1 **Is bigger always better? Neither body size nor aggressive behavior are good**

2 **predictors to measure the degree of specialization of hummingbird interaction**

3 **networks in rocky outcrops**

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24   **Abstract-** Interspecific competition can strongly influence community structure and

25   shape niche breadth and overlap. One of the main factors that determine the

26   hummingbird community structure is competition for food. Hummingbirds functional

27   attributes, such as beak length and body mass, influence nectar acquisition in the

28   flowers, shaping foraging niches according to hummingbird dominance and foraging

29   strategy. This study evaluates how the hummingbirds' functional and behavioral

30   attributes are related to plants assemblage in rocky outcrops' habitats. We tested the

31   following hypothesis: H1) Functional traits (beak length and body mass) are related to

32   the richness and frequency of pollen grain morphotypes carried by hummingbirds; H2)

33   Dominant and territorial hummingbirds carry a lower richness and frequency of pollen

34   types when compared to subordinate hummingbirds, and H3) Hummingbird species

35   carry different types of pollen grains. We conducted the study between September 2018

36   and March 2019 in a *Campo Rupestre* (rocky outcrops) in Southeastern Brazil.

37   Hummingbirds were captured with a trap built based on trapdoors. We recorded their

38   beak size and body masses, marked with commercial bird rings and ink on parts of the

39   body, and then released. Behavioral responses to artificial feeders were collected

40   regarding each visit's time and duration and the outcome of aggressive interactions. The

41   pollen adhered to the body parts was collected and identified in the laboratory. Our

42   results showed that neither body size nor aggressive behaviors influenced pollen

43   richness and frequency in rocky outcrops. Beak length was the most important

44   hummingbirds' attribute that influenced pollen richness, but not pollen frequency. Short-

45   billed hummingbirds carried the greatest richness of pollen grains. Pollen grain richness

46   and frequency were not related to hummingbird body mass or aggressive behavior. The

47   hummingbird-pollen grain interaction network has shown to be generalized in the pollen

48   grain transport. We conclude that hummingbirds' beak length is the central

49   morphological variable to measure pollen grain transport. It has direct implications for

50   the pollination of different plant species.

51   **Keywords:** interaction network, pollen transportation, territorial behavior, Trochilidae.

52

53 **Introduction**

54   Diet specialization, the use of a subset of available resources, is considered

55 one of the major mechanisms permitting species co-occurrence through reduced niche

56 overlap (Chesson 2000; Levine and HilleRisLambers 2009). Diet specialists often have

57 morphological adaptations that allow them to extract resources more efficiently than

58 species with generalist feeding morphologies (Forister et al. 2012).

59   Morphological attributes of hummingbirds, such as beak and tongue lengths,

60 and flowers, such as the corolla size, are directly related to the acquisition of nectar by

61 hummingbirds (Sick 1997, Fogden et al. 2014, Rico-Guevara et al. 2019). When

62 feeding, hummingbirds can carry a certain amount of pollen grains glued to different

63 parts of their bodies (Von Matter et al. 2010, Rico-Guevara et al. 2019). Flowers with a

64 large corolla opening are efficient in depositing pollen grains in the bodies of

65 hummingbirds (Buzato et al. 2000). Body mass is a morphological variable of great

66 importance in hummingbirds' interactions (Feinsinger 1976, Araya-Salas et al. 2018).

67 Short-billed hummingbirds are generally characterized as functionally generalized

68 pollinators, visiting many flowers with short corollas (Von Matter et al. 2010, Fogden et

69 al. 2014, Maruyama et al. 2016). On the other hand, hummingbirds with long and

70 curved beaks are adapted to the exploitation of flowers with long corollas (Collins &

71 Paton 1989, Buzato et al. 2000, Fogden et al. 2014).

72   Body size and body mass have been related to the dominance hierarchy of

73 hummingbirds in different assemblages. They can influence the composition of

74 hummingbird species exploring a given food source, explaining in part the niche

75 specialization observed in this group of birds (Wolf et al. 1976, Feinsinger & Colwell

76 1978, Lopez-Segoviano et al. 2018, Marquez-Luna et al. 2019). Overall, larger

77 hummingbird species tend to dominate, excluding smaller species from high-quality

78   energy resources (Araujo-Silva and Bessa 2010; Justino et al. 2012; Mendiola-Islas et

79   al. 2016, Marquez-Luna et al. 2019). However, smaller species can also establish and

80   defend foraging territories against larger contenders (Wolf et al. 1976; Antunes 2003).

