

1 **Trophic guild and forest type explain phyllostomid bat abundance variation from**
2 **human habitat disturbance.**

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14 **Trophic guild and forest type explain phyllostomid bat abundance variation from**
15 **human habitat disturbance.**

16 **Highlights**

- 17 ☐ No phylogenetic signal was found in the abundance of bats in disturbed habitats.
- 18 ☐ The abundance of bats in disturbed habitats depends on the trophic guild.
- 19 ☐ Forest altitude influences the abundance of bats in disturbed habitats.
- 20 ☐ Animal-feeding bats reduced their abundance in disturbed habitats regardless of
21 disturbance type and forest type.

22 **Abstract**

23 The loss of tropical forest cover caused by land-use change is causing a reduction in
24 functional groups, such as trophic guilds. Phyllostomid bats (family Phyllostomidae) are
25 essential in the Neotropics since they occupy up to six trophic guilds, and are pollinators,
26 seed dispersers, and regulators of vertebrate and invertebrate populations. In this study, a
27 series of meta-analyses were performed in order to analyse their response to habitat
28 disturbance. Data were obtained through a comprehensive literature review whereby we
29 measured the abundance of phyllostomid bats in disturbed habitats and conserved forests.
30 We found that the abundance of phytophagous bats depends on the type of habitat
31 disturbance and the type of forest where it occurs. On the other hand, animal-feeding bats
32 reduce their abundance in any disturbed habitat regardless of disturbance type and forest
33 type. No phylogenetic signal was found in the response of bats to habitat disturbance, nor
34 was the response found to be dependent on the type of crop, the age of the secondary forest,

35 or the distance to a conserved forest. These results demonstrate that feeding and the type of
36 forest where the disturbance occurs are important aspects to understand the reduction of
37 animal populations in the face of habitat destruction processes. This has implications on the
38 conservation of species and their function in ecosystems.

39 **Keywords**

40 Chiroptera, Neotropical leaf-nosed bats, land-use change, phylogenetic signal, meta-analysis,
41 distance to conserved forest.

42 **1. Introduction**

43 Tropical ecosystems are losing their forest cover due to changes in land use resulting from
44 the development of different human activities (Venter et al. 2016; Potapov et al. 2017).
45 Urbanization, logging, agriculture, and livestock are the main land uses responsible for the
46 current deforestation (Potapov et al. 2017). In many cases, these can cause a reduction in the
47 abundance of species (Dirzo et al. 2014; Newbold et al. 2015) and the subsequent loss of
48 ecosystem functions due the reduction in functional groups. For example, a reduction in
49 trophic guilds that fulfil specific functions, such as pollination, seed dispersal, and control of
50 populations within ecosystems, results in an imbalance of ecosystem functionality (Díaz et al.
51 2013; Dirzo et al. 2014; Newbold et al. 2020).

52 In the Neotropics, leaf-nosed bats (Phyllostomidae) are essential in ecosystem
53 functionality. They are pollinators and seed dispersers of more than 700 plants species, and
54 they are also predators of vertebrates and invertebrates, thus acting as regulators of their
55 populations (Muscarella & Fleming 2007; Kalka et al. 2008; Kunz et al. 2011). The family

56 Phyllostomidae consists of 11 subfamilies, 60 genera, and 212 species (Cirranello et al. 2016)
57 distributed throughout the tropics and subtropics of America, including the Antilles (Villalobos
58 & Arita 2010). Species diversity patterns of phyllostomids are considered one of the greatest
59 adaptive radiations among vertebrate families due to the wide ecological and morphological
60 variation they exhibit (Freeman 2000; Dumont et al. 2014). This morphological variation is
61 reflected in six trophic guilds: nectarivores, frugivores, insectivores, carnivores, sanguivores,
62 and omnivores (Freeman 2000; Rex et al. 2010; Rojas et al. 2011). In addition, phyllostomids
63 have been considered good bioindicators in Neotropical forests, since their species richness
64 and relative abundance is reduced by human habitat disturbance (Fenton et al. 1992;
65 Medellín et al. 2000; Jones et al. 2009).

66 Previous studies suggest that the reduction in the populations of phyllostomid species
67 depends on the trophic guild to which they belong because not all trophic guilds are affected
68 in the same way by habitat disturbance (Medellín et al. 2000; Klingbeil & Willig 2009; Willig et
69 al. 2019). In general, frugivorous and nectarivorous bats are considered tolerant to habitat
70 disturbance, whereas insectivorous and carnivorous bats are considered sensitive. However,
71 when analysing the response of bats from different trophic guilds in different types of habitat
72 disturbance, contradictory results arise. This contradictory pattern has been observed in
73 nectarivorous (Ochoa 2000; Williams-Guillén & Perfecto 2010; Durán & Pérez 2015),
74 insectivorous (Murillo-García & Bedoya-Durán 2014), and sanguivorous phyllostomid bats
75 (Quinto-Mosquera et al. 2013; Gonçalves et al. 2017). The latter, traditionally considered as
76 tolerant to human disturbance activities, such as livestock, appear to be sensitive (Quinto-
77 Mosquera et al. 2013; Gonçalves et al. 2017).

