</b>	<b>4984</b>	

955

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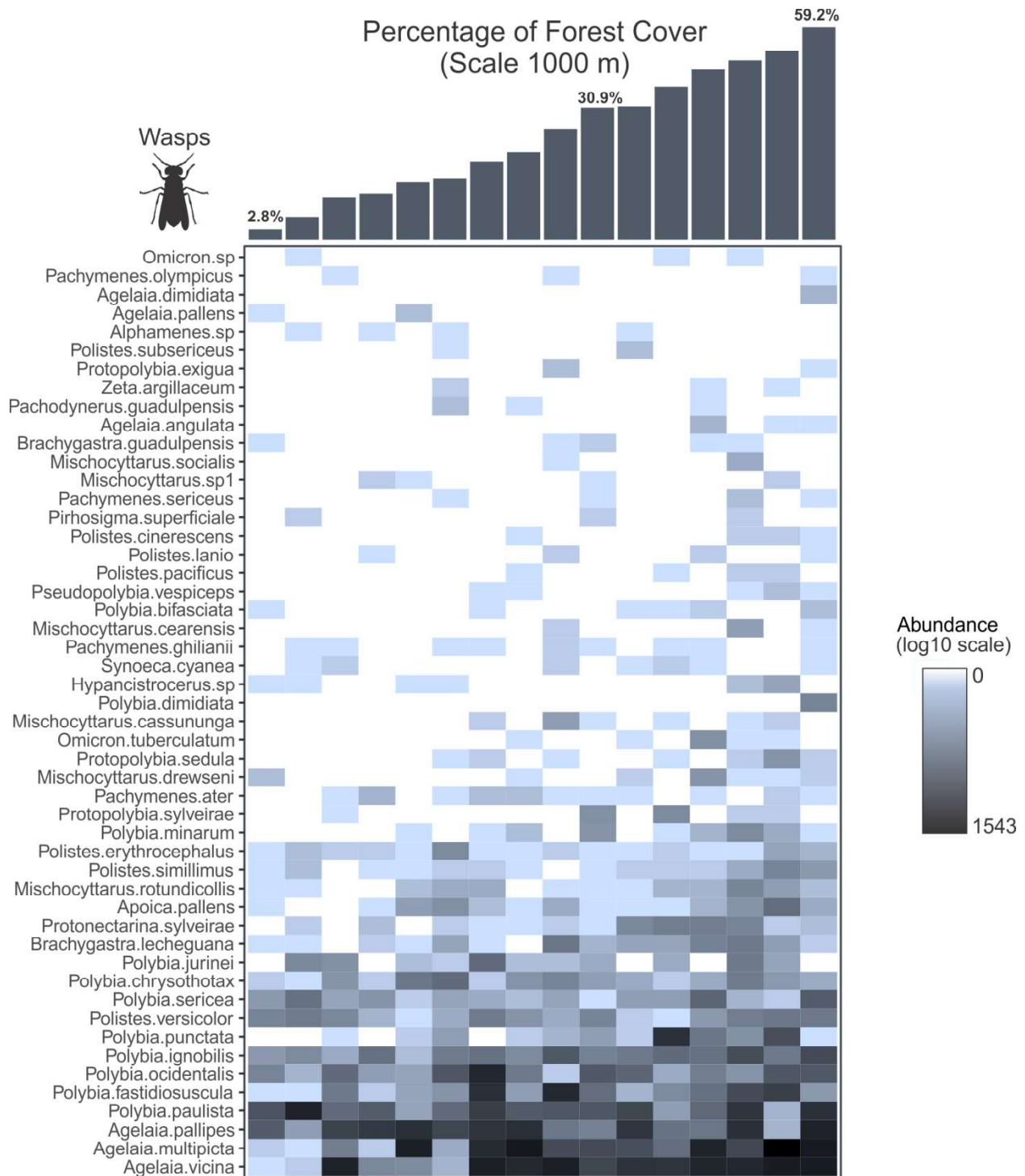
