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1 Fine-scale temporal dynamics of flower visitors
2 sheds light on insect-assemblage overlap
3 between sexes in a dioecious Ecuadorian palm.
4

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21

22 **Abstract**

23 Background: Dioecious plants generally display sexual dimorphism in male and female floral traits
24 resulting in differential pollinator attraction. Consequently, the partitioning of floral visitors
25 between male and female flowers and their timing of visits to both sexes is of critical importance
26 to ensure plant's reproductive success. Palm inflorescences are visited by abundant and diverse
27 insect communities, yet the temporal patterns of insect visits on both sexes remain poorly known.

28 Methods: We characterized the composition of a community of flower-visiting arthropods
29 associated with the dioecious ivory palm (*Phytelephas aequatorialis*, Spruce) in a pre-montane
30 forest of Ecuador. We monitored the temporal variations in insect visits along the flowering of 12
31 inflorescences (8 female and 4 male) using interception traps recovered every 4-hours.

32 Results: We report 59 morphospecies in the arthropod community, dominated by three beetle
33 families: Staphylinidae, Nitidulidae and Curculionidae. Male inflorescences were more abundantly
34 visited than female, but visitors of the latter were taxonomically more diverse. Among the 16
35 pollinator candidates identified, 9 visited both inflorescence sexes synchronously at dusk /night
36 whereas the others did so asynchronously during the day.

37 Conclusion: Our study provides new insights into the pollination mechanism of *P. aequatorialis*.
38 We found evidence of differential pollinator attraction between floral sexes, which may be
39 explained by the sexual dimorphism of both flowers. Synchronicity in dusk/night visits of both
40 inflorescence sexes suggests a sexual synchronization of the signal used to attract pollinators.

41 **Keywords:**

42 *Areaceae, Phytelephas aequatorialis*, beetles, sexual dimorphism, cloud forest

43

44 1. INTRODUCTION

45 Pollination is one of the most vital ecosystem services for humanity as it enhances production in
46 75% of globally important crops and allows the survival of nearly 90% of flowering plants (Klein
47 *et al.* 2007, Ollerton *et al.* 2011). This service is increasingly threatened due to habitat loss, use of
48 pesticides, and climate change, which all affect the populations of pollinators (Potts *et al.* 2016). A
49 sustained pollination service for both cultivated and wild ecosystems requires better documenting
50 and understanding pollination mechanisms, particularly for plant-pollinator interactions, to identify
51 key levers on which act to maintain them. Identifying the actors at play during pollination (i.e. most
52 effective pollinators) is even more critical in tropical areas where local human communities rely
53 on both cultivated and natural plant species for their socio-economical activities (De la Torre *et al.*
54 2008). Nevertheless, the complexity of the fragmented landscape and the paucity of ecological
55 knowledge for most pollinator species and their interactions with plants in the tropics, as well as
56 their dynamics in space and time, impede a sound analysis of the sustainability of pollination
57 service in the face of ongoing global changes (Vamosi *et al.* 2006, Kaiser-Bunbury *et al.* 2017).

58 Among pollination systems, those involving dioecy - a reproductive system where
59 individuals in a population are subdivided into female and male entities - are particularly
60 remarkable yet poorly known. Widespread across plant families, dioecy is considered to be
61 relatively rare compared to other reproductive systems (6% of flowering plant species), even
62 though the proportion of dioecious plants tends to increase in tropical regions (Renner & Ricklefs
63 1995, Matallana *et al.* 2005, Renner 2014, Käfer *et al.* 2017). An interesting characteristic of
64 numerous dioecious plants is that male and female individuals exhibit distinctive morphological,
65 physiological and life-history traits, which have been explained by differential requirements in
66 resource acquisition and allocation, genetic constraints, environmental responses as well as

67 contrasted investments in reproduction (Barrett & Hough 2013). Dioecious plants are unable to
68 self-pollinate due to sex separation and thus require an external vector, generally animal, for pollen
69 transport (Bawa 1980, Renner & Ricklefs 1995). Consequently, reproductive traits of males and
70 females can respond differently to pollinator-mediated selection (Waelti *et al.* 2009), which may
71 manifest by a sexual dimorphism in floral display (number and size of flowers), scent (quantity and
72 quality) and accessibility to pollinators (Ashman 2009, Barrett & Hough 2013). Sexual dimorphism
73 has important consequences for the reproductive success because a differential attraction of
74 pollinators between sexes could affect the direction and the intensity of pollen movement from
75 male to female reproductive organs. For example, male plants commonly possess small individual
76 flowers aggregated in inflorescences resulting in a larger floral display than females, and generally
77 provide pollen, nectar, and shelter in exchange of visits. By contrast, females are often described
78 as non-rewarding (Ashman 2009, Barrett & Hough 2013). Therefore, a change in pollinator
79 occurrence (diversity, abundance, and/or phenology) could modify the pollen movement rate
80 between sexes, potentially reducing the reproductive success of the plant. Detailed information on
81 the communities of visitors associated with both sexes in dioecious plants is mandatory to
82 understand the consequences of any variation in pollinator occurrence.

83 Dioecy *sensu stricto* is relatively uncommon in the Arecaceae family (palms), but appear to be
84 a recurrent trend in the Neotropical palms when considering temporal and functional dioecy. .
85 Dioecy is the dominant sexual system in two of the 5 subfamilies, including the Ceroxyloideae in
86 which sexual dimorphism manifests in species as a spectacular difference in both size and aspect
87 of male and female inflorescences (Henderson 1986, 2002, Ervik *et al.* 1999, Barfod *et al.* 2011,
88 Nadot *et al.* 2016). The inflorescences of palms are often visited by a highly diverse and abundant
89 insect fauna, among which only a few species have an efficient role in pollination (Núñez-

90 Avellaneda & Rojas-Robles 2008, De Medeiros *et al.* 2019, Barbosa *et al.* 2020). Many palm
91 species have evolved reproductive strategies involving the emission of floral scent and
92 thermogenesis for the attraction of effective pollinators (Küchmeister *et al.* 1998, Knudsen *et al.*
93 2001, Meekijjaroenroj *et al.* 2007, Pincebourde *et al.* 2016). Among them, the most effective
94 species are generally beetles (commonly derelomine weevils (Curculionidae, Derelomini) and
95 mystropine sap beetles (Nitidulidae, Mystropini)). These insects have evolved a mutualistic
96 relationship with the host palm: adults feed on pollen and females oviposit inside staminate
97 inflorescences ; larvae achieved their development by feeding on decaying staminate tissues after
98 dehiscence , whereas pistillate flowers are pollinated by deception, i.e. without providing any
99 apparent rewards (Listabarth 1992, 1996, Anstett 1999, Sakai 2002, Barfod *et al.* 2011, De
100 Medeiros *et al.* 2019). In these deceptive systems, the synchronicity between pollinators' activity,
101 pollen availability in staminate (male hereafter) inflorescences, and stigma receptivity in pistillate
102 (female hereafter) inflorescences is of critical importance to ensure plants' reproductive success.
103 Although the arthropod fauna and the ecological role of individual flower-visiting species has
104 thoroughly been studied for several palm species (for example *Ceroxylon* sp. ; Kirejtshuk &
105 Couturier 2009, Carreño-Barrera *et al.* (2020) and *Mauritia flexuosa* ;Mendes *et al.* (2017) , our
106 knowledge of the insect communities interacting with most of dioecious palm flowers, and their
107 fluctuations in abundance and composition during the flowering remains fragmentary.

108 In this study, we characterized the composition and the daily activity patterns at a fine temporal
109 scale of a community of flower-visiting arthropods associated with the dioecious ivory palm
110 (*Phytelephas aequatorialis*, Spruce) in a pre-montane forest of Ecuador. *Phytelephas*
111 *aequatorialis*, locally known as “tagua”, exhibits an extreme sex-related divergence in floral
112 morphology (Ervik *et al.* 1999, Montúfar *et al.* 2013). As other species in the tribe

113 Phytelephantoidae, staminate inflorescences are large, conspicuous, while pistillate inflorescences
114 are smaller and visually concealed (see methods section for more detailed in the floral morphology
115 of *P. aequatorialis*). The composition of female floral scents is unknown in *P. aequatorialis* (Ervik
116 *et al.* 1999), but could presumably use the same attractant odor as male flowers as both sexes in
117 other phytelephantoid species produce a qualitatively and quantitatively similar, abundant emission
118 of scent (Ervik *et al.* 1999).. Both sexes are thermogenic, producing heat at the bud stage. Male
119 inflorescences cool down immediately after anthesis whereas heat production continues several
120 days after anthesis in females (Pincebourde *et al.* 2016). The partitioning of floral visitors between
121 female and male inflorescences and the daily activity of these visitors has not been thoroughly
122 studied.

123 The two main objectives of this study were: 1) To study community richness and abundance of
124 insect visitors associated with male and female inflorescences of the ivory palm. We expect a
125 certain degree of similarity in the assemblage of flower-visiting arthropod between both sexes as a
126 consequence of pollinator sharing, but with differences due to the extreme differences in floral size
127 and morphology, that could result in divergences in both scent composition and visual cues, – our
128 study aimed at quantifying the degree of overlap in the communities of visitors between the two
129 sexes.; and 2) to document the temporal variations of these communities. We expected that the
130 temporal pattern of visits of candidate species for pollination should be synchronized between both
131 sexes, assuring pollen movement between sexes.

132

133 2. METHODS

134 2.1. STUDY MODEL AND SITE – This study took place in a 10-ha plot in the *Reserva Otongachi*,
135 a mid-altitude forest located between 850 to 1150 m a.s.l. in the Western Ecuadorian slopes (0°19'
136 S, 78°56' W). The study model and the experimental site are detailed in Supplementary Information
137 S1.