81   Hummingbirds of medium-large body masses are more efficient than… in expelling

82   smaller species from food resources (Lanna et al. 2017, Lopez -Segoviano et al. 2018).

83   Generally, medium-sized hummingbirds and small-medium straight beaks are territorial

84   species, dominant in defense of the food resource (Feinsinger 1976). Thus, it is

85   expected that medium-large body masses hummingbirds present less richness and less

86   frequency of pollen adhered to their bodies when compared to small body masses

87   species.

88   Dominance or subordination of hummingbirds can lead them to adopt two

89   strategies for acquiring their food: 1) territorialism or, 2) trapline (Stiles 1975,

90   Feinsinger & Colwell 1978). Hummingbirds that are subordinate and do not defend

91   territories must forage for greater distances, visiting a more significant number of

92   flower species, which can increase the richness and frequency of pollen grains adhered

93   to their bodies. Since dominant hummingbirds defend and have exclusive access to

94   more energetic food resources, they do not need to forage for greater distances, gaining

95   more benefits than subordinate hummingbirds (Lanna et al. 2017). Dominant and more

96   aggressive hummingbirds may have, then, less richness and less frequency of pollen

97   grains adhered to their bodies (Lanna et al. 2017).

98   Thus, hummingbirds' and plants' morphological attributes can facilitate or

99   hinder the relationship between them when referring to pollination (Sick 1997), which

100   may influence the transport and transfer of pollen grain from one flower to another

101   (Sick 1997, Von Matter et al. 2010).

102   The interaction between plants that provide food to birds (in the form of nectar

103   or fruits) and birds that provide positive services to the plants (in the way of pollen

104   transfer or seed dispersal) has attracted the attention of biologists since Darwin's time

105   (Bascompte and Jordano, 2007, Maruyama et al. 2016, Vizentin-Bugoni et al. 2016).

106   Studies are now using complex interaction network metrics to describe bird-plant

107   mutualistic interactions and are contributing to the development of the conceptual

108   framework of ecological networks (Bascompte and Jordano, 2007; Ings et al., 2009;

109   Heleno et al., 2014; Gu et al., 2015; Rodríguez -Flores et al. 2019, Simmons et al.

110   2019). A pattern is emerging from these studies: the interspecific interactions between

111   plant-hummingbird present an uneven distribution between species (i.e., the degree of

112   dependence of one species to another), with some hummingbirds interacting with

113   several plant species and others interacting with few plant species (Rezende et al. 2007).

114   In the context presented above, in our study, we investigate whether

115   morphological traits (beak length and body mass) and behavioral traits (dominance

116   hierarchy) influence the richness and frequency of pollen grains transported in the

117   hummingbirds in outcrops in southeastern Brazil. We also investigate the influence of

118   these traits in metrics of the plants-hummingbird ecological network. We tested the

119   following hypotheses: H1) The richness and frequency of pollen grains transported in

120   the hummingbird body are influenced by beak length and body mass. We expected

121   short-billed hummingbirds to carry more richness and pollen frequency because they

122   visit more flowers than long-billed hummingbirds. H2) Dominance behavior will

123   influence the richness and frequency of pollen grains in the hummingbird body. We

124   expect that dominant hummingbirds will carry a lower richness and frequency of pollen

125   grain than subordinate hummingbirds because they spend more time feeding and

126   defending a single spot of a preferred resource. H3) The hummingbird-plant interactions

127   will present specializations with a lower overlap in the composition of morphotypes.

128   We expect hummingbirds' morphological and behavioral characteristics to influence the

129   richness and frequency of pollen carried by the birds with a lower overlap in the pollen

130   types composition.

131   **Methods**

132   **Study area**

133   The study was conducted between September 2018 and March 2019 in a

134   *Campo Rupestre* (rocky outcrops) site located in Ouro Preto city, Minas Gerais,

135   Southeastern Brazil (20°22'16.62" S, 43°30'23.43" W). The altitude is 1,397m, and the

136   climate is humid-mesothermal (humid temperate, with dry winters and hot and rainy

137   summers; Álvares et al. 2013).