78 Several studies have been conducted in order to explore this controversy. It has been
79 found that omnivorous and frugivorous bats are tolerant to livestock grassland, whereas
80 carnivorous, insectivorous, nectarivorous, and sanguivorous bats become sensitive to this
81 type of disturbance (Gonçalves et al. 2017). Another study that considered different types of
82 habitat disturbance showed that carnivorous and insectivorous bats are sensitive to habitat
83 disturbance, frugivores and nectarivores tolerate agroforestry crops, and all trophic guilds,
84 including omnivores and sanguivores, are sensitive to monocultures and grasslands (García-
85 Morales et al. 2013). This is consistent with the results of a recent study that found that the
86 functional and taxonomic diversity of Neotropical bats decreases in habitats less similar to
87 conserved forests (i.e. high contrast), such as crops, grasslands, and early-stage secondary
88 forests (Farneda et al. 2019). However, it is not clear how bats belonging to different trophic
89 guilds would respond to urbanization, logging, and tourism. In addition, considering the wide
90 geographic distribution of phyllostomids, it is still unknown if the type of forest where the
91 disturbance occurs could affect their relative abundance. Moreover, there are factors that
92 have not been considered, such as the distance between conserved forests and disturbed
93 habitats, and the phylogenetic signal in the response to disturbance. Previous studies have
94 shown that the abundance of frugivorous bats decreases in wooded crops and grasslands as
95 the distance to a patch of conserved forest increases (Galindo-González & Sosa 2003), which
96 is similar to what has been found in birds and trees (Socolar et al. 2019). It is important to
97 note that, because we are performing observations with bat species, it is necessary to
98 determine the phylogenetic signal based on the phylogenetic relationship between species,
99 since their relatedness could generate statistical non-independence (Münkemüller et al.

100 2012). Finally, since the last meta-analysis carried out in 2013, more than twenty studies have
101 been conducted in the Neotropics in order to understand the response of phyllostomids to
102 habitat disturbance. These studies can allow to make a new quantitative revision about the
103 effect of habitat disturbance on phyllostomid abundance.

104 Therefore, the objective of this study was to answer, through a series of meta-
105 analyses, the following questions:

106 i) Is the relative abundance of trophic guilds occupied by phyllostomids different
107 according to the type of habitat disturbance? We expected frugivorous, nectarivorous, and
108 omnivorous bats to be more abundant, or maintain a similar abundance, in disturbed forests,
109 such as secondary forests, crops, mixed habitats with crops and grasslands, forests with
110 selective logging, forests with tourism, and urban areas, compared to conserved forests.
111 These types of human disturbances allow the presence of pioneer plants in these disturbed
112 habitats or their surroundings, favouring phytophagous bats or those that include pioneer
113 plants in their diet (Peters et al. 2006; Castro-Luna et al. 2007; Saldaña-Vázquez et al. 2010;
114 Prone et al. 2012; Cisneros et al. 2015; Willig et al. 2019). We expected sanguivores to
115 increase their abundance, or maintain a similar abundance, in secondary forests, crops, and
116 mixed habitats with crops and grasslands, compared to conserved forests. The proximity of
117 these habitats to human settlements and their domestic animals represents a potential source
118 of food (Delpietro et al. 1992; Bobrowiec et al. 2015). Conversely, we expected carnivores
119 and insectivores to be more abundant in conserved forests, compared to all other types of
120 habitat disturbance, since deforestation promotes a reduction in prey and roosting sites
121 (Bernard & Fenton 2003; Jones et al. 2017).

122 ii) Is the relative abundance of trophic guilds of phyllostomids dependent on crop
123 intensity and secondary forest age? We expected carnivores and insectivores to be sensitive
124 regardless of crop intensity or secondary forest age, based on our previous predictions. In the
125 case of sanguivores, we expected their response to not be related to crop intensity or forest
126 age, since it is believed that their response depends rather on the proximity to human
127 settlements, as mentioned above. We expected frugivores, nectarivores, and omnivores to be
128 tolerant to low intensity crops (e.g. agroforestry) and sensitive to high intensity crops (e.g.
129 monocultures), since pioneer plants have been observed to be abundant in low intensity
130 crops, and their abundance decreases as intensity increases (Williams-Guillén & Perfecto
131 2010). We also expected these three guilds to remain tolerant throughout the different ages of
132 secondary forests, since pioneer plants are abundant in these habitats due to the succession
133 process (Castro-Luna et al. 2007; de la Peña-Cuéllar et al. 2012; Farneda et al. 2018).