138 2.2. FLOWER-VISITOR TRAPPING AND IDENTIFICATION – We monitored insect
139 communities visiting the inflorescences of twelve ivory palm trees (eight females and four males)
140 between October 16 and December 16, 2018. We sampled flower-visiting insects every 4 hours
141 from the beginning (bud opening) to the end (color change and scent of rotting tissue) of the
142 anthesis of these inflorescences by using interception traps. Details on trap design, trapping
143 protocol, dates and climatic conditions during the study period are provided in Supplementary
144 information S2. Briefly, interception traps were made of a transparent foil sheet (H = 57 cm and L
145 = 26 cm) held vertically in the vicinity of each focal inflorescence and equipped with a collector
146 filled with water and a wetting agent acting as a surfactant to prevent captured arthropods from
147 escaping. Each trap was installed from the start of the flower anthesis, and trapping stopped within
148 24 to 48 hours and 28-52h after the beginning of the anthesis in male and female palms respectively.
149 The collectors were retrieved and replaced by new ones every four hours. Overall, we collected
150 114 samples of 4-hour trapping periods during this survey, with 85 samples collected on female
151 inflorescences and 29 collected on male inflorescences. This totals 456 hours of trapping (female:
152 340 hours, mean 42.5 ± 7.7 h per inflorescence; male: 116 hours, mean 29 ± 7.6 h per
153 inflorescence).

154 All arthropods were assigned to morphospecies, with insects further classified into a
155 taxonomic family according to Delvare and Aberlenc (1989). Insect vouchers were deposited in
156 the QCAZ entomological collection at Pontificia Universidad Católica del Ecuador in Quito,

157 Ecuador. Macrophotos are available at <https://www.inaturalist.org/projects/biodiversity-in-the->
158 [tagua-palm-forests-of-ecuador](https://www.inaturalist.org/projects/biodiversity-in-the-tagua-palm-forests-of-ecuador).

159 2.3. DATA ANALYSES

160 2.3.1. SAMPLING COMPLETENESS – We used the Fisher’s alpha index to assess whether the
161 sampling intensity was sufficient to capture most of the diversity of the insect community-(Slik *et*
162 *al.* 2015) for both inflorescence sexes. This index is widely used to characterize species abundance
163 patterns and is less sensitive to changes in sample size than any other index of diversity (Devaurs
164 & Gras 2010). For each sex, we plotted Fisher’s alpha indices against sampling effort, i.e., the
165 increase in the number of 4-hours period sampling. As the sampling effort of individuals increases,
166 a rarefaction curve typically approaches an asymptote when further species are recorded, while the
167 rarest or occasional visitors remain unrecorded (Gotelli & Colwell 2001, Chao & Chiu 2016).

168 2.3.2. MULTIMODAL SPECIES ABUNDANCE DISTRIBUTION MODEL – We explored the
169 pattern of Species Abundance Distributions (SADs) according to sex. SAD is a useful tool to
170 identify species’ commonness and rarity in ecological communities (McGill *et al.* 2007, Matthews
171 & Whittaker 2014). For each floral sex, we built a Preston plot and we evaluated the presence of
172 different modes (peak in species number for a given class of abundance) in the SADs using a
173 Gamma-binomial model, also known as “gambin” (Ugland *et al.* 2007, Matthews, Borregaard, *et*
174 *al.* 2014), proposed in the eponymous R package (Matthews *et al.* 2018). The gambin model
175 generally provides a good fit for the empirical SAD dataset (Matthews *et al.* 2018). We plotted
176 unimodal, bimodal, and trimodal gambin models according to each floral sex, and then evaluated
177 the quality of the fit using the Akaike’s Information Criterion (AIC).

178 2.3.3. The idea behind the multimodal SADs is that different modes represent different categories
179 of species grouped according to given biological traits (Matthews & Whittaker 2015, Antão *et al.*
180 2017). We used the SAD to distinguish rare morphospecies, with no or a few role in pollination,
181 from abundant morphospecies more likely involved in the pollination of the palm. Additionally,
182 we measured the body length and body width of each morphospecies from available photos taken
183 with a stereomicroscope and a graduated scale in the background (Table S1). TEMPORAL
184 VARIATION IN FLOWER-VISITING ARTHROPODS – We tested whether the daily activity of
185 the main morphospecies differed along the day and between male and female inflorescences by
186 analyzing the timing of their visits to both floral sexes. We first selected the morphospecies with a
187 potential role as pollinators by excluding those only trapped in only one floral sex. Then, we ranked
188 these potential pollinators according to their abundance and retained all those that exceed a
189 threshold >99% of total abundance on both inflorescence sexes.

190 We carried out a non-metric multidimensional scaling (nMDS) using the Bray-Curtis index to
191 examine the dissimilarity in assemblages of the main morphospecies between the 4-hours periods
192 of the day and the flower sexes. We assessed the difference in composition of the flower-visiting
193 community between floral sexes at each period using an analysis of similarity (ANOSIM, Clarke
194 1993).

195 Finally, we predicted the trend in morphospecies abundance on male and female inflorescences
196 along the 4-hours periods of the day. We fitted a mixture model to the observed abundance of
197 captures at each 4-hours period with a zero-inflated negative binomial distribution using the *pscl*
198 package in R (Jackman, 2008). The zero-inflated model with binomial negative distribution
199 provided a better fit than the generalized linear model (GLM) with Poisson or negative binomial
200 distribution, or than the zero-inflated model with Poisson distribution, as judged by a lower AIC

201 value. The negative binomial distribution structure allowed accounting for overdispersion resulting
202 in large differences in morphospecies captures among 4-hours periods and individual
203 inflorescences. The zero-inflated component controlled for the large number of zero counts in
204 observations. We modeled the number of flower-visitor captures as the response variable, and
205 visitor species (categorical, 16 morphospecies), 4-hour trapping periods (categorical, 6 levels), and
206 inflorescence sex (categorical, female and male) and their pairwise interactions as predictor
207 variables.

208 **3. RESULTS**

209 3.1. COMMUNITY COMPOSITION AND SAMPLING COMPLETENESS – Overall, 30,591
210 floral visitors belonging to 59 morphospecies were trapped over the whole sampling period. In
211 terms of morphospecies abundance, Coleoptera represented 81.1% of the total assemblage,
212 followed by Hymenoptera (2.9%) and Diptera (2.5%). Coleoptera were dominated by three
213 taxonomic families, namely Staphylinidae (47.3% of the Coleoptera), Nitidulidae (10.4%), and
214 Curculionidae (8.6%). As 99% of Acari (13.1% of the assemblage) were captured in only one 4-
215 hours sample, we discarded them from relevant taxa for pollination (Table S1).

216 The plateau of the Fisher's alpha index curve after ten 4-hours sampling periods indicated
217 that our sampling effort was sufficient to capture most of the diversity of flower-visiting arthropods
218 for both floral sexes (Figure 2b). The diversity of flower visitors was higher for female
219 inflorescences compared to male inflorescences (Figure 2b; 57 vs. 44 morphospecies,
220 respectively). Curves interpolating the abundance relative to the sampling effort showed higher
221 capture rates on male inflorescences, reinforced by the extrapolation curves that showed almost
222 twice more captures on males compared to females after 100 4-hours sampling periods (Figure 2a).

223 3.2. MULTIMODAL DISTRIBUTION MODEL AND BODY SIZES – The bimodal gambin
224 model on SAD always provided the best fit to the data according to the X^2 goodness-of-fit and AIC
225 (AIC; male = 229, female = 304), followed by the trimodal model (AIC; male = 236, female = 310)
226 and the unimodal model (AIC; male = 249, female = 313) (Figure 3a-b). For male inflorescences,
227 32% of morphospecies were associated with the octaves of the first mode i.e., with 1 or 2
228 individuals captured. For females, the octaves associated with the first mode contained 53% of the
229 morphospecies i.e., represented by 1 to 16 individuals.

230 Flower-visitor morphospecies displayed a wide range in body size, from 0.94 mm in length
231 and 0.54 mm in width (morphospecies PTIL1) to 15 mm in length and 7 mm in width
232 (morphospecies SC1).

233 3.3. TEMPORAL VARIATION OF THE MAIN VISITORS – Among all 59 flower-visitor
234 morphospecies, 84.2% (42 morphospecies) were captured on both floral sexes. Among these, 99%
235 of the individuals captured on both sexes were represented by only 16 morphospecies (Figure 4)
236 on which we focused our subsequent analyses. Fifteen morphospecies were representatives of
237 Coleoptera and one of Diptera (SPH1). Coleoptera included seven families, namely Staphylinidae
238 (5 morphospecies), Curculionidae (4 morphospecies), Nitidulidae (2 morphospecies), Histeridae,
239 Scarabaeidae, Silvanidae, and Ptilidae (one morphospecies each).

240 The nMDS analysis with these 16 main morphospecies revealed that insect community
241 composition visiting male or female inflorescences was significantly different during the period
242 1200-1600 h ($P < 0.05$) (Figure 5). For the other 4-hours periods, the R-value < 0.1 indicated high
243 similarity between insect communities visiting both sexes, excluding the 2000-0000 h period where
244 communities did not completely overlap. The two crepuscular periods (0400-0800 h and 1600-
245 2000 h) had the highest overlapping value. Overall, insect communities did not differ between

246 floral sexes (ANOSIM, $R = 0.06$; $P = 0.119$), but they did so when comparing the 4-hours periods
247 (ANOSIM, $R = 0.30$; $P = 0.001$).