138   **Hummingbird capture**

139   The study was divided into two stages: 1) capture of hummingbirds, held in

140   September and November 2018, and 2) sampling of hummingbirds' dominance

141   behaviors, which were carried out in January and February 2019, in two periods

142   (morning and afternoon), totaling 195 hours in 30 non-consecutive days. The study

143   summed a sampling effort of 438 hours.

144   Hummingbirds were captured with a trap built based on trapdoors used in

145   hunting wild birds. It consists of a crate 50-60cm wide and 50cm high. All sides of the

146   box were closed with a fine screen (green net). On one side of 60cm, a door was kept

147   open with a 30cm bamboo rod. A string was attached to the door's support rod, which,

148   when pulled, caused the door to close, trapping the hummingbirds inside.

149   Hummingbirds were attracted to the trap's interior with artificial drinking

150   fountains filled with a 25% sugar concentration solution (Lanna et al. 2017). The

151   drinkers were offered from 6:00 am to 6:00 pm, two days before data collection. In the

152 following three days, the hummingbirds were captured from 2:00 pm to 6:00 pm to

153 ensure that these individuals had visited natural flowers during the morning. The

154 sampled individuals were marked with commercial bird rings and ink on three parts of

155 the body (chest, tail, and back). This method was preferred to minimize possible loss of

156 pollen due to the manipulation of hummingbirds in ornithological nets traditionally used

157 in this type of work (Borgella et al. 2001, Avalos et al. 2011). The capture of

158 hummingbirds was authorized by the Brazilian Agency of Environment and Renewable

159 Sources (SISBIO license number 51082-1). We measure each bird's beak length using a

160 digital caliper (model ZAAS 1.004®) and body mass, using a Pesola precision scale

161 (LogNature®).

162   The pollen adhered to the body, forehead, throat, and beak of the individuals

163 was removed using small portions of glycerin gelatin stained with fuchsin (Beattie

164 1971) and stored in Eppendorf for subsequent preparation of the slides for

165 identification. Identification of morphotypes was performed considering the

166 ornamentation, shape, and size of the pollen grains (Murcia & Feinsinger 1996, Fonseca

167 et al. 2016).

168

169 **Hummingbird behavior**

170   We documented the interactions among hummingbirds by conducting

171 behavioral observations at a distance using an artificial drinking fountain to attract

172 hummingbirds (following Lanna et al., 2017). The artificial drinker contained three 200

173 ml (Mr. Pet®) artificial flowers and was filled with a 25% sugar solution. The fountain

174 was remained available throughout the day, and the mixture was always replaced every

175 morning (Lanna et al. 2016, Lanna et al. 2017).

176   Dominance behaviors were recorded from 6 am to 10 am and from 2 pm to 4

177   pm on five consecutive days. Birds were observed at a distance of 8m, using a 10x50

178   binocular (Nikon TX Extreme), and the hummingbirds were identified according to

179   Sigrist (2009). For each observation, we recorded the hummingbird species, the time

180   and duration of each visit, and the outcome of aggressive interactions. The aggressive

181   interactions were characterized by a hummingbird chasing (without contact) and/or

182   attacking other hummingbirds (Cotton 1998, Camfield 2006). The winner was identified

183   as the hummingbird that returned to feed or perch nearby after it had successfully

184   defended and/or chased off another hummingbird from the feeder. For behavioral data

185   collection, the focal sampling was used to record all agonistic behavior occurrences

186   (Altmann 1974).

187   **Statistical analysis**

188   We determined pollen grain frequency in the hummingbirds' bodies by

189   summarizing the abundance of pollen morphotypes in each hummingbird species

190   divided by the number of individuals of each hummingbird species. Morphotypes with a

191   frequency lower than 3% were removed because these types could represent possible

192   contamination of pollen grains from a plant species deposited on the flower by any

193   other floral visitor (Talavera et al. 2001).