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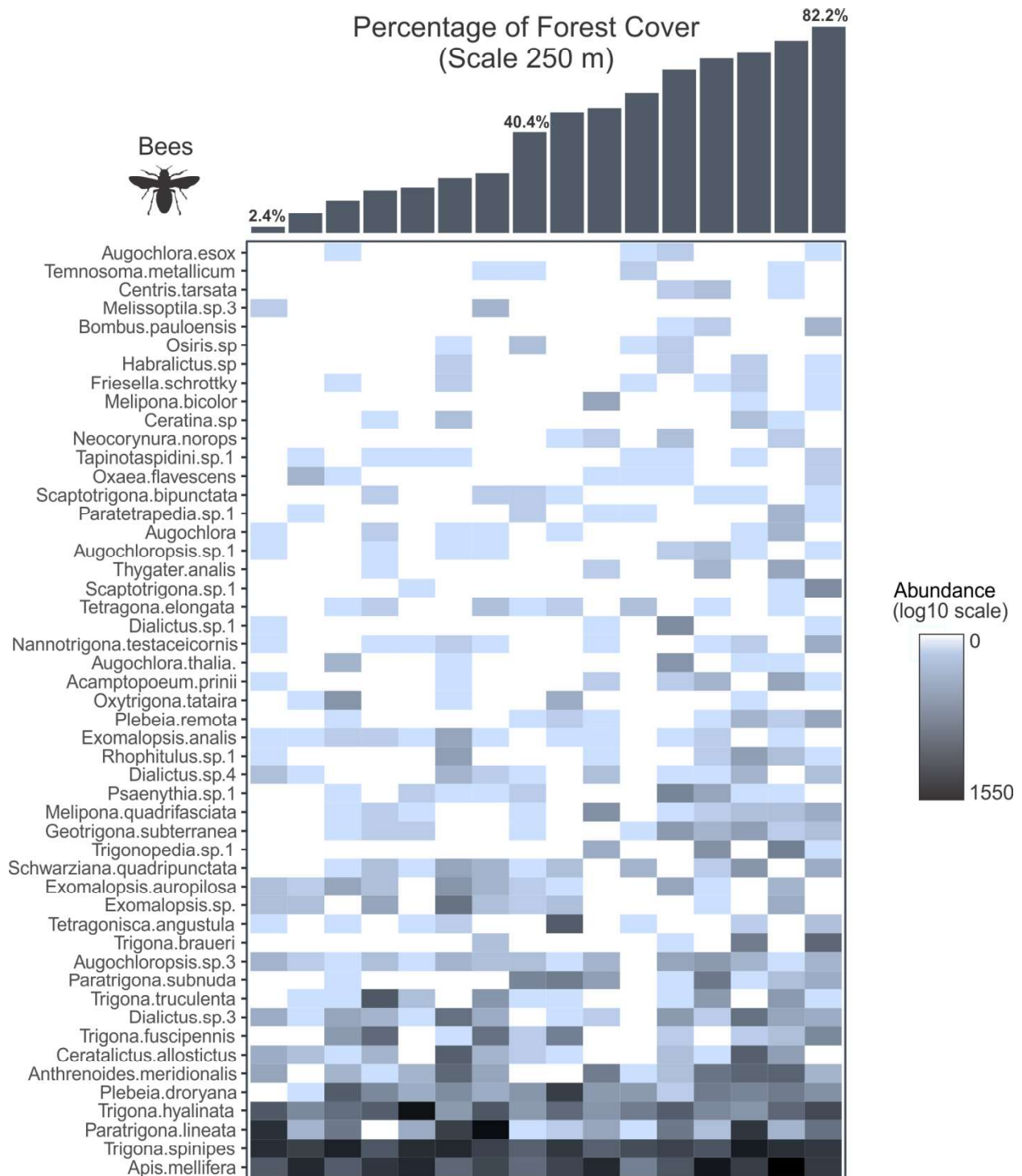