248 Our zero-inflated negative binomial model applied to the abundance of the 16 main
249 morphospecies revealed that captures on inflorescences differed significantly among
250 morphospecies ($X^2 = 201$, $P < 0.001$) and according to the six 4-hours periods of the day ($X^2 = 227$,
251 $P < 0.001$). They did not differ between floral sexes ($X^2 = 0.166$, $P = 0.684$), although we detected
252 an interactive effect between period and sex ($X^2 = 55.316$, $P < 0.001$) (Table S2). The zero-inflated
253 part of the model indicated that the 1200-1600 h period significantly influenced the probability for
254 a given morphospecies to be differentially captured on males and females. The count part of the
255 model indicated that, overall, captures were significantly higher on male than female inflorescences
256 (Table S2). The activity pattern predicted by the model allowed to separate the 16 morphospecies
257 into three distinct periods (Figure 6, Table S2): six crepuscular morphospecies active at sunset
258 (1600-2000 h) (CU1, ND1, ND5, ND8, ST4, and SC1), three nocturnal morphospecies (CU2, CU3,
259 and CU8), and seven diurnal morphospecies with an activity distributed throughout the day (ST3,
260 ST5, ST6, HS1, ND10, ND6, and SPH1). Crepuscular and nocturnal morphospecies presented a
261 similar pattern on both floral sexes, whereas diurnal morphospecies did not peak simultaneously
262 on both sexes, except ST5 (Figure 6). For a summary of model statistics, see Table S2.

263 **4. DISCUSSION**

264 A SPECIOSE ASSEMBLAGE WITH A FEW POLLINATOR CANDIDATES – Our sampling
265 revealed a diverse species assemblage associated with the flowers of *P. aequatorialis* in the
266 Otongachi reserve forest (Ecuador). Three beetle families (Staphylinidae, Nitidulidae, and
267 Curculionidae) largely dominated in both species number and abundance, associated with less

268 represented families of other beetles, bees (Apidae) and flies (Drosophilidae, Spaeroceridae),
269 consistent with observations of Ervik et al. (1999). Such diversity in the assemblage associated
270 with flowers was described in other palms (Henderson 1986, Listabarth 1992, Kuchmeister *et al.*
271 1997, Núñez Avellaneda 2014, De Medeiros *et al.* 2019, Barfod *et al.* 2011, De Medeiros *et al.*
272 2019) and the dominance of beetles as visitors was reported in 30% of palm species (Barfod *et al.*
273 2011). Our study revealed that 84 % of the visitors detected in the assemblage (42 morphospecies)
274 could be potentially involved in the pollination of *P. aequatorialis* due to their presence in both
275 flower sexes. Such diversity raises many questions about the direction of interactions among insects
276 (i.e., antagonistic or mutualistic), the specificity to their host palm, and the variation of these
277 interactions in time and space. *P. aequatorialis* could fall in the “open framework of interactions”
278 (Barfod *et al.* 2011) where pollinators with limited role in pollination could be of higher importance
279 to pollinate the palms according to changing conditions, like seasonality of geographic variations.
280 The dominance of Coleoptera in our survey raises the question of a beetle-oriented sampling bias
281 related to the trap design. The trap configuration (one transparent simple-pane hung between two
282 funnels) and its positioning (blocking a large part of the potential access to the inflorescence for
283 flying visitors) are more adapted to target flying active beetles (e.g. Lamarre *et al.* 2012). However,
284 a large amount of Hymenoptera was also captured, and one Diptera morphospecies is among the
285 most collected morphospecies of this survey, demonstrating the ability of this trap design in
286 capturing various orders of flying insects. We cannot exclude that very small species are absent or
287 poorly sampled due to their ability to avoid the trap. Further studies with an improved trap system
288 (e.g. cross-vanes windows trap or trap baited with flower-mimicking visual and/or scented cues)
289 could resolve this potential sampling bias.

290 Despite this large diversity of visitors shared by both floral sexes, a core of 16
291 morphospecies totalized 99% of visits. Species abundance in a community is an important factor
292 to predict their relative effectiveness for pollination (Ollerton 2017) and is commonly used to
293 identify palm pollinators, among other variables such as pollen load (Núñez-Avellaneda & Rojas-
294 Robles 2008, Carreño-Barrera *et al.* 2020). Nevertheless, the very limited knowledge of the biology
295 of these morphospecies and the absence of data on the individual performance of pollination
296 considerably limit the identification of efficient pollinators (Ne'eman *et al.* 2009). Several authors
297 have reported an intensive use of the male floral tissues by Coleoptera. Derelomine weevils
298 (Curculionidae) and mystropine beetles (Nitidulidae) are almost always found among the most
299 abundant visitors on flowers of both sexes (Núñez *et al.* 2005, Franz & Valente 2006, Kirejtshuk
300 & Couturier 2010, Restrepo Correa *et al.* 2016), and are often considered as main pollinators in
301 palms. These insects feed on pollen and oviposit inside male floral tissues, and their larvae achieve
302 their development in decaying inflorescence (Listabarth 1996, De Medeiros *et al.* 2019). It was
303 reported that they visit and deposit pollen on female inflorescences without receiving food
304 resources, and do not exploit the floral tissues as they do with male inflorescences. Bernal and
305 Ervik (1996) have described the construction of egg chambers in the floral receptacles on *P.*
306 *seemannii* male inflorescences by pollinating rove beetles of the genus *Amazoncharis*
307 (Staphylinidae Aleocharineae). These authors did a parallel between the fleshy structure and the
308 fast development of these inflorescences and that of the mushrooms on which feed some families
309 of Staphylinidae. Silvanidae and Ptilidae families are known to be mushroom feeders (Hammond
310 & Lawrence 1989), so it is not excluded that the two morphospecies present in our list of putative
311 pollinators of *P. aequatorialis* also use floral tissue as feeding and oviposition sites as
312 *Amazoncharis* do.

313 Such a diverse and abundant community of floral visitors may suggest high costs for both ivory
314 palm sexes (De Medeiros *et al.* 2019), because of the risk to attract different types of antagonists,
315 such as folivores, herbivores, or pollinators that may transmit fungal infection (e.g. Dötterl *et al.*
316 2009). For example, the destructive process associated with brood pollination aforementioned can
317 exert a high cost on the plant (Dufay & Anstett 2004, Dufay 2010). In *P. aequatorialis*, the impact
318 on male fitness of tissue consumption by adult visitors could be mitigated by the large size of the
319 inflorescence and the high amount of pollen produced. Moreover, the insect larvae develop on male
320 flowers after pollen emission, which would not affect the fitness of male inflorescences. It may
321 even be a benefit for the male plant to host these insects since the adult insects emerging from old
322 inflorescences can visit and carry the pollen of the next inflorescences produced by their host palm
323 (Dufay 2010). Nonetheless, attractiveness to brood pollinators could be very costly for female
324 fitness, as attacked floral tissue, especially ovules, alters seed production and therefore fitness.

325 POLLINATOR-MEDIATED SELECTION OF FLORAL DIMORPHISM – We found that male
326 inflorescences of *P. aequatorialis* were overall more visited than females, which has been
327 confirmed by the predictions of the activity model for 15 out 16 candidate pollinators. According
328 to sexual selection theory, sexual dimorphism observed in many dioecious plants can result from
329 different strategies or selective pressures exerted on males and females (Renner & Ricklefs 1995,
330 Ashman 2009, Waelti *et al.* 2009, Barrett & Hough 2013). Males tend to harbor showy floral traits
331 that maximize their reproductive success while competing for access to females, but they pay the
332 cost of signaling to antagonists. On the contrary, females are predicted to evolve discrete floral
333 morphology and signaling to pollinators to limit their attractiveness to herbivores, which are more
334 detrimental for females than males. Inflorescences of the species in the genus *Phytelephas* are one
335 of the most extreme examples of sexual dimorphism known in plants (Ervik *et al.* 1999), and our
336 expectation that males are quantitatively more attractive to visitors than females was confirmed.

337 Interestingly, our results showed a higher diversity of visitors on female inflorescences, with
338 more rare, less abundant morphospecies compared to males, contrasting with other studies on palm
339 pollinators (De Medeiros *et al.* 2019, Barbosa *et al.* 2020). Rare species, i.e., recorded in a few
340 samples in species inventories, are generally considered as “migrants” with good dispersal ability,
341 and, therefore with higher probability to be trapped by “chance” (Matthews, Borges, *et al.* 2014).
342 Given that the duration of female anthesis is longer than male anthesis in *P. aequatorialis* (4-5 days
343 vs 24h-48h), the resulting longer trapping time may have increased the probability to trap species
344 unrelated to pollination and may partially explain the higher species diversity observed on females.
345 Another, not exclusive explanation is that the proximity in the ivory palm crown of female
346 inflorescences with leaves and mature infructescences, as well as the frequent presence of epiphytic
347 plants, could result in inadvertent trapping of insect guilds usually not attracted by the
348 inflorescences. For example, we collected a few individuals belonging to three Scolytinae
349 morphospecies, which are mainly considered bark and seed borers (we found Scolytinae larvae in
350 galleries bored inside attacked seeds; TA, pers. obs.). Unfortunately, our knowledge is insufficient
351 for attributing recorded morphospecies to functional groups and deepening this hypothesis.

352

353 4.3. FLOWER VISITORS ALL DAY BUT MAINLY ACTIVE AT DUSK: IMPLICATIONS 354 ON THE TAGUA PALM POLLINATION

355 The 16 main pollinators exhibited two distinct activity patterns in male and female
356 inflorescences: 1) morphospecies that presented a short, dusk or early-night activity perfectly
357 synchronous on both floral sexes, and 2) morphospecies with a long activity period, spread over
358 the day, which does not culminate in a synchronic way on both sexes (except one morphospecies).
359 Our results contrast with the daytime activity of flower visitors reported by Ervik *et al.* (1999) for

360 male ivory palms observed during the same period of the year as our study (October-November).
361 As these authors conducted only qualitative inspections of inflorescences at different times of the
362 day, we cannot exclude they missed narrow activity windows of some visitors. The variation in the
363 activity of these different morphospecies results in a continuous temporal succession of visitors
364 during the diel cycle and throughout the flowering period. In other palm species, several studies
365 have reported a partitioning of floral visitors between the day and night periods (Küchmeister *et*
366 *al.* 1997, Silberbauer-Gottsberger *et al.* 2001, Brieva-Oviedo *et al.* 2020, Barbosa *et al.* 2021). This
367 extended visiting period could represent a strategy of the palm to increase the pollination success,
368 by exploiting functionally diverse insects with potentially variable contributions to pollination (De
369 Medeiros *et al.* 2019).