194   Pearson's correlation analysis was performed to verify whether the

195   hummingbird's beak length was correlated with its body mass. Subsequently,

196   Generalized Linear Models were built, and, in the case of non-significant variables, the

197   models were reduced to the minimum ideal model (Zuur et al. 2009). We created four

198   models, two related to the hummingbird's morphology, and the other two related to the

199   hummingbird behavior. To analyze if the hummingbird's morphology affected the

200   pollen richness and the frequency of pollen morphotypes (as response variables) and the

201   beak length and body mass as explanatory variables (the error distributions were

202   Poisson and Gaussian, respectively). And, to analyze if the hummingbird behavior

203   affected the pollen richness and the frequency of pollen morphotypes (the response

204   variables), the models had the number of victories in agonistic combats and the time the

205   species spent feeding as explanatory variables (the error distribution were negative

206   binomial and Gaussian, respectively).

207   A mutualistic network was built to evaluate the relationship between the

208   frequency of each pollen grain morphotype transported by the hummingbird. We used a

209   quantitative matrix with hummingbirds in the columns and pollen morphotypes in the

210   lines (Blüthgen et al. 2006). The indexes used were: complementary specialization (H2')

211   and modularity (Q). The H2'index is derived from Shannon entropy, which describes

212   the diversity of interactions (distribution of the interactions' weight in the interaction

213   network). It is suggested to be robust for differences in the sampling effort and the size

214   of the analyzed network (Fründ et al. 2016). Values close to 0 indicate high

215   specialization, and values relative to 1 indicate high generalization (Newman 2006,

216   Blüthgen et al. 2007). The Q index shows the most related species within the network,

217   ranging from 0 to 1. Values close to 0 indicate no connection between individuals, and

218   close to 1 indicates individuals high connected in the network (Dormann and Strauss

219   2014). We used the bipartite package to calculate and analyze the interaction network

220   (Dormann et al. 2009) of the software R version 3.1.0 (R Development Core Team

221   2017).

222   **Results**

223   Eight species of hummingbirds were recorded (Table 1)in the study. Of these,

224   only *Phaethornis eurynome* was not observed during behavioral sampling. Pearson's

225   correlation analysis showed that the length of the beak (mm) and body mass (g) of

226 hummingbirds were not correlated variables. In our study, the highest richness of pollen

227 grain morphotypes was recorded in *Amazilia lactea* (s = 8), and the lowest richness was

228 recorded in *Phaethornis pretrei* (s = 1) (Table 1). The highest frequency of pollen grain

229 morphotypes was found in *Phaethornis pretrei* (n = 96.02%), and the lowest frequency

230 in *Heliodoxa rubricauda* (n = 27.02%) (Table 1). The hummingbird species with the

231 highest body mass was *Eupetomena macroura* (8.5g), and the lowest was *Chlorostilbon*

232 *lucidus* (4.0g) (Table 1). The species with the longest beak was *Phaethornis pretrei*

233 (33.5mm), and the shortest beak was *Amazilia lactea* (14.3mm) (Table 1).

234 _____Insert Table 1_____

235   Forty-seven morphotypes of pollen-grains adhered to the hummingbirds'

236 bodies were identified. With the removal of the morphotypes that had a frequency

237 below 3%, the final richness was 15 pollen grains morphotypes. In this study, the

238 species that obtained the highest number of victories in interspecific and intraspecific

239 agonistic combats was *Heliodoxa rubricauda* (n = 840), and the least amount was

240 *Chlorostilbon lucidus* (n = 1) (Table 1). The species that spent the longest time feeding

241 was *Chlorostilbon lucidus* (35 sec), and the shortest time was *Eupetomena macroura*

242 (1.3 sec) (Table 1).

243   The richness of pollen grain morphotypes was inversely related to the length

244 of the hummingbird beak ($F_{1,\ 6.3218}$ = 25.755, p <0.004) (Figure 1; Table 2) and did not

245 vary with hummingbirds' body mass ($F_{1,\ 0.008}$ = 0.0287, p <0.873). The frequency of

246 pollen grain morphotypes did not vary significantly depending on the length of the beak

247 ($F_{1,\ 828.07}$ = 0.8126, p <0.409) and on the body mass of hummingbirds ($F_{1,\ 521.35}$ = 0.4560,

248 p <0.536) (Table 2).

249 _____Insert Figure 1 and Table 2_____

250   Dominance behaviors in the artificial feeder did not vary with the richness and

251   frequency of pollen grain morphotypes found in hummingbirds (Table 3).