**Fig. 1.** Location of study sites in southeastern Brazil: a) Minas Gerais (MG) and São Paulo (SP) states in southeastern Brazil and the study region along the border of SP and MG, b) the sampled landscapes (black points) within the study region and c) land use maps of the studied landscape. In b) letters A, B and C represent the locations of the following cities: A = Espírito Santo do Pinhal, B = São João da Boa Vista, and C = Poços de Caldas. The dark gray line in b) represents the border between MG and SP. The land use maps in c) are 1 km radius and show the gradient of forest cover from 2.8 % (landscape 9) to 59.3% (landscape 7).

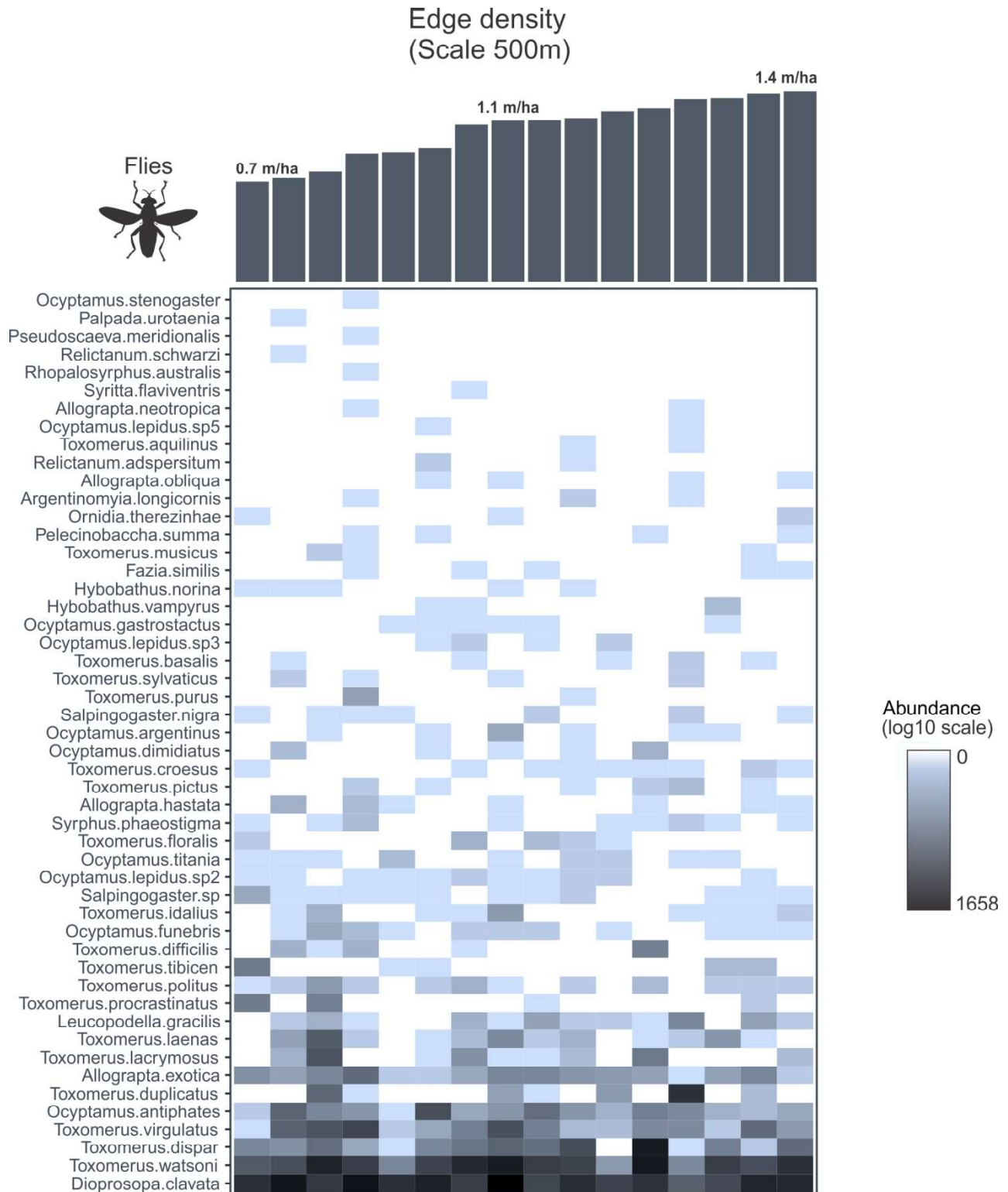




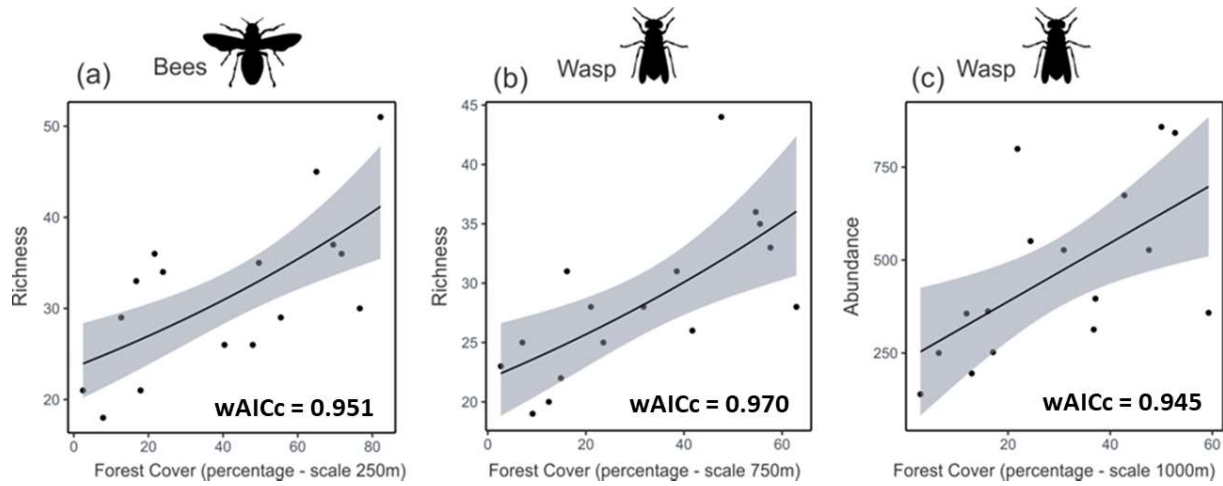
**Fig. 2.** Abundance of the 50 most abundant wasp species in coffee producing landscapes across the gradient of forest cover at the 1000 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.



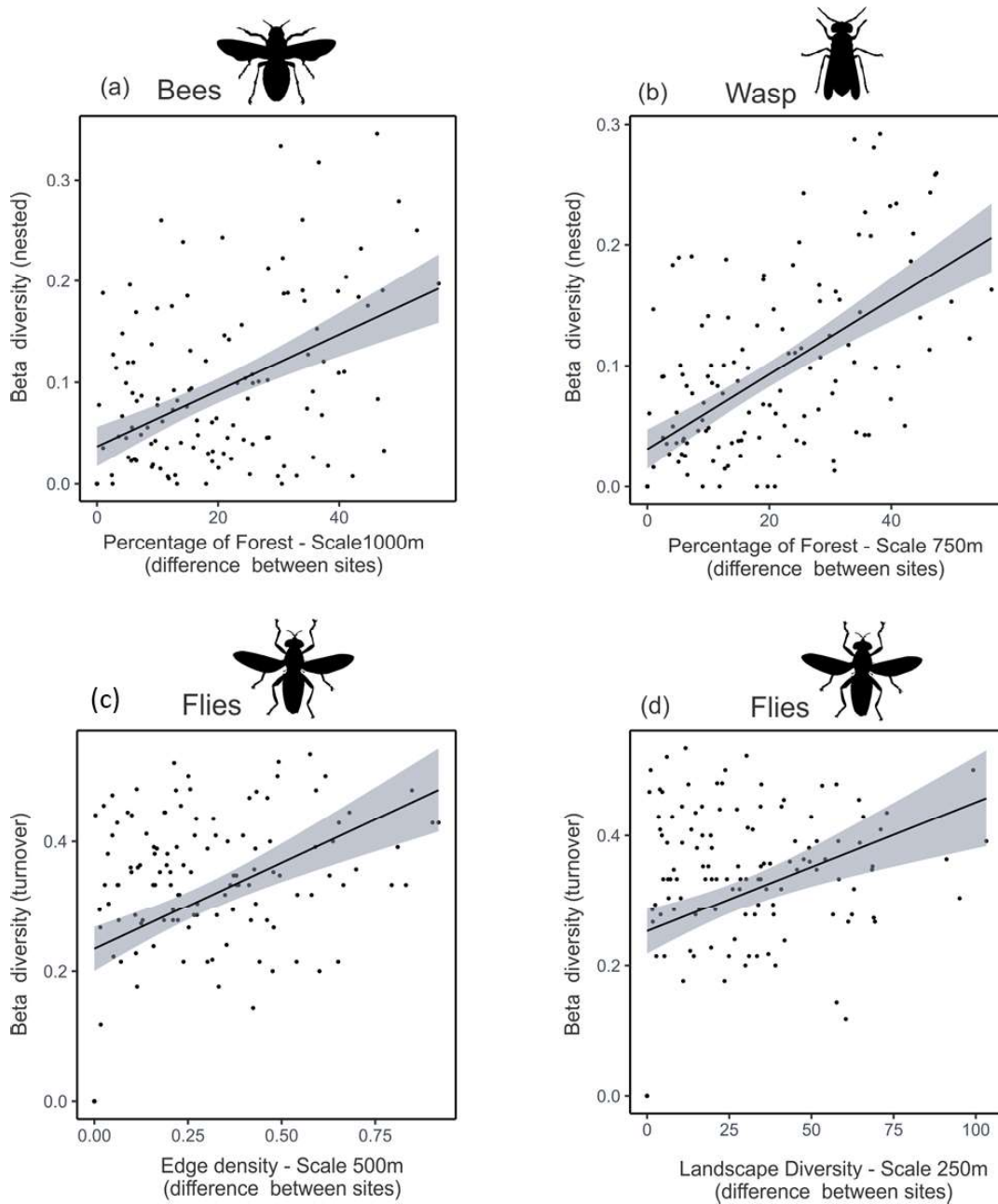
**Fig. 3.** Abundance of the 50 most abundant bee species in coffee producing landscapes across the gradient of forest cover at the 250 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.