370 We found evidence for a pattern of activity centered at dusk and night across nine of the 16
371 most abundant floral visitors. The crepuscular activity of flower visitors is frequently observed in
372 palms pollinated by beetles (Silberbauer-Gottsberger 1990, Kuchmeister *et al.* 1997, Silberbauer-
373 Gottsberger *et al.* 2001, but see Núñez *et al.* 2005 that deal with diurnal and nocturnal pollination
374 by mystropine beetles) . By exhibiting high differences in physical parameters compared with the
375 day period, dusk, night, and dawn periods present some advantages for the pollination process.
376 Plants that emit large flowers can reduce water loss through evapotranspiration due to a lower air
377 temperature and higher humidity, while reduced air turbulence and wind velocity can promote
378 flight in small pollinators (Borges *et al.* 2016, Borges 2018). Miyake & Yahara (1998)
379 demonstrated that nocturnal pollinators contributed more to cross-pollination than diurnal
380 pollinators because they consumed less pollen and dispersed farther. A short, crepuscular activity
381 window has been described for tropical pollinators (Borges *et al.* 2016), including palm pollinators
382 for which visiting activity synchronized on inflorescences of both sexes. For example, the 30-

383 minute dusk activity of the derelomine weevils *Grasidius hybridus* is perfectly synchronized on
384 male and female inflorescences of *Elaeis oleifera* (Auffray *et al.* 2017). To our knowledge, there
385 is no explanation of why nocturnal activity for tropical pollinators is short, however it could be a
386 strategy to limit inter-specific competition (Fründ *et al.* 2011) or an adaptation to climatic
387 constraints (e.g. an adaptation to avoid daily rain maxima; Núñez *et al.* (2005)).

388 Our study provides new insights into the pollination mechanism of *P. aequatorialis*. The
389 temporal dynamic and the synchronicity in visits on both flower sexes for nine of the main visitors
390 support the hypothesis that insects are attracted by a remote signal synchronously displayed at dusk
391 and night by male and female flowers. In many plant species with strong sexual dimorphism, the
392 plant-pollinator interaction relies on the mimicking by non-rewarding sex (generally the female)
393 of the signals used to attract pollinators by the rewarding sex (Ashman 2009). Several visitor
394 morphospecies in the genus *Phytelephas* use male inflorescences as breeding sites (Bernal & Ervik
395 1996, Ervik *et al.* 1999), but it is unknown if female inflorescences provide any rewards in
396 exchange for visits. Heat reward was demonstrated in only a few instances (e.g. Seymour *et al.*
397 2003). In our system, female inflorescences seem to produce heat for several days including during
398 periods of low ambient temperature at dusk and night periods (see figure 2 in Pincebourde *et al.*
399 2016; TA, pers. obs.). Therefore, we cannot exclude that the candidate pollinators visiting female
400 flowers during these short periods of the day obtain heat reward. Nevertheless, the thermal
401 requirements of those morphospecies remain largely unknown. Our finding that most of the flower
402 visitors are active at dusk means that these nocturnal insects must find floral resources under low
403 light conditions (Borges 2018, Cordeiro *et al.* 2019), which requires sensory adaptations to find
404 flowers. The inflorescence recognition by visual (color) cues is perhaps less efficient, especially
405 from distance, during this daytime (Borges 2018) suggesting insects rely more on COVs emission

406 (Borges 2018, Cordeiro *et al.* 2019) and floral heating to find flowers. Insects visiting the
407 inflorescences of *Phytelphas* are thought to be attracted by the dominant volatile compound p-
408 methylanisole (Ervik *et al.* 1999). In agreement with previous authors, we hypothesize
409 that pollinator attraction relies on a high chemical resemblance between male and female
410 inflorescences (i.e., intersexual chemical mimicry) and that this similarity prevents the dusk- and
411 night-active pollinators to discriminate among floral sexes, allowing female inflorescences to
412 receive visits. Further studies on the chemical components involved in insect-ivory palm
413 interactions, and its reliance on thermogenesis (Pincebourde *et al.* 2016), should shed a new light
414 on this fascinating pollination system.

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428 RM and OD obtained the funding; RM, SXPU, AB, and OD conceptualized the study; SXPU
429 collected the data and created the database, under the supervision of RM, AB, and OD. TA analyzed
430 the data, and prepared the graphics; TA and RM wrote the original version; TA, RM, SP, MG,
431 SXPU, AB, and OD reviewed and wrote the final document, and the revised version.

432 **Disclosure statement**

433 The corresponding author confirms on behalf of all authors that there have been no involvements
434 that might raise the question of bias in the work reported or in the conclusions, implications, or
435 opinions stated.

436

437 Table 1: Output of the zero-inflated negative binomial model, considering the species (16 most
 438 abundant morphospecies captured on both male and female flowers), the hours (4-hour periods of
 439 the sampling) the sex of the flowers, as well as the interaction terms between these variables. The
 440 response variable was the number of captures.

	<i>df</i>	χ^2	<i>P</i>
HOURS	5	224.06	< 2.2E-16 ***
SPECIES	15	179.92	< 2.2E-16 ***
SEX	1	0.02	0.88
HOURS * SPECIES	75	368.43	< 2.2E-16 ***
HOURS * SEX	5	58.68	2.279E-11 ***
SPECIES * SEX	15	44.82	0.0001175 ***

441

442 Figure Legends

443 Figure 1: Photographs of a male (a) and female inflorescences (b) at the anthesis stage. Interception
444 trap used for capturing flying insects held in the vicinity of male flower (c). Female ivory palm in
445 a pasture environment (d). Scale bars represent 40cm.

446 Figure 2: Rarefaction curve showing the increase of A) the arthropod abundance and B) The
447 Fisher's alpha index, with an increasing number of four-hour periods of sampling, for female (red)
448 and male (blue) inflorescences. Open points represent the average of 50 replicates randomly
449 selected among all samples collected for each gender. Error bars indicate SD. Dotted lines represent
450 the extrapolation using A) a linear model, and B) a gam function.

451 Figure 3: Preston plot of the abundance distribution of morphospecies captured on A) male
452 inflorescences and B) female inflorescences. The y-axis is the number of morphospecies and the
453 x-axis is the species abundance in log₂ representing true doubling classes of abundance (the first
454 bar represents species with abundance 1, the second one species with abundances 2–3, then 4–7,
455 8–15, etc.). The black line fits a gambin bimodal distribution model. Boxplots were used to
456 compare the body width distribution of morphospecies between the two respective modes to which
457 they belong for C) male inflorescences and D) female inflorescences. Wilcoxon test: ns = non-
458 significant; ** < 0.01

459 Figure 2: Mean abundance (log₁₀) of the 16 putative pollinator morphospecies collected on male
460 (blue) and female (red) flowers of Tagua palm in the Otongachi reserve. Error bars are SD. The 16
461 flower-visiting morphospecies represented 99% of the total captures from both female and male
462 flowers. Each morphospecies is coded by letters corresponding to the taxonomic family:
463 Coleoptera: ST = Staphylinidae, CU = Curculionidae, ND = Nitidulidae, HS = Histeridae, SC =

464 Scarabaeidae; SILV = Silvanidae; PTIL = Ptilidae, Diptera: SPH = Sphaeroceridae, see table S1
465 for more details.

466 Figure 3: Non-metric multidimensional scaling (nMDS) analysis on the community of the 16 main
467 flower-visitors of the Tagua palm at 4-hour periods and according to the sex of the flower (open
468 circle = female, open triangle = male). Graphs show convex hulls containing all points according
469 to the flower sex, faceted by 4-hours periods. For each 4-hours period, *sign.* <0.05 indicate a
470 significant difference in male and female communities, or no difference if > R-value indicate the
471 similarity between communities; $0.25 < R < 0.5$ = different with some overlap; $0.1 < R < 0.25$ =
472 similar but with no high overlap; $R < 0.1$ = similar.

473 Figure 4: Number of captured morphospecies on female (red) and male (blue) flowers at each 4-
474 hours period. Points and solid lines are model estimates for each 4-period and flower sex and
475 shaded ribbons are the estimated intervals of the model at 95% confidence. Morphospecies are
476 grouped according to their daily period of maximum activity: blue boxes = crepuscular
477 morphospecies, black boxes = nocturnal morphospecies, and orange boxes = diurnal
478 morphospecies. See table S1 for details on morphospecies codes.