134 iii) Is the relative abundance of phyllostomid trophic guilds in disturbed habitats related
135 to the distance to conserved forests? We expected bats, despite their ability to fly, to
136 decrease their abundance in disturbed habitats as the distance to conserved forests
137 increased, which is similar to patterns observed in terrestrial mammals, other bats, and birds
138 (Galindo-González & Sosa 2003; Socolar et al. 2019; Pardo et al. 2019). We expected this
139 because most diurnal refuges of bats are in conserved habitats (Cortés-Delgado & Sosa
140 2014).

141 iv) Is the relative abundance of phyllostomid trophic guilds related to the forest where
142 human disturbance occurs? We expected bats to be sensitive to different types of habitat
143 disturbance in forests with higher elevation but not in lowland tropical forests, as has been

144 observed in another animal groups (Dalsgaard et al. 2018). This is because there is a greater
145 availability of food in lowland tropical forests (<1000 meters), which facilitates the increase in
146 bat populations and maintains a greater diversity of bat species compared to forests of higher
147 elevation (Rex et al. 2008; Martins et al. 2015).

148

149 **2. Methods**

150 2.1. Literature search

151 We conducted an extensive review of the available literature through Google scholar. The
152 keywords used were “phyllostomidae”, “abundancia”, “alteración”, “perturbación”,
153 “murciélagos”, “abundance”, “perturbation”, and “bats”. We did not include words in
154 Portuguese because most studies published in this language regularly include a title, abstract,
155 and keywords in English. We did not limit the search by year of publication. We selected
156 studies that sampled phyllostomids in disturbed habitats and at least one conserved forest. All
157 the studies considered in the analysis included: number of captures of each bat species per
158 site, distance between sampled sites, and a description of the type of habitat disturbance.
159 When studies did not report the distance among sampled sites, we extracted it from the study
160 site map (when present) with ImageJ 1.52a (Schneider et al. 2012).

161

162 2.2. Database

163 We obtained a total of 22 studies presenting useful data (Supporting Information). The 22
164 studies summarized 763 bat species observations (i.e. number of cases, k) conducted in six
165 countries (Fig. 1). The observations comprised 107 phyllostomid bat species belonging to 42
166 genera and 11 trophic guilds, based on (Rojas et al. 2011), and seven types of disturbance
167 (Table 1) and five forest types, according to the ecological zones defined by the FAO (2012).

168

169 2.3. Phylogenetic signal in phyllostomid abundance

170 We identified two potential sources of non-independence in our data. The first one was the
171 possibility of phylogenetic signal in the species abundance observed in disturbed habitats
172 (Nakagawa et al. 2017). To assess this effect, we evaluated the presence of phylogenetic
173 signal by making a phylogenetic tree of the species present in our database. The second
174 source was related to the author involved in the investigation (Nakagawa et al. 2017), when
175 more than one species data item coming from the same author could be similar or biased. To
176 deal with this effect, we included author as a random effect in our meta-analysis (see below).

177 For the estimation of phylogenetic signal in species abundance in disturbed habitats, we
178 constructed a new phylogeny for the Phyllostomidae species present in our abundance
179 dataset, since not all species with observations of abundance were present in previous
180 Phyllostomidae phylogenies (Baker & Hooper 2003; Datzmann et al. 2010; Rojas et al. 2011);
181 Shi and Rabosky (2015)). Characters used were DNA sequences obtained from the Genbank
182 database (NCBI) for Cytochrome Oxidase I (COI), Recombination activating 2 (RAG2), and
183 Cytochrome B (CYTB) genes from 157 phyllostomid species and one mormoopid species

184 (*Pteronotus parnellii*), which was used as an outgroup (Supporting Information). We aligned
185 all sequences with MUSCLE using the default parameters (Edgar 2004). We performed a
186 multilocus phylogenetic reconstruction in BEAST v1.8.4 (Suchard et al. 2018) for the
187 Bayesian inference. We linked the trees and the molecular substitution model for all genes.
188 We used the GTR+I+G molecular substitution model, strict clock model, and constant size
189 model for the construction of the tree (Kingman 1982). We did three independent runs for one
190 hundred million generations and sampled every one thousand generations. We discarded the
191 first 2.5 million generations of each run as a burn-in. We used TRACER v1.8.2 (Rambaut et
192 al. 2018) to estimate the effective sample size for each parameter (all resulting effective
193 sample sizes exceeded 100) and its convergence, and to calculate the mean, upper, and
194 lower bounds of the 95% highest posterior density interval (95% HPD). We combined the
195 trees sampled from each independent run (10000) using LogCombiner and TreeAnnotator
196 (Heled & Drummond 2010). The obtained grouping of species was consistent with
197 phylogenetic trees generated in other studies (Rojas et al. 2011; Shi & Rabosky 2015).