252   Hummingbirds' body mass also did not change concerning the number of victories in

253   agonistic interactions on artificial feeders (Table 3).

254   _____Insert Table 3_____

255   The interaction network between hummingbirds and pollen grain morphotypes

256   showed median values of modularity (Q= 0.533) (Figure 2) and the complementary

257   specialization index H2'(0.675) (Figure 3), indicating medium connectivity between

258   hummingbirds and plants and a tendency for generalization of these relations.

259   _____Insert Figures 2 and 3_____

260

Discussion

262   Our results showed that neither body size nor aggressive behaviors influenced

263   pollen richness and frequency in rocky outcrops. Beak length was the most crucial

264   hummingbirds' attribute that influenced pollen richness, but not pollen frequency. We

265   expected short-billed hummingbirds to carry a higher richness of pollen morphotypes

266   with higher frequency because they need to visit more flowers than long-billed

267   hummingbirds. We found that the length of the beak of hummingbird species proved to

268   be the most important morphological trait related to the richness of plants visited

269   (measured by the pollen grains richness) and less important to explain the frequency of

270   pollen grains transported. This greater richness of pollen grains is probably the result of

271   an adjustment of the hummingbirds' beak with the flowers they feed on (Sick 1997,

272   Fogden et al. 2014, Rico-Guevara et al. 2019). Due to that adjustment, the interaction

273   network between hummingbirds and pollen grains was moderately specialized,

274   reflecting the importance of hummingbirds in different plants' pollination process.

275   The short-billed hummingbird species in our study (*A. lactea*, *T. glaucopis,*

276 and *C. lucidus*) carried a higher pollen grain richness. These species are considered

277 functional generalists because they can visit a great diversity of native and exotic plants

278 (Maruyama et al. 2016), mainly plants with short corollas (Maruyama et al. 2016).). At

279 the other extreme, the longest, curved-billed hummingbird species (*P. eurynome* and *P.*

280 *petrei*) carried a lower richness of pollen grains when compared to the intermediate-

281 billed species (*A. cirrochloris*, *H. rubricauda,* and *E. macroura*) and to the short-billed

282 (*A. lactea*, *T. glaucopis,* and *C. lucidus*). These two *Phaethornis* hummingbirds are

283 considered specialized in feeding nectar from long tube bromeliad flowers found in the

284 Atlantic forest, restricting access to nectar for short-billed species hummingbirds

285 (Buzato et al. 2000, Maruyama et al. 2016, Sonne et al. 2019). The morphological

286 match and phenological overlap are important factors predicting plant–hummingbird

287 interactions, showing the role of these characteristics in organizing plant–hummingbird

288 communities (Brown & Bowers 1985, Vizentin-Bugoni et al. 2014). Thus, the lowest

289 richness of pollen grains found in *Phaethornis* species may reflect the lack of long,

290 tubular flowers in the study area, remembering that our study was conducted in the

291 *Campo Rupestre* area where more plant species have open and narrow corollas (Giulietti

292 et al. 1997).

293   On the other hand, the frequency of pollen grains was not significantly related

294 to the beak length. Our results indicate that the potential pollinators' effectiveness may

295 be mediated more closely by the abundance of pollinators (hummingbirds) than the

296 trait-matching compatibility. The potential pollinators are the pollinator's total

297 contribution to the plant's fitness, measure, for example, by the number of pollen grains

298 deposited (Schupp et al. 2017, Missagia and Alves 2018). Although hummingbirds'

299 beak was not a good predictor to explain a higher frequency of pollen grains in our

300   study, the result points to a tendency for long, curved-billed species to carry a higher

301   frequency of pollen grains than short-billed species. However, it is crucial to consider

302   the environment where the present study was carried out. A rocky outcrop is a less

303   complex and more unpredictable habitat; although deemed a megadiverse, it presents

304   less flower diversity than forest habitats (Silveira et al. 2016). Maybe, more complex,

305   flower-diverse habitats, like forests and urban environments, could increase the

306   frequency of pollen carried by short-billed hummingbirds, due mainly to differences in

307   plant (flower) composition (Maglianesi et al. 2014).