479



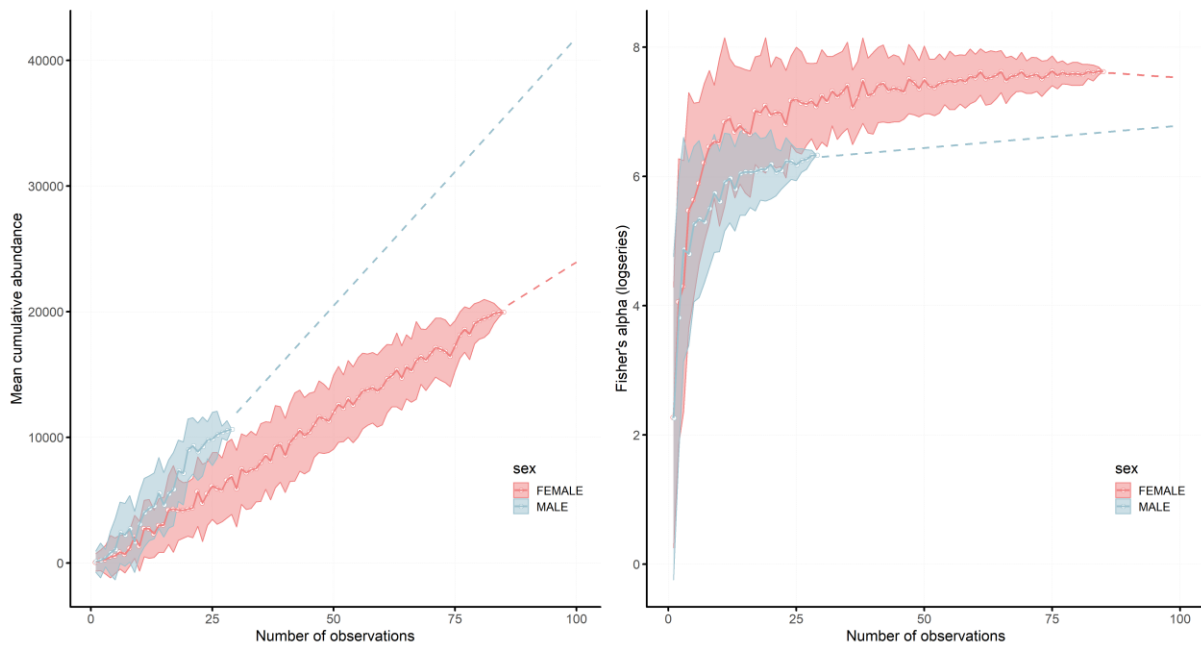
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482 Figure 5: Photographs of a male (a) and female inflorescences (b) at the anthesis stage. Interception

483 trap used for capturing flying insects held in the vicinity of male flower (c). Female ivory palm in
484 a pasture environment (d). Scale bars represent 40cm.

485

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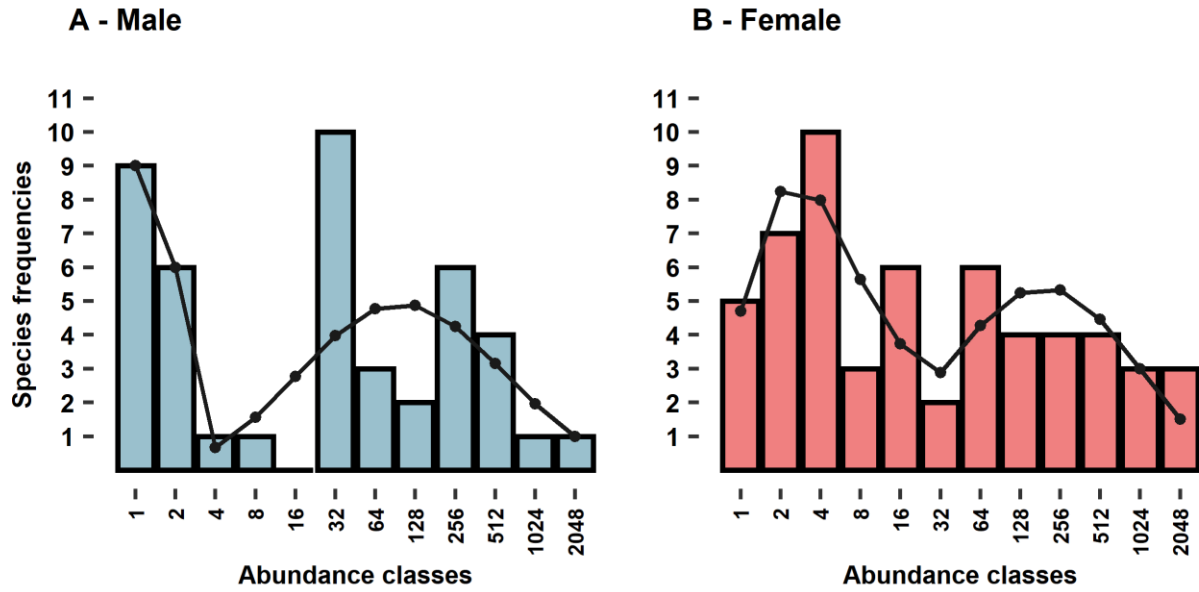
487

488 Figure 2: Rarefaction curve showing the increase of A) the arthropod abundance and B) The
489 Fisher's alpha index, with an increasing number of four-hour periods of sampling, for female (red)
490 and male (blue) inflorescences. Open points represent the average of 50 replicates randomly
491 selected among all samples collected for each gender. Error bars indicate SD. Dotted lines represent
492 the extrapolation using A) a linear model, and B) a gam function.

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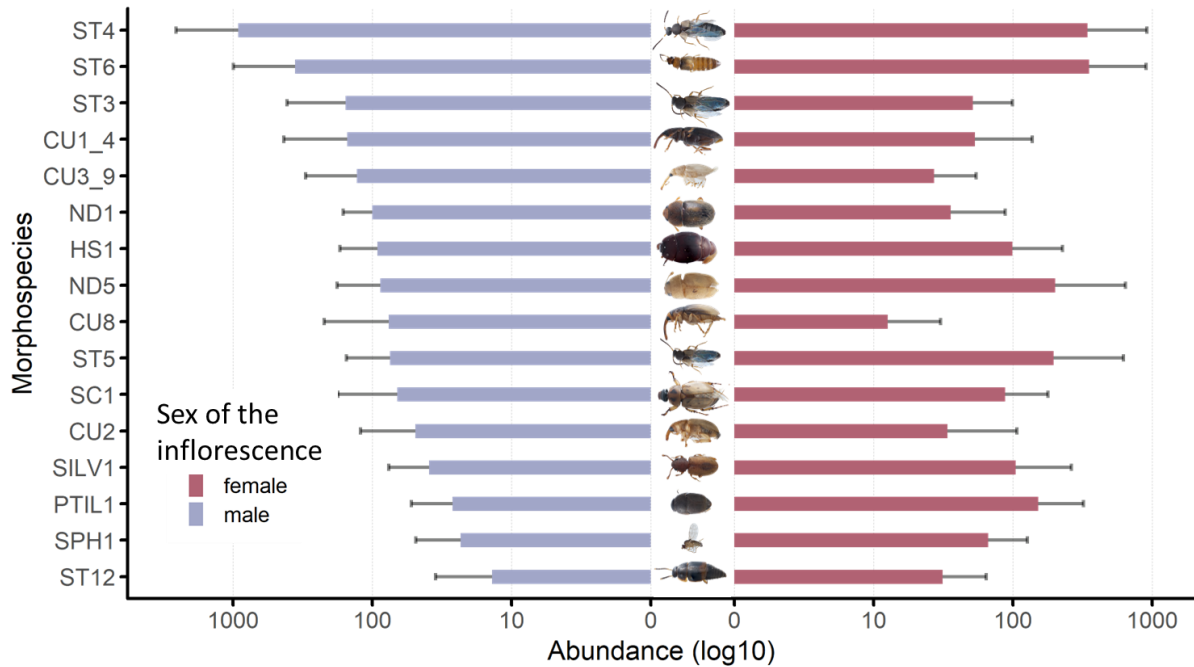
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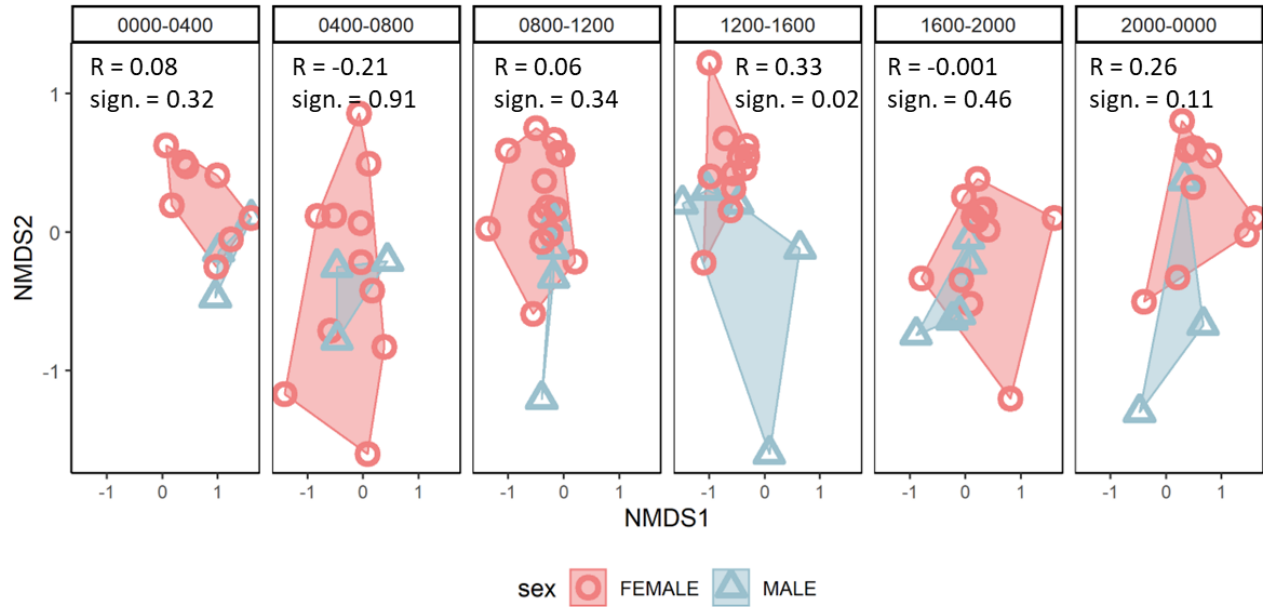


496
 497 Figure 3: Preston plot of the abundance distribution of morphospecies captured on A) male
 498 inflorescences and B) female inflorescences. The y-axis is the number of morphospecies and the
 499 x-axis is the species abundance in log₂ representing true doubling classes of abundance (the first
 500 bar represents species with abundance 1, the second one species with abundances 2–3, then 4–7,
 501 8–15, etc.). The black line fits a gambin bimodal distribution model.