198 We looked for a phylogenetic signal in the abundance of bat species by performing a
199 randomization test in the R computational environment (R Core Team 2018). We used the
200 obtained phylogenetic tree (Fig. 2) and its branch lengths to perform the randomization test,
201 which evaluates the variation expected in a quantitative trait under a Brownian motion model
202 of evolution compared with values obtained by shuffling trait data across the tips. Higher
203 values and statistically significant values of the K index indicate a stronger phylogenetic signal
204 (Blomberg et al. 2003). Species abundance values used in the randomization test were the
205 mean of the proportion of bats captured in disturbed habitats for each species. To obtain

206 these values, we performed a multivariate meta-analysis of the proportion of the abundance
207 of species captured in disturbed habitats, taking species as a fixed factor and the author that
208 reported the abundance value as a random factor (Viechtbauer 2010).

209 Given that not all phyllostomid species with abundance were present in the
210 phylogenetic tree, we pruned the branches using the "Picante" package (Kembel et al. 2010).
211 In this way, species in the tree corresponded to those in the database used in the meta-
212 analysis. Of the 158 species in the tree and 107 species in the database, only 91 were used
213 in the analysis (Supporting Information). We used the "Geiger" package (Harmon et al. 2008)
214 to create a file that contained the species, the effect size, and the phylogenetic lengths. The
215 phylogenetic signal was tested with the "phytools" package (Revell 2012) using 1000
216 randomizations. Due to the absence of phylogenetic signal in the proportion of bat abundance
217 in the assessed species ($K=0.35$, $P= 0.204$, Fig. 2), the meta-analyses below were performed
218 without phylogenetic correction.

219

220 2.4. Effect of habitat disturbance on abundance of phyllostomid trophic guilds

221 We performed five meta-analyses corresponding to each question in our objectives and their
222 respective moderator variables: 1) habitat disturbance type, 2) crop type, 3) secondary forest
223 age, 4) distance between conserved and disturbed sample sites, and 5) habitat disturbance
224 type inside each forest type. The selected effect size was the proportion of individuals
225 captured in the disturbed habitat from the total of individuals captured per species in both
226 habitats (conserved and disturbed); hereafter referred to as "bat abundance". In each meta-

227 analysis, the author of the study was considered as a random factor (Nakagawa et al. 2017).
228 All analyses were performed using the package “Metafor” (Viechtbauer 2010) in the R
229 computational environment (R Core Team 2018).

230 We used Cochran's Q index as a measure of heterogeneity for each analysis.
231 Heterogeneity is important in meta-analyses because it allows to evaluate if the variation in
232 the collected effect sizes is explained by population variation or by chance (Harrison 2011;
233 Nakagawa et al. 2017). In addition, if heterogeneity is significant, it means that variation in
234 effect size could be explained by moderator variables (i.e. forest type, distance, etc.). In order
235 to examine the publication bias in our data set, we performed a regression test (Egger et al.
236 1997; Nakagawa et al. 2017). A significant result in the regression test indicates that effect
237 sizes (i.e. bat abundance) are balanced. Finally, we did not perform a meta-analysis for
238 carnivorous (C) guilds due to the low number of observations in the database ($k = 2$).

239

240 **3. Results**

241 Bat abundance in disturbed habitats was 0.46 from the total abundance observed ($P < 0.0001$,
242 $CI = 0.42 - 0.48$, $k = 763$), and the observations were significantly heterogeneous
243 ($Q = 28237.5540$, $d.f. = 762$, $P < 0.0001$). Therefore, the response of bats to habitat disturbance
244 was classified as sensitive because the confidence intervals (CI) of the abundance estimate
245 in disturbed habitats was lower than 0.5 and, thus, did not overlap with this value.

246 In general, we found that frugivores (F), frugivores-nectarivores (FN), insectivores-
247 nectarivores (IN), insectivores-nectarivores-frugivores (INF), and nectarivores (N) were

248 tolerant to habitat disturbance. On the other hand, insectivores (I), sanguivores (S),
249 insectivores-frugivores (IF), carnivores-frugivores (CF), and insectivores-carnivores-frugivores
250 (ICF) were sensitive to habitat disturbance (Supporting Information). In addition, for these last
251 three trophic guilds (IF, CF and ICF), the heterogeneity of the adjusted models was not
252 significant (Supporting Information). Therefore, we did not evaluate the effect of the
253 moderator variables on the abundance of these guilds.