308   The richness and frequency of pollen grain morphotypes were not influenced

309   by the hummingbirds' body masses, as expected. Lighter hummingbirds, such as the

310   Phaethornithinae (*P. eurynome* and *P. pretrei*) and the Trochilinae (*C. lucidus*, *A.*

311   *lactea,* and *T. glaucopis*), were expected to carry more morphotypes and more pollen

312   grains. Species that are subordinate avoid combats with more dominant species.

313   Therefore, they need to visit more plant species, which would increase the chances of

314   having more pollen of different plant species in their bodies. Thus, hummingbirds' body

315   mass and dominance behavior were not variables that explained the differences in the

316   number of pollen grains transported. In contrast, some authors cite that the behavior and

317   the body mass are the most important variables for structuring the hummingbird

318   assembly in a resource spot (Sick 1997, Forgden et al. 2014, Lanna et al. 2017). More

319   aggressive and dominant species can share the territory with more peaceful and less

320   hostile species (Stiles 2008, Lanna et al. 2017, Lopez-Segoviano et al. 2018). Marques-

321   Luna et al. (2019) found that the dominant species of hummingbirds in the assemblage

322   (*L. clemenciae* and *C. thalassinus*) weigh more than 6 g, representing the largest

323   hummingbird species in the community. The higher rank within the dominance

324   hierarchy was associated with large body size species, which coincides with that

325   reported by different authors (Dearborn 1998; Justino et al. 2012). However, the bigger

326   species are not always the most aggressive and dominant, observed by Martin and

327   Ghalambor (2014) and Márquez-Luna et al. (2019), where smaller species of

328   hummingbirds dominated bigger ones in some of the interactions.

329   The interaction network between hummingbirds and pollen grain morphotypes

330   tended to be generalized, with an overlap of pollen grain morphotypes carried by each

331   hummingbird species. Most of the hummingbirds recorded in the present study

332   belonged to the Emerald clade (*Chlorostilbon*, *Eupetomena*, *Amazilia*, *Thalurania,* and

333   *Aphantochroa*), formed by evolutionarily recent and more generalist hummingbirds.

334   The *Phaetornis* genus belongs to the Hermit clade, formed by evolutionarily older and

335   more specialized hummingbirds (Rodrigues-Flores et al. 2019). Because of the

336   hummingbird species involved, we expected and observed in this study a heterogeneous

337   connectivity distribution, with a tendency to generalize the species interaction in the

338   network, because most hummingbirds visited more plant species and few hummingbirds

339   visited few of the plants.

340   Hummingbirds present a preference in selecting their food resource (Stiles

341   1975, Feinsinger et al. 1979, Maruyama et al. 2014, Lanna et al. 2017). This

342   specialization can be related to the flower morphology (Maglianesi et al. 2014, Fonseca

343   et al. 2016) and to hummingbird morphology (beak length) (Maglianesi et al. 2014).

344   However, it was shown that hummingbirds relaxed their specialized relationships and

345   became less specific in their interactions in non-forested areas (Morrison and

346   Mendenhall, 2020). Our research was conducted in a *Campo Rupestre* area, where trees

347   are rare, reinforcing our result of a lower specialization in our interaction network.

348   Thus, most hummingbirds explored many flowers, ornithophilous or not, while the

349   hermits remained to explore few plant species.

15

350   We conclude that the hummingbirds' beak's length is the most important

351   variable to explain the richness, specialization, and segregation in the transport of pollen

352   grains by hummingbirds in rocky outcrops. As suggested by Maglianesi et al. (2014),

353   hummingbird species' morphological traits influence ecological specialization patterns.

354   The beak's morphology seems to be more important than body mass in determining the

355   niche partition within the community. In this way, the beak of hummingbirds is of great

356   importance for the pollination process of many species of plants.

357

358   **Acknowledgments**

363

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547 **Table 1:** Physical attributes of the recorded hummingbirds, average time spent feeding,

548 and the number of victories in the agonistic interactions while serving in the drinking

549 fountain. Richness and frequency of pollen grains morphotypes transported by each

550 hummingbird species.