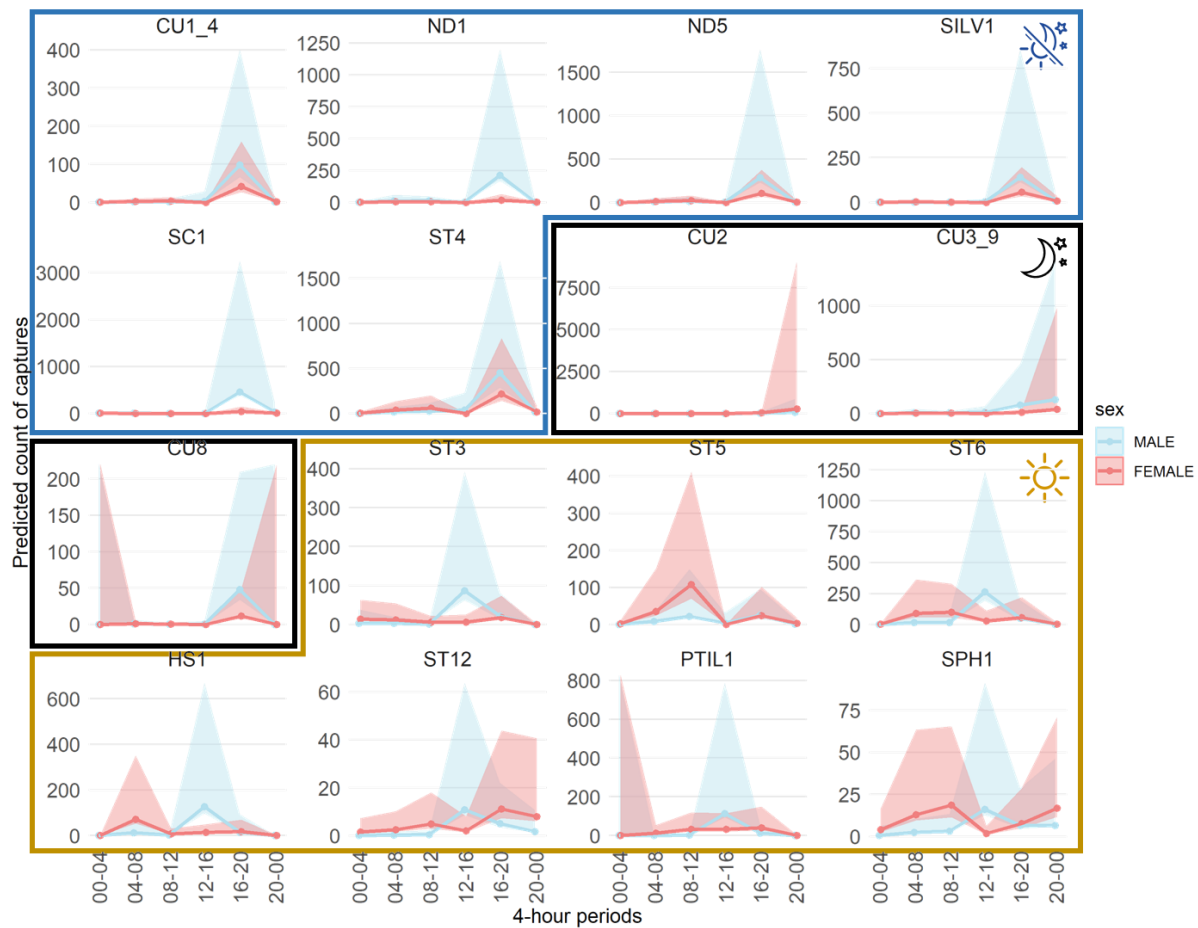
502



503
 504 Figure 6: Mean abundance (log10) of the 16 putative pollinator morphospecies collected on male
 505 (blue) and female (red) flowers of Tagua palm in the Otongachi reserve. Error bars are SD. The 16
 506 flower-visiting morphospecies represented 99% of the total captures from both female and male
 507 flowers. Each morphospecies is coded by letters corresponding to the taxonomic family:
 508 Coleoptera: *ST* = *Staphylinidae*, *CU* = *Curculionidae*, *ND* = *Nitidulidae*, *HS* = *Histeridae*, *SC* =
 509 *Scarabaeidae*; *SILV* = *Silvanidae*; *PTIL* = *Ptilidae*, *Diptera*: *SPH* = *Sphaeroceridae*, see table S1
 510 for more details.



511
 512 Figure 7: Non-metric multidimensional scaling (nMDS) analysis on the community of the 16 main
 513 flower-visitors of the Tagua palm at 4-hour periods and according to the sex of the flower (open
 514 circle = female, open triangle = male). Graphs show convex hulls containing all points according
 515 to the flower sex, faceted by 4-hours periods. For each 4-hours period, *sign.* <0.05 indicate a
 516 significant difference in male and female communities, or no difference if > 0.05. R-values indicate
 517 the similarity between communities; $0.25 < R < 0.5$ = different with some overlap; $0.1 < R < 0.25$
 518 = similar but with no high overlap; $R < 0.1$ = similar.



519
 520 Figure 8: Number of captured morphospecies on female (red) and male (blue) flowers at each 4-
 521 hours period. Points and solid lines are model estimates for each 4-period and flower sex and
 522 shaded ribbons are the estimated intervals of the model at 95% confidence. Morphospecies are
 523 grouped according to their daily period of maximum activity: blue boxes = crepuscular
 524 morphospecies, black boxes = nocturnal morphospecies, and orange boxes = diurnal
 525 morphospecies. See table S1 for details on morphospecies codes.

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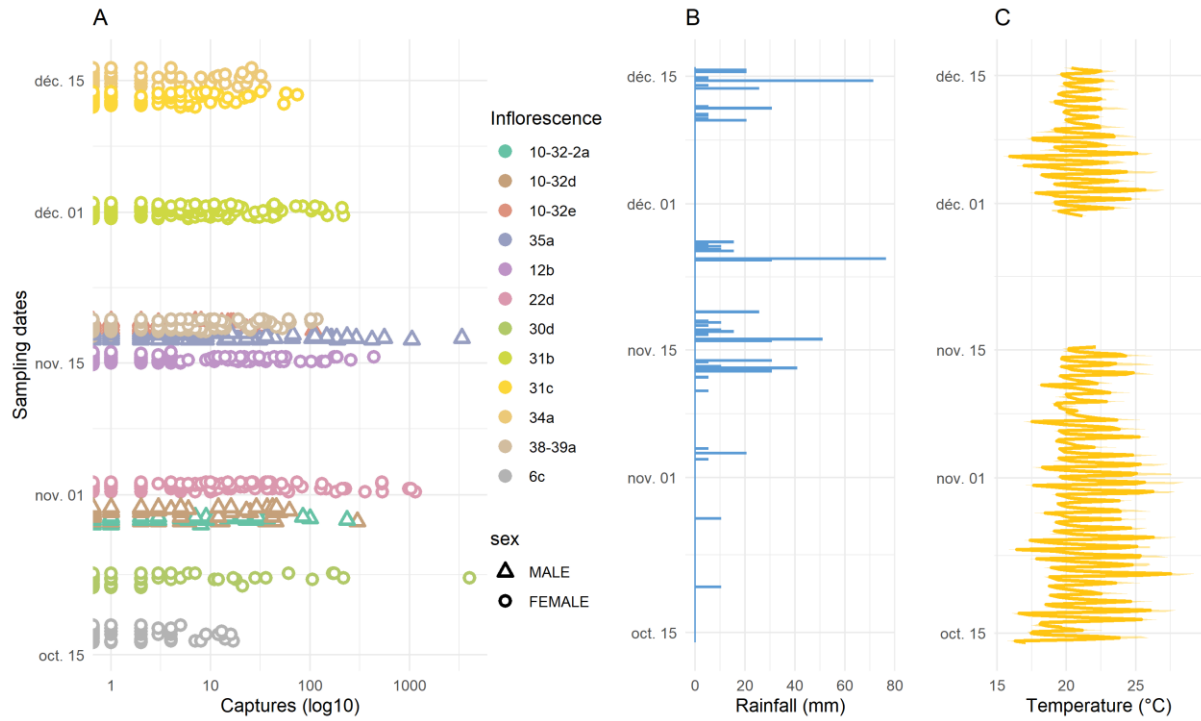
741 **Supplementary information S1**

742 Trapping method

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744 Variations in abundance and composition of flower-visitor community during the flowering period
745 of the palms were assessed by sampling visitor insects with interception trapping. Interception
746 traps were made of a transparent foil sheet (H = 57 cm and L = 26 cm), stretched out between
747 two funnels (H = 32 cm and diameter = 26 cm), and held vertically in the vicinity of each focal
748 flower (Fig. 1C). The bottom funnel was equipped with a collector so that flying insects colliding
749 with the transparent foil fell into. The collector was filled with water and a wetting agent acting
750 as a surfactant to prevent captured arthropods from escaping. Each trap was installed from the
751 start of the flower anthesis i.e., when the peduncular bract (the bud integument covering the
752 flower) opened, followed by either the quick elongation for the male inflorescence or the
753 revealing of the tepals for the female inflorescence (Ervik et al. 1999). The collectors were
754 retrieved and replaced by new ones every four hours. Because male flowers decay quickly,
755 trapping was stopped within 24 to 48 hours after the beginning of the anthesis. Female anthesis
756 may last several days so that trapping was stopped 28-52h after the opening. Insect fauna trapped
757 in each collector was transferred into a plastic tube and conserved in 70° alcohol before
758 identification and counting in the lab.

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 761 Figure S2: A) Distribution of captures, B) rainfall (mm) and C) temperatures (°C) per 4-hour
 762 sampling period during the study dates. In A), each symbol represents the number of individuals
 763 of a given visitor morphospecies captured by unit sampling. The twelve studied palms are
 764 differentiated according to colors, and the gender of the flower is indicated by triangles or
 765 squares, for females and males, respectively.