254 We evaluated the different moderator variables of bat abundance in disturbed habitats
255 for bats from trophic guilds with significant heterogeneity (F, FN, IN, INF and N). We did not
256 find differences in the abundance of these trophic guilds among different crop types
257 (Supporting Information) despite the significant heterogeneity of the adjusted model ($P < 0.05$,
258 Supporting Information). Secondary forests age and distance from conserved forests were
259 partly explained by trophic guild ($\eta^2_{\text{distance}} = 0.1-0.5$, Supporting Information); however, there
260 was no significance in their heterogeneity ($P > 0.05$, Supporting Information).

261 In the meta-analysis with habitat disturbance type as moderator, we found that only F,
262 N, and INF responded significantly different (Table 2). We found that F were sensitive to
263 logging, grassland, and urbanization, but tolerant to secondary forest and crops. Nectarivores
264 were sensitive to urbanization and tolerant to secondary forest and crops. Finally, INF were
265 sensitive to logging, grassland, and crops, but they were tolerant to secondary forest and
266 mixed habitats such as grassland-crops.

267 Our nested analysis indicated that the response of bats depends on the forest type
268 where the disturbance occurs only in the case of F and FN (Table 3). Frugivores were

269 sensitive to secondary forest if it occurred in the Tropical Mountain System but tolerant when
270 it occurred in the Tropical Rainforest. They were also sensitive to urbanization if it occurred in
271 the Tropical Moist Forest or the Tropical Mountain System but tolerant when it occurred in the
272 Tropical Rainforest. Frugivores-nectarivores were sensitive to secondary forest if it occurred
273 in the Tropical Mountain System but tolerant when it occurred in the Tropical Dry Forest or
274 Tropical Rainforest and were sensitive to crops if they occurred in the Tropical Mountain
275 System but tolerant when they occurred in the Tropical Rainforest.

276

277 **4. Discussion**

278 Our results show that populations of phyllostomid bats are sensitive to human habitat
279 disturbance, which contrasts with what was found in a previous meta-analysis (García-
280 Morales et al. 2013). However, we found that this response depends on the trophic guild to
281 which the species belong. We observed that frugivores (F), frugivores-nectarivores (FN),
282 insectivores-nectarivores (IN), insectivores-nectarivores-frugivores (INF), and nectarivores (N)
283 were tolerant to habitat disturbance, whereas insectivores (I), sanguivores (S), insectivores-
284 frugivores (IF), carnivores-frugivores (CF), and insectivores-carnivores-frugivores (ICF) were
285 sensitive. These results agree with previous observations of the effect of habitat disturbance
286 on phyllostomid abundance (Fenton et al. 1992; Medellín et al. 2000; Ávila-Gómez et al.
287 2015).

288 Even though I and S showed significance in the heterogeneity of the adjusted models,
289 they remained sensitive in subsequent analyses with moderator variables. The response to

290 habitat disturbance by sensitive guilds could be explained by initial deforestation causing the
291 loss of potential refuges. For example, S use holes in living trees as well as caves or cracks in
292 rocks (Voss et al. 2016; Gonçalves et al. 2017), while I and C use holes in living trees or
293 arboreal termite nests (Bernard & Fenton 2003; Kalko et al. 2006; Jones et al. 2017). In
294 addition, I and C present fidelity and permanence towards this resource. Moreover, the prey
295 of these species are more abundant in conserved forests (Kalko et al. 1999; de la Peña-
296 Cuéllar et al. 2012).

297 4.1 Habitat disturbance type

298 Different types of habitat disturbance promote different changes in food and other resources
299 used by phyllostomids and, thus, not all bats can tolerate disturbance in a similar way. We
300 found F and N to have the highest variation in abundance response in relation to disturbance
301 type. This pattern was previously observed by García-Morales et al. (2013).

302 We also found that F and N were tolerant to secondary forests and crops, which is
303 consistent with previous studies (Fenton et al. 1992; Klingbeil & Willig 2009). This response
304 may be due to the abundance of chiropterochorous or chiropterophilous species among
305 pioneer plants in these habitats, thus favouring F and N (Castro-Luna et al. 2007; Muscarella
306 & Fleming 2007; Castro-Luna & Galindo-González 2012). Frugivores were also tolerant to
307 forests with tourism; however, our results are not conclusive because we only included one
308 study with this type of habitat disturbance. This study was conducted near a conserved forest
309 and a secondary forest, which explains the high abundance of this trophic guild (Murillo-
310 García & Bedoya-Durán 2014). On the other hand, we expected F and N to be tolerant to

311 urban zones and forests with selective logging, as has been observed in previous studies
312 (Peters et al. 2006; Ferreira et al. 2010; Prone et al. 2012). However, we found the opposite,
313 which could be explained by our analysis being performed at the trophic guild level, whereas
314 studies that found these guilds to be tolerant were performed at the genus level (Saldaña-
315 Vázquez et al. 2010; Saldaña-Vázquez & Schondube 2016). Finally, we found F to be
316 sensitive to livestock grasslands, which is consistent with our expectations and the study by
317 García-Morales et al. (2013).