Hummingbird species	Number of individuals	Pollen morphotype richness	Pollen morphotype frequency (%)	Victories in agonistic interactions	Time spent feeding (sec)	Beak length (mm)	Body mass (g)
Amazilia lactea	11	8	41.68	73	9.4	14.3	4.3
Aphantochroa cirrochloris	3	4	95.00	453	7.3	17.0	6.5
Chlorostilbon lucidus	2	5	38.89	1	35.0	15.3	4.0
Eupetomena macroura	1	4	40.06	37	1.2	21.0	8.5
Heliodoxa rubricauda	8	4	27.02	840	6.7	17.4	7.0
Phaethornis eurynome	2	2	95.97	-	-	33.5	5.3
Phaethornis pretrei	8	1	96.02	14	3.7	28.8	5.7
Thalurania glaucopis	14	7	94.01	225	8.5	15.7	4.8

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553 **Table 2:** Results of the GLM models for richness and abundance of pollen grains

554 morphotypes collected in hummingbirds according to the functional attributes body

555 mass plus beak length.

Response variable	Explanatory variable	DF	Deviance	F	Estimative	P
Pollen richness	Beak length	1	6.322	25.755	-0.126	0.004**
Pollen richness	Body mass	1	0.009	0.029	0.014	0.873
Pollen frequency	Beak length	1	828.07	0.813	2.338	0.408
Pollen frequency	Body mass	1	521.35	0.456	-6.208	0.536

556 ** Statistical significance; DF = degrees of freedom

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558 **Table 3**: Richness and frequency of pollen grain morphotypes as a function of the total

559 time spent in feeding and the number of victories in agonistic interactions.

Response variable	Explanatory variable	DF	Deviance	F	Estimative	P
Pollen frequency	Time spent feeding	1	446.17	0.407	2.410	0.551
Pollen frequency	Victories	1	131.83	0.106	-0.033	0.760
Pollen richness	Time spent feeding	1	8.696	1.913	0.336	0.225
Pollen richness	Victories	1	0.105	0.021	-0.002	0.890