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773 **Supplementary information S2**

774 **2.1 Study model and site**

775 The ivory palm is a medium-size, understory palm endemic to western Ecuador. The species
776 displays a wide ecological range since its populations grow from sea level up to 1500 m a.s.l and
777 can be naturally found in a variety of forest environments, such as premontane and montane,
778 tropical, deciduous, and semi-deciduous forests (Montúfar *et al.* 2013, Brokamp *et al.* 2014,
779 Escobar *et al.* 2019). Despite a wide distribution and locally abundant populations, the ivory palm
780 is classified by UICN as “near threatened” (Montúfar 2003) due to the high rate of forest
781 degradation affecting more than 75% of Western Ecuador (Dodson & Gentry 1991, Sierra 2013).
782 Because of their commercial value, adult palms are often left stand when forests are converted into
783 agriculture or pastures. However, regeneration on these lands is severely affected by the inability
784 of seedlings to develop in these degraded habitats (Montúfar *et al.* 2013).

785 The size of ivory palm ranges from 1 to 15 m with 8-15 pinnate leaves reaching 6-8 m in
786 length. Inflorescences are interfoliar and usually with multiples on the same trunk. Unisexual
787 female and male inflorescences are similar in appearance at the bud stage (except for size) but
788 differ significantly in morphology at anthesis, i.e. the flowering stage. The cylindrical-shaped bud
789 is protected by two fibrous, foliar-originated tissues. The most external tissue, the prophyll detaches
790 early during the growth of the bud, while the coriaceous, orange-color peduncular bract covers the
791 inflorescence until anthesis. The male bud can reach 1m long and 8-12 cm wide, while the female
792 bud is about half smaller. At anthesis, the bud breaks lengthwise and releases a whitish-yellow
793 inflorescence. The conspicuous male (staminate) inflorescence is cylindrical and grows up to 2,5
794 m in length and 20 cm in diameter with 300 – 500 crowded flower clusters arranged along a fleshy
795 rachis. Male inflorescence unfolds completely a few hours after the bud opening and falls along

796 the palm trunk (Figure 1B). Female (pistillate) inflorescences have a head-like form with 20-25
797 crowded, tentacular-like flowers inserted at the extremity of a strong 40-50 cm long peduncle
798 (Figure 1A). Each flower is a 10 cm-length tubular style basally flanked with a group of 20-30
799 staminodes (aborted male flowers) surrounded by tepals and sepals. The gynoecium has 4-10 united
800 carpels, with one ovule per carpel. Infructescence is spheric-shaped (25-40 cm diameter), with 15
801 to 25 conical fruits containing each 4-7 seeds which require 2 to 7 years to mature according to
802 altitude and climatic conditions (Brokamp *et al.* 2014). The hard and whitish endosperm is used
803 for button manufacturing, handicraft industry, and other industrial applications or new usages (e.g.
804 bioplastic, microbeads; Barfod *et al.* 1990; Brokamp *et al.* 2014; Ghysels *et al.* 2019).

805 The reserve is a 150-ha patch of primary–secondary forest surrounded by pastures and small
806 farms. The density and the male: female sex ratio of the ivory palm population was at 42 adult
807 palms / ha and 1.77, respectively. In this region, seasons are well separated into a dry (June–
808 November: 65 ± 16 mm per month) and a rainy period (December–May: 315 ± 90 mm per month;
809 Cárdenas & Dangles 2012) with an annual average precipitation of 2300 mm. Air temperatures
810 range between 17 and 28 °C (mean 21 ± 1.89 °C).

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819 **Table S1.** Composition of floral visitors observed on anthesizing female and male inflorescences
 820 of *Phytelephas aequatorialis* in the Otongachi natural reserve. Body size (length and width in
 821 mm) of each species is indicated in the right marge.

	Females			Males			Body size (mm)	
	<i>N</i> = 8			<i>N</i> = 4			length	width
	O	sum	mean ± sd	O	sum	mean ± sd		
Coleoptera								
Chrysomelidae								
CR1	3	11	4 ± 1	1	2	2	7	?
CR2	3	4	1 ± 1	1	4	4	6	3
CR3	2	2	1 ± 0	-	-	-	5	3
CR4	3	4	1 ± 1	-	-	-	7	4
CR5	1	1	1	1	1	1	6	3,5
CR6	1	7	7	3	8	3 ± 2	6	?
CR7	1	1	1	-	-	-	6	3
Curculionidae								
Curculioninae								
CU1_4*	8	428	54 ± 84	4	604	151 ± 279	2,5	0,9
CU2*	5	271	54 ± 89	2	196	98 ± 79	1,7	0,75
CU3_9*	6	218	36 ± 25	4	514	128 ± 173	2,8	0,8
CU7	-	-	-	1	1	1	4,3	1,20
CU8*	6	101	17 ± 19	3	304	101 ± 166	3,3	1,1
CU10	1	2	2	1	1	1	4,5	?
CU11	1	3	3	-	-	-		
Scolytinae								
SCO1	3	7	2 ± 2	1	1	1	2,4	0,7
SCO2	2	2	1 ± 0	1	1	1	3,7	1,15
SCO3	1	1	1	-	-	-	1,5	1
Histeridae								
HS1*	8	794	99 ± 129	4	366	92 ± 79	3,2	1,97
Monotomidae								
ND9	1	1	1	-	-	-	2,5	?
Nitidulidae								
ND1*	7	287	41 ± 54	4	400	100 ± 61	2,5	1,5
ND2	6	198	33 ± 51	4	52	13 ± 16	1,5	0,5
ND3_4	7	114	16 ± 24	4	37	9 ± 6	1,8	0,6
ND5*	8	1616	202 ± 440	4	350	88 ± 92	1,6	0,8
ND7	4	87	22 ± 28	2	46	23 ± 24	1,6	0,8
ND11	1	2	2	-	-	-	1,9	0,8
ND12	1	1	1	-	-	-		
Ptiliidae								
PTI1*	8	1217	152 ± 170	4	106	26 ± 26	0,94	0,54
Scarabaeidae								
SC1*	7	707	101 ± 90	3	264	88 ± 125	15	7
Silvanidae								
SILV1*	6	841	140 ± 171	4	156	39 ± 37	1,6	0,6
Staphylinidae								
ST1	8	74	9 ± 13	4	32	8 ± 11	14	2,5
ST2	8	133	17 ± 15	3	36	12 ± 12	4,76	0,90
ST3*	7	412	59 ± 46	4	622	156 ± 252	2,8	0,55
ST4*	8	2745	343 ± 574	4	3667	917 ± 1647	2,6	0,75
ST5*	8	1574	197 ± 426	4	298	74 ± 79	3,3	0,76
ST6*	8	2817	352 ± 555	4	1427	357 ± 635	1,8	0,58

ST7	6	39	6 ± 5	1	1	1	4,34	1,0
ST8	3	51	17 ± 16	-	-	-		
ST9	6	79	13 ± 17	1	1	1	1,8	1,0
ST10	2	6	3 ± 3	-	-	-	4,30	1,35
ST11	7	106	15 ± 17	2	54	27 ± 30	5,6	1,6
ST12*	8	250	31 ± 33	3	55	18 ± 23	3,0	1,42
Dermaptera								
Dermaptera								
DER1	3	5	2 ± 1	-	-	-	16	4
DER2	3	3	1 ± 0	-	-	-	14	4
Diptera								
Diptera div.								
DIP1	1	30	30	-	-	-	?	?
DIP2	1	22	22	-	-	-	?	?
Drosophilidae								
DR1	2	10	5 ± 4	2	33	16 ± 6	2	?
DR2	2	6	3 ± 1	2	45	22 ± 18	2	?
Sphaeroceridae								
SPH1*	8	533	67 ± 61	4	93	23 ± 26	?	?
Hemiptera								
HEMI1	8	26	3 ± 3	1	2	2	?	?
Hymenoptera								
Apidae								
AP1	6	21	4 ± 3	2	48	24 ± 11	10	4
AP2	5	12	2 ± 1	1	3	3	?	?
AP3	5	19	4 ± 3	4	121	30 ± 22	6	?
AP4	1	2	2	1	2	2	6	?
AP5	-	-	-	2	671	336 ± 42	?	?
AP6	2	5	2 ± 2	1	1	1	?	?
Lepidoptera								
LEP1	2	17	8 ± 6	2	3	2 ± 1	5	1
Other arthropods								
Acari								
AC1	3	4025	1342 ± 2302	-	-	-	?	?
Pseudoscorpiones								
PSE1	4	4	1 ± 0	2	3	2 ± 1	?	?
PSE2	3	4	1 ± 1	1	1	1	4	1,5

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823 N: number of inflorescences equipped with a trap; O: number of inflorescences on which the floral

824 visitor was trapped; *: Denote morphospecies with a putative role as pollinator (cumulated

825 abundance > 99% among morphospecies shared on both male and female flowers). The body size

826 parameters (width and length) were estimated from scaled photographs. “?” Denotes the inability

827 to estimate the size due to the absence of photographs or a poor orientation of the morphospecies

828 on the photo.

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832 Table S1: Results of the zero-inflated negative binomial model (count part and zero part).
 833 Estimates indicate the direction and magnitude of influence each factor has on captures. P-value
 834 indicates whether the estimate is statistically significant ($P < 0.05$). Red text indicates positive
 835 estimates; blue text indicates negative estimates.