**Fig. 4.** Abundance of the 50 most abundant flower fly species in coffee producing landscapes across the gradient of edge density at the 500 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.



**Fig. 5.** The best-supported models and spatial scales (the highest wAICc value) of the relationship with forest cover for species richness of bees (a) and wasps (b), and abundance of wasps (c) in southeastern Brazil. Wasps and bees had similar responses at all spatial extents.



**Fig. 6.** The best-supported models and spatial scales for the nested component of beta diversity of bees (a) and wasps (b) versus the differences in forest cover (%) between paired landscapes and the turnover component of beta diversity of flower flies (c and d) versus the differences in edge density and landscape diversity between paired landscapes. Similar results were observed at all spatial extents.

**Table 1**

Competing models used to explain patterns of each insect group in coffee producing landscapes in southeastern Brazil. Y indicates species richness and abundance of each focal group (bees, wasps and flower flies).

<b>Models</b>	<b>Fixed effects</b>
Forest cover	Y ~ % Forest cover
Landscape diversity	Y ~ Shannon diversity index
Edge density	Y ~ Edge density index
Null	Y ~ 1

**Table 2**

Plausible models to explain species richness and abundance of wasps, bees and flower flies within coffee producing landscapes in southeastern Brazil. wAICc = weight of evidence of the models. All selected models have  $\Delta\text{AICc} = 0.0$ . Asterisks indicate the level of significance of the models (model fit). (+) indicates positive correlation between response variables and forest cover at all four spatial scales.

Taxon	Response variable	Model	Spatial extents (meters)			
			250	500	750	1000
			wAICc	wAICc	wAICc	wAICc
Wasp	Richness	Forest cover (+)	0.937***	0.957***	0.970***	0.961***
	Abundance	Forest cover (+)	0.460***	0.813**	0.770**	0.945**
Bee	Richness	Forest cover (+)	0.951***	0.938***	0.815***	0.890***
	Abundance	Null	-	-	-	-
Flower flies	Richness	Null	-	-	-	-
	Abundance	Null	-	-	-	-

\*\* P < 0.01; \*\*\* P < 0.001

**Table 3**

Coefficients of determination ( $R^2$ ) of the permutation test statistics of each explanatory variable and residuals of the redundancy analysis for explaining beta diversity components (Nested and Turnover) of wasps, bees and flower flies within coffee producing landscapes in southeastern Brazil.

<b>Taxon</b>	<b>Component</b>	<b>Spatial extents</b>	<b>Forest cover</b>	<b>Edge density</b>	<b>Landscape diversity</b>
<b>Bees</b>	Nested	250	12.44 / 0.45*	-	-
		500	10.29 / 0.42*	-	-
		750	11.50 / 0.45*	-	-
		1000	11/50 / 0.48*	-	-
<b>Wasp</b>	Nested	250	15.85 / 0.51***	-	-
		500	16.15 / 0.49**	-	-
		750	16.83 / 0.55***	-	-
		1000	14.76 / 0.53**	-	-
<b>Flower flies</b>	Turnover	250	-	2.38 / 0.11*	1.99 / 0.14**
		500	-	2.17 / 0.16**	-
		750	-	2.13 / 0.13*	-
		1000	-	2.13 / 0.13*	-

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$