560 DF = degrees of freedom

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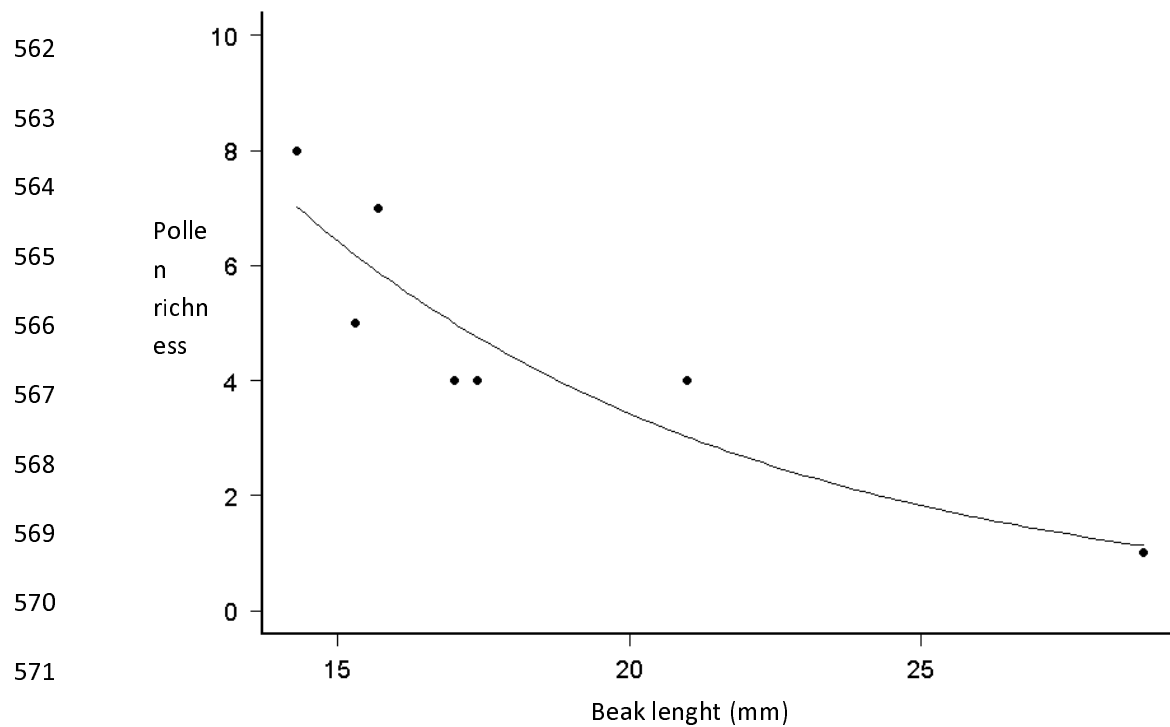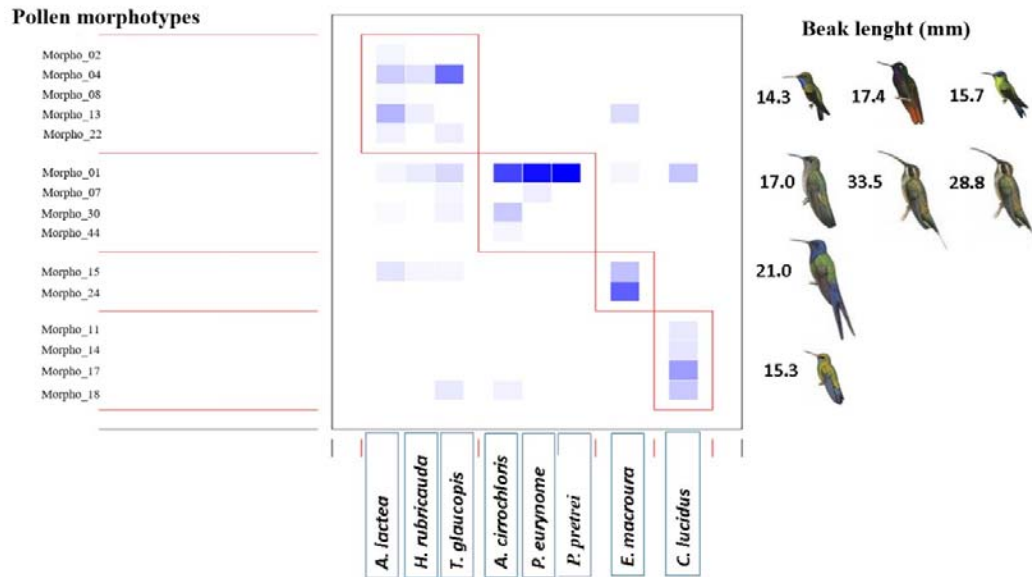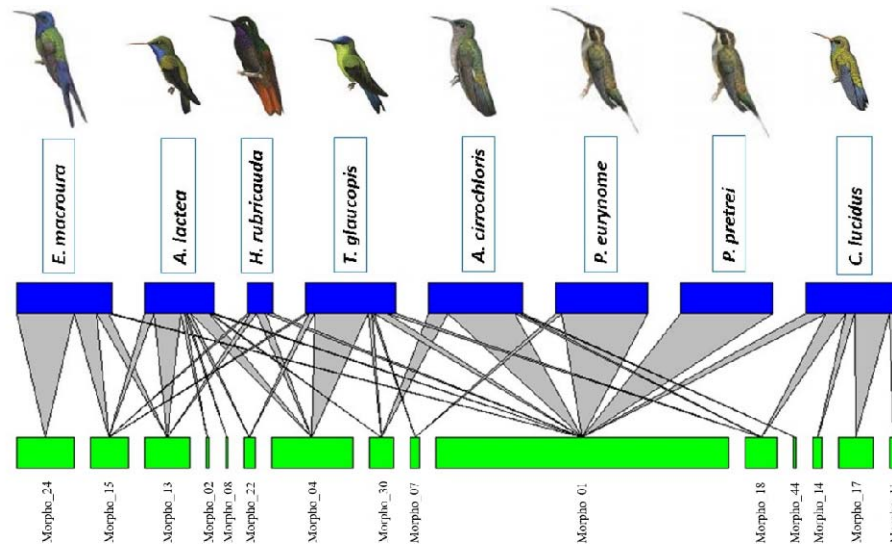563
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Figure 1: Relationship between richness of pollen grains morphotypes carried by hummingbirds and the length of the beak.

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Figure 2: Interaction network (modules) formed by the hummingbird species and the pollen grains morphotypes concerning their beak lengths. The most vibrant colors represent the highest frequency of pollen carried by them.

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Figure 3: Interaction network representing the overlapping trophic niche of hummingbirds based on the frequency of pollen grain transported by them.

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