Count model coefficients (negbin with log link):

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)					
CU1 MALE 1600-2000	5.021e+00	6.724e-01	7.467	8.19e-14	***
Hours (1600-2000)					
0000-0400	-6.499e+00	1.114e+00	-5.831	5.51e-09	***
0400-0800	-4.794e+00	8.527e-01	-5.622	1.89e-08	***
0800-1200	-6.302e+00	8.900e-01	-7.081	1.43e-12	***
1200-1600	-4.113e+00	1.353e+00	-3.040	0.002366	**
2000-0000	-5.454e+00	1.114e+00	-4.895	9.81e-07	***
Species (CU1_4)					
CU2	-2.358e+00	1.059e+00	-2.228	0.025895	*
CU3_9	-9.928e-01	1.031e+00	-0.963	0.335623	
CU8	-1.184e+00	8.922e-01	-1.327	0.184371	
HS1	-2.511e+00	1.040e+00	-2.415	0.015722	*
ND1	2.275e-01	9.677e-01	0.235	0.814123	
ST12	-3.444e+00	8.742e-01	-3.940	8.16e-05	***
ND5	5.493e-01	1.024e+00	0.536	0.591617	
PTIL1	-2.592e+00	8.839e-01	-2.932	0.003367	**
SILV1	-1.392e-01	9.997e-01	-0.139	0.889251	
SC1	1.049e+00	1.073e+00	0.978	0.328195	
SPH1	-3.232e+00	8.744e-01	-3.697	0.000219	***
ST3	-1.983e+00	8.295e-01	-2.390	0.016837	*
ST4	1.063e+00	8.211e-01	1.295	0.195482	
ST5	-1.824e+00	8.322e-01	-2.191	0.028440	*
ST6	-1.182e+00	8.451e-01	-1.398	0.162048	
Gender (MALE)					
FEMALE	-1.532e+00	6.605e-01	-2.320	0.020349	*
Hours (1600-2000): species (CU1_4)					
CU2					
0000-0400	-4.387e-02	1.466e+00	-0.030	0.976119	
0400-0800	1.448e+00	1.167e+00	1.241	0.214614	
0800-1200	6.816e-02	1.279e+00	0.053	0.957488	
1200-1600	1.872e+00	1.544e+00	1.212	0.225411	
2000-0000	6.988e+00	1.935e+00	3.611	0.000306	***

CU3_9

0000-0400	1.465e-01	1.578e+00	0.093	0.926072	
0400-0800	1.422e+00	1.110e+00	1.281	0.200197	
0800-1200	3.734e+00	1.089e+00	3.428	0.000607	***
1200-1600	2.432e+00	1.560e+00	1.559	0.118999	
2000-0000	5.793e+00	1.862e+00	3.111	0.001867	**

CU8

0000-0400	-1.925e+01	1.487e+04	-0.001	0.998967	
0400-0800	8.709e-01	1.105e+00	0.788	0.430814	
0800-1200	1.444e+00	1.170e+00	1.234	0.217206	
1200-1600	-9.011e-01	1.979e+00	-0.455	0.648825	
2000-0000	-1.422e+01	1.291e+03	-0.011	0.991206	

HS1

0000-0400	-2.274e-01	1.603e+00	-0.142	0.887141	
0400-0800	4.781e+00	1.151e+00	4.155	3.26e-05	***
0800-1200	4.021e+00	1.120e+00	3.589	0.000332	***
1200-1600	6.402e+00	1.469e+00	4.357	1.32e-05	***
2000-0000	1.065e+00	1.484e+00	0.718	0.472759	

ND1

0000-0400	3.857e-02	1.395e+00	0.028	0.977940	
0400-0800	1.991e+00	1.057e+00	1.884	0.059623	.
0800-1200	3.584e+00	1.092e+00	3.283	0.001026	**
1200-1600	-2.213e+00	2.072e+00	-1.068	0.285470	
2000-0000	1.298e+00	1.392e+00	0.932	0.351104	

ST12

0000-0400	2.738e+00	1.248e+00	2.195	0.028197	*
0400-0800	1.851e+00	1.084e+00	1.708	0.087653	.
0800-1200	3.996e+00	1.084e+00	3.685	0.000229	***
1200-1600	4.919e+00	1.476e+00	3.331	0.000864	***
2000-0000	4.463e+00	1.337e+00	3.338	0.000845	***

ND5

0000-0400	-1.921e+00	1.585e+00	-1.212	0.225608	
0400-0800	1.231e+00	1.040e+00	1.184	0.236516	
0800-1200	3.260e+00	1.079e+00	3.020	0.002530	**
1200-1600	-4.154e-01	1.610e+00	-0.258	0.796390	
2000-0000	1.260e+00	1.460e+00	0.863	0.387985	

PTIL1

0000-0400	-1.897e+01	7.956e+03	-0.002	0.998097	
0400-0800	2.155e+00	1.105e+00	1.951	0.051107	.
0800-1200	4.601e+00	1.043e+00	4.413	1.02e-05	***
1200-1600	6.375e+00	1.470e+00	4.336	1.45e-05	***
2000-0000	4.674e-03	1.555e+00	0.003	0.997601	

SILV1

0000-0400	1.151e+00	1.243e+00	0.926	0.354688	
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0400-0800	2.322e-01	1.083e+00	0.214	0.830216	
0800-1200	1.530e+00	1.119e+00	1.367	0.171522	
1200-1600	1.676e-01	1.622e+00	0.103	0.917738	
2000-0000	2.853e+00	1.325e+00	2.153	0.031314	*
SC1					
0000-0400	2.600e+00	1.214e+00	2.142	0.032210	*
0400-0800	2.406e-01	1.178e+00	0.204	0.838141	
0800-1200	5.749e-01	1.107e+00	0.519	0.603574	
1200-1600	-2.321e+00	1.984e+00	-1.170	0.242064	
2000-0000	2.840e+00	1.296e+00	2.192	0.028401	*
SPH1					
0000-0400	4.006e+00	1.206e+00	3.322	0.000893	***
0400-0800	3.862e+00	1.081e+00	3.573	0.000353	***
0800-1200	5.702e+00	1.048e+00	5.438	5.39e-08	***
1200-1600	5.087e+00	1.461e+00	3.482	0.000497	***
2000-0000	5.565e+00	1.322e+00	4.208	2.58e-05	***
ST3					
0000-0400	4.368e+00	1.289e+00	3.390	0.000700	***
0400-0800	2.896e+00	1.127e+00	2.570	0.010164	*
0800-1200	3.743e+00	1.114e+00	3.358	0.000784	***
1200-1600	5.526e+00	1.470e+00	3.760	0.000170	***
2000-0000	3.046e-02	1.705e+00	0.018	0.985747	
ST4					
0000-0400	9.111e-01	1.186e+00	0.768	0.442285	
0400-0800	1.573e+00	9.976e-01	1.576	0.114931	
0800-1200	3.506e+00	1.066e+00	3.289	0.001005	**
1200-1600	1.654e+00	1.482e+00	1.116	0.264490	
2000-0000	2.172e+00	1.396e+00	1.556	0.119694	
ST5					
0000-0400	2.330e+00	1.272e+00	1.832	0.066908	.
0400-0800	3.705e+00	1.020e+00	3.634	0.000279	***
0800-1200	6.328e+00	1.150e+00	5.504	3.71e-08	***
1200-1600	2.288e+00	1.569e+00	1.458	0.144750	
2000-0000	2.721e+00	1.451e+00	1.875	0.060853	.
ST6					
0000-0400	1.543e+00	1.226e+00	1.259	0.208061	
0400-0800	3.794e+00	1.062e+00	3.572	0.000355	***
0800-1200	5.377e+00	1.065e+00	5.047	4.50e-07	***
1200-1600	5.842e+00	1.467e+00	3.981	6.85e-05	***
2000-0000	1.849e+00	1.352e+00	1.368	0.171355	
Hours (1600-2000): Gender (MALE)					
Female					
0000-0400	1.773e+00	8.253e-01	2.148	0.031712	*
0400-0800	1.420e+00	5.207e-01	2.726	0.006402	**

0800-1200	1.404e+00	4.851e-01	2.893	0.003814	**
1200-1600:	-2.511e+00	5.666e-01	-4.432	9.32e-06	***
2000-0000	6.256e-01	7.106e-01	0.880	0.378626	

Species (CU1_4): Gender (MALE)

Female

CU2	2.300e+00	1.050e+00	2.190	0.028555	*
CU3_9	-3.199e-01	9.252e-01	-0.346	0.729546	
CU8	1.971e-01	9.608e-01	0.205	0.837460	
HS1	1.899e+00	8.689e-01	2.185	0.028869	*
ND1	-8.376e-01	8.391e-01	-0.998	0.318194	
ST12	2.409e+00	8.406e-01	2.866	0.004154	**
ND5	6.159e-01	9.081e-01	0.678	0.497608	
PTIL1	2.824e+00	8.806e-01	3.207	0.001340	**
SILV1	6.921e-01	8.762e-01	0.790	0.429637	
SC1	-7.981e-01	9.347e-01	-0.854	0.393174	
SPH1	1.829e+00	8.072e-01	2.266	0.023472	*
ST3	1.418e+00	8.556e-01	1.657	0.097462	.
ST4	8.599e-01	7.917e-01	1.086	0.277387	
ST5	1.555e+00	8.664e-01	1.795	0.072614	.
ST6	1.776e+00	8.061e-01	2.203	0.027601	*
Log(theta)	-1.073e+00	1.374e-01	-7.809	5.76e-15	***

Zero-inflation model coefficients (binomial with logit link):

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.64672	0.55913	-2.945	0.003228	**

Gender

FEMALE	0.93857	0.54566	1.720	0.085425	.
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Hours

0000-0400	-0.24323	2.98840	-0.081	0.935130	
0400-0800	1.25889	0.68341	1.842	0.065465	.
0800-1200	-0.24998	1.15648	-0.216	0.828866	
1200-1600	2.01738	0.60881	3.314	0.000921	***
2000-0000	1.42904	0.69081	2.069	0.038578	*

Sex (MALE): hours (1600-2000)

Female

0000-0400	0.69730	3.02522	0.230	0.817706	
0400-0800	-0.72241	0.74013	-0.976	0.329040	
0800-1200	0.06480	1.19478	0.054	0.956746	
1200-1600	-2.88833	0.92417	-3.125	0.001776	**
2000-0000	-0.05452	0.75583	-0.072	0.942493	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.342

Number of iterations in BFGS optimization: 146

836

Log-likelihood: -3137 on 130 Df