318

319 4.2. Crop type and secondary forest age

320 We found that crop type and secondary forest age did not affect the abundance of
321 phyllostomid trophic guilds. This could be explained by our study including a high number of
322 studies on agroforestry crops versus only one on monocultures. Similarly, in the case of
323 secondary forest age, most studies evaluated secondary forests of 15 years or less, whereas
324 very few looked at secondary forests of 50 years or more. The results may change with data
325 with the same number of cases per crop type according to intensity and secondary forests of
326 different ages.

327

328 4.3. Distance to conserved forests

329 We found that the distance to conserved forests does not influence the abundance of
330 phyllostomid trophic guilds in disturbed habitats. Other studies show the opposite effect in
331 non-flying mammals, bats, birds, and trees (Galindo-González & Sosa 2003; Cleary et al.

332 2016; Socolar et al. 2019; Pardo et al. 2019). The lack of a significant effect of distance to
333 conserved habitats on bat abundance in disturbed habitats may be related to the variation in
334 habitat disturbance type in our study and the ability of phyllostomids to fly large distances
335 either to migrate or forage (Arnone et al. 2016; Esbérard et al. 2017; Medellín et al. 2018). In
336 order to determine the effect of these two variables on bat abundance in disturbed habitats,
337 studies that evaluate the effects of habitat disturbance on bat abundance comparing
338 disturbance type and phyllostomid vagility are necessary.

339

340 4.4. Forest type

341 Our results show that the abundance of F and FN can vary depending on the type of forest
342 where the habitat disturbance occurs. Both trophic guilds decreased their abundance, from
343 tolerant to sensitive, in secondary forests of tropical mountain systems (forests with altitudes
344 higher than 1000 meters). The same happened with FN, which became sensitive in crops
345 located in tropical mountain systems. On the other hand, F became tolerant in urban zones
346 when they occurred in tropical rainforests (forests with an altitude lower than 1000 meters).

347 The abundance and richness of phyllostomids could change according to altitude,
348 since higher species richness and abundance has been reported in lowland forests (Sampaio
349 et al. 2003; Rex et al. 2008), whereas abundance has been observed to decrease in habitats
350 with altitudes above 1000 meters (McCain 2007; Martins et al. 2015; de Carvalho et al. 2019).
351 Therefore, habitat disturbance could have a major impact on phyllostomid populations in
352 highlands compared to lowlands. In addition, the diversity of plants is high in lowlands but

353 decreases after 1000 meters (Gentry 1988), which explains the sensitivity of phytophagous
354 bats to habitat disturbance in highland forests. Other studies have shown the importance of
355 protecting high altitude tropical forests because human activities put ecosystem services at
356 risk, for example, the protection and purification of freshwater (Martínez et al. 2009;
357 Armenteras et al. 2011). Our results support this idea and highlight the importance of the
358 conservation of highland tropical forests.

359

360 **5. Conclusions**

361 Although some bats are tolerant to habitat disturbance, because these habitats can provide
362 food and refuges, our results do not suggest that they replace the resources provided by a
363 conserved forest. Bats move through the matrix using both anthropic environments and
364 conserved forests overnight (Ripperger et al. 2015). Therefore, conserved forests will always
365 be essential to maintain phyllostomid bat populations of different trophic guilds. We conclude
366 that the response of phyllostomid guilds to human habitat disturbance is complex and does
367 not depend on phylogenetic signal. Sensitivity occurs regardless of disturbance type or forest
368 type. It is advisable to enrich the anthropogenic matrix with forest cover and
369 chiropterochorous or chiropterophilous species to promote colonization by bats and other
370 animals in order to facilitate their functions and ecosystem services (Kunz et al. 2011; Castro-
371 Luna & Galindo-González 2012).

372 The literature used in this meta-analysis was limited because some published studies
373 do not describe the type of habitat disturbance. Also, some studies do not use a control site

374 (conserved forest) and they do not show a map or coordinates of the sampled sites. We
375 highlight the absence of studies in Central America and the Antilles, which is partly due to the
376 limitations already mentioned. For future research, it is necessary to have more information
377 about phyllostomid species variables, such as body mass, flight strategies, foraging range,
378 and type of refuge used. These can be decisive in understanding the complex response of
379 phyllostomid guilds to habitat disturbance.

380

381 **Appendix A. Supplementary data**

382 The supplementary data to this article are available online.

383 **Conflicts of interest:**

384 The authors of this article have no conflict of interest to declare.

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388

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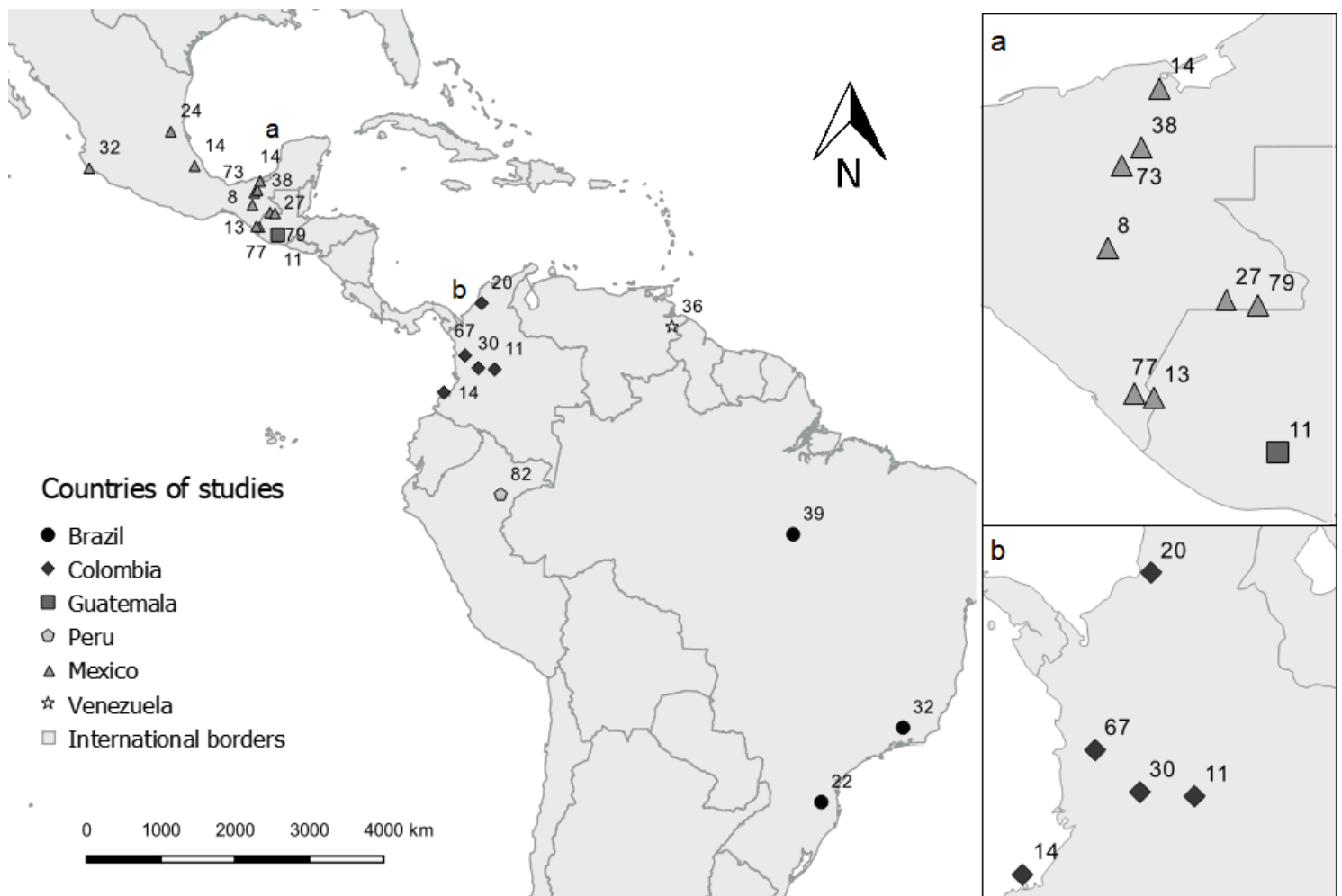
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603 **Figures**



604 Figure 1. Map of the locations of the studies used for the generation of the database. Each
605 point indicates the number of cases that contributed to the analysis. Boxes on the right show
606 a close up of the areas marked as a and b on the main map.

611 **Tables**

612 Table 1. Definition of the seven types of habitat disturbance and the number of cases for each
613 one.

Disturbance type	Definition	Number of cases (<i>k</i>)
Crops	All land used for growing a product regardless of its type and intensity. These were subclassified into: monoculture, polyculture, agroforestry, and urban crops.	262
Grassland	Land covered to a greater extent by grass in an induced manner and for livestock purposes.	21
Grassland-Crops	Mixed use of land by induced grassland for livestock and crops.	20
Logging	Forest intervened by selective logging.	107
Secondary forest	Secondary vegetation where, after the removal of the forest, there has been a process of natural succession. The number of years the process takes without any type of human intervention was taken.	292
Tourism	Forest intervened with the presence of trails and buildings for tourism purposes.	7
Urban zone	Sites with vegetation within the urban matrix, such as home gardens and urban parks.	54

614

615 Table 2. Response of frugivorous (F), nectarivorous (N), and insectivorous-frugivorous-
616 nectarivorous (INF) bats to different types of habitat disturbance.

Trophic guild (k)	QM ^a (d.f.)	Disturbance type	Estimate ^b	CI ^c	P
F (462)	1019.5690 (7)	Logging ^d	0.2029	0.0932-0.312	0.0003
		Tourism ^e	0.751	0.634-0.869	<0.0001
		Secondary forest ^e	0.556	0.459-0.653	<0.0001
		Crops ^e	0.558	0.461-0.656	<0.0001
		Grassland ^d	0.215	0.115-0.315	<0.0001
		Grassland-crops	0.221	0-0.662	0.325
		Urban zone ^d	0.3202	0.219-0.421	<0.0001
		Global analysis	0.4808	0.454-0.507	<0.0001
N (41)	413.7397 (6)	Logging	0.552	0.418-0.687	<0.0001
		Tourism	0.823	0.451-1	<0.0001
		Secondary forest ^e	0.785	0.686-0.885	<0.0001
		Crops ^e	0.641	0.522-0.7605	<0.0001
		Grassland-crops	0.5	0.0799-0.9201	0.0197
		Urban zone ^d	0.219	0-0.452	0.0651
		Global analysis	0.566	0.478-0.653	<0.0001
		INF (26)	504.4064 (6)	Logging ^d	0.226
Secondary forest ^e	0.813			0.712-0.913	<0.0001
Crops ^d	0.359			0.245-0.473	<0.0001
Grassland ^d	0.129			0-0.4707	0.4577
Grassland-crops ^e	0.962			0.839-1	<0.0001
Urban zone	0.363			0.0013-0.725	0.0492
Global analysis	0.473			0.349-0.596	<0.0001

617 ^aCochran's Q index value for the heterogeneity test

618 ^bis the proportion of bat abundance estimated for each model.

619 ^cConfidence interval of the estimate value

620 ^dare sensitive and do not transpose their confidence intervals with ^e

621 ^eare tolerant and do not transpose their confidence intervals with ^d

622 Table 3. Response of frugivorous (F) and frugivorous-nectarivorous (FN) bats to disturbance
 623 type in different forest types: Tropical Rainforest (TRF), Tropical Dry Forest (TDF), Tropical
 624 Moist Forest (TMF), Tropical Mountain System (TMS), and Subtropical Mountain System
 625 (STMS).

Trophic guild (<i>k</i>)	QM ^a (d.f.)	Disturbance type	Forest type	Estimate ^b	CI ^c	p
F (462)	1213.5333 (15)	Secondary forest	TDF	0.576	0.341-0.811	<.0001
			TMF	0.284	0-0.617	0.0943
			TMS ^d	0.233	0-0.469	0.0527
			TRF ^e	0.627	0.515-0.738	<.0001
		Crops	STMS	0.295	0-0.627	0.0818
			TMS	0.587	0.349-0.826	<.0001
			TRF	0.588	0.476-0.699	<.0001
		Grassland	TMS	0.0264	0-0.263	0.827
			TRF	0.144	0.028-0.2603	0.015
		Urban zone	TMF ^d	0.0451	0-0.377	0.7901
			TMS ^d	0.068	0-0.4015	0.6894
			TRF ^e	0.6061	0.4098-0.8024	<.0001
		Global analysis		0.4808	0.454-0.5074	<.0001
		FN (52)	223.4907 (12)	Secondary forest	TDF ^e	0.7304
TMF	0.75				0.0594-1	0.0333
TMS ^d	0.0385				0-0.388	0.829
TRF ^e	0.697				0.563-0.831	<.0001
Crop	STMS			0.823	0.454-1	<.0001
	TMS ^d			0.116	0-0.446	0.489
	TRF ^e			0.628	0.493-0.762	<.0001
Grassland	TMS			0.0385	0-0.395	0.832
	TRF			0.168	0-0.3809	0.121
Global analysis				0.524	0.443-0.6043	<.0001

626 ^aCochran's Q index value for the heterogeneity test

627 ^bis the proportion of bat abundance estimated for each model.

628 ^cConfidence interval of the estimate value
629 ^dare sensitive and do not transpose their confidence intervals with ^e
630 ^eare tolerant and do not transpose their confidence intervals with ^d