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Farneda, F, Meyer, CFJ and Grelle, CEV

<http://dx.doi.org/10.1111/btp.12736>

Title	Effects of land-use change on functional and taxonomic diversity of Neotropical bats
Authors	Farneda, F, Meyer, CFJ and Grelle, CEV
Type	Article
URL	This version is available at: http://usir.salford.ac.uk/id/eprint/53407/
Published Date	2019

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1 LRH: Farneda, Meyer and Grelle

2 RRH: Bat biodiversity loss in countryside landscapes

3 **Effects of land-use change on functional and taxonomic diversity of Neotropical**
4 **bats**

5 Fábio Z. Farneda¹, Christoph F. J. Meyer², Carlos E. V. Grelle^{1,3}

6 ¹Department of Ecology, Federal University of Rio de Janeiro, PO Box 68020, 21941-902

7 Rio de Janeiro, Brazil.

8 ²School of Environment and Life Sciences, University of Salford, M5 4WT Salford, United

9 Kingdom.

10 ³Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, 22460-030 Rio de Janeiro,

11 Brazil.

12 Correspondence

13 Farneda Z.F., Department of Ecology, Federal University of Rio de Janeiro, 21941-902 Rio

14 de Janeiro, Brazil. Email: fabiozarneda@gmail.com

15 Funding information

16 Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES); Conselho

17 Nacional de Desenvolvimento Científico e Tecnológico (CNPq); Fundação para a Ciência e

18 a Tecnologia (FCT), Grant/Award Number: PTDC/BIA-BIC/111184/2009.

19 Received____; revision accepted____.

20 **Abstract**

21 Human land-use changes are particularly extensive in tropical regions, representing one of
22 the greatest threats to terrestrial biodiversity and a key research topic in conservation.
23 However, studies considering the effects of different types of anthropogenic disturbance on
24 the functional dimension of biodiversity in human-modified landscapes are rare. Here, we
25 obtained data through an extensive review of peer-reviewed articles and compared 30
26 Neotropical bat assemblages in well-preserved primary forest and four different human-
27 disturbed habitats in terms of their functional and taxonomic diversity. We found that
28 disturbed habitats that are structurally less similar to primary forest (pasture, cropland and
29 early-stage secondary forest) were characterized by a lower functional and taxonomic
30 diversity, as well as community level-functional uniqueness. These habitats generally
31 retained fewer species that perform different ecological functions compared to higher-
32 quality landscape matrices, such as agroforestry. According to functional trait composition,
33 different bat ensembles respond differently to landscape change, negatively affecting
34 mainly gleaning insectivorous bats in pasture, narrow-range species in cropland, and
35 heavier animalivorous bats in secondary forest. Although our results highlight the
36 importance of higher-quality matrix habitats to support elevated functional and taxonomic
37 bat diversity, the conservation of bat species that perform different ecological functions in
38 the mosaic of human-modified habitats also depends on the irreplaceable conservation
39 value of well-preserved primary forests. Our study based on a pooled analysis of individual
40 studies provides novel insights into the effects of different human-modified habitats on
41 Neotropical bat assemblages.

42 **Key-words:** Chiroptera; conservation biology; countryside ecosystems; functional traits;
43 habitat loss; land-use change; matrix quality; wildlife-friendly farming

44 **1. Introduction**

45 Given the unrelenting pace of land-use change across the tropics, being able to make
46 accurate predictions about the persistence of biodiversity and associated ecosystem services
47 across the complex, increasingly fragmented and human-dominated landscapes of the
48 Anthropocene is crucial for informing conservation strategies and policy (Barlow et al.,
49 2007; Jetz, Wilcove, & Dobson, 2007; Phalan et al., 2013). Tropical deforestation
50 accounted for 32% of global forest loss between 2000 and 2012, nearly half of which
51 occurred in South America (Hansen et al., 2013). Resulting landscapes typically comprise a
52 mosaic of human-modified habitats that include remnants of old-growth forest, cattle
53 pasture, cropland, secondary forest regenerating after clearance or burning, agroforestry
54 systems, wood plantations and logged forest (Barlow et al., 2007; Gardner et al., 2009;
55 Chazdon, 2014; Reid, Fagan, Lucas, Slaughter, & Zahawi, 2018).

56 In human-modified landscapes, the effects of edge, area and isolation on biota may
57 be more or less pronounced, depending on how similar the matrix is structurally to the
58 original habitat (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013; Laurance et al.,
59 2017). Furthermore, matrix quality and permeability may regulate the use of corridors and
60 stepping stones by species and strongly influence their occurrence and abundance (Kupfer,
61 Malanson, & Franklin, 2006; Watling, Nowakowski, Donnelly, & Orrock, 2011; Didham,
62 Kapos, & Ewers, 2012). Community-wide functional contributions depend not only on
63 which species and functional traits are present, but also on species abundances (Stuart-
64 Smith et al., 2013; Gagic et al., 2015). As the ecological effects of a species are generally
65 proportional to its abundance or biomass, functional diversity (i.e. the value and variation
66 of traits between species that affect its performance, fitness and ecological functions, Weiss

67 & Ray 2019) weighted by abundance offers promising insights into how community
68 assembly mechanisms are influenced by environmental changes (de Bello, Lepš, Lavorel,
69 & Moretti, 2007), and more accurately reflects functional community structure compared to
70 metrics based on simple species counts (Mouillot, Graham, Villéger, Mason, & Bellwood,
71 2013; Stuart-Smith et al., 2013; Gagic et al., 2015).

72 From a functional perspective, phyllostomid bats are a well-suited indicator group
73 for studying effects of landscape changes in the tropics because they display high species
74 richness, abundance, variation in morphology, foraging behavior and fulfill crucial roles as
75 pollinators, seed dispersers, prey and predators (Kunz, Torrez, Bauer, Lobova, & Fleming,
76 2011; Meyer, Struebig, & Willig, 2016). Few studies to date have explored the impact of
77 human-induced habitat changes on the diversity and structure of Neotropical bat
78 assemblages focusing on the functional dimension of biodiversity (but see Cisneros, Fagan,
79 & Willig, 2015; Garcia-Morales et al., 2016; Farneda et al., 2018a; Pereira, Fonseca, &
80 Aguiar, 2018). These studies generally point to an inverse relationship between functional
81 diversity and land-use intensity, suggesting that the preservation of a large proportion of the
82 ecological functions in a community requires the conservation of vast areas of primary
83 forests. However, so far no attempt has been made to generalize beyond these single case
84 studies by comparing Neotropical bat assemblages in well-preserved forest and different
85 human-disturbed habitats in terms of functional diversity based on a comprehensive
86 analysis of available datasets.

87 The present study used a pooled analysis of individual ecological studies to evaluate
88 how changes in multiple human-modified habitats affect the taxonomic and functional
89 dimensions of Neotropical phyllostomid bats. Additionally, we investigated how key
90 ecological functions provided by bats are being imperiled by land-use intensification. Our

91 general hypothesis was that functional and taxonomic diversity increase with decreasing
92 land-use intensity and disturbance. We predicted that, (1) functional and taxonomic
93 diversity and community-level functional uniqueness (sensu Ricotta et al., 2016) would be
94 strongly affected by structural complexity and patch-matrix contrast of each landscape,
95 being lower in high-contrast matrices (pasture, cropland and early-stage secondary forest)
96 and higher in relatively low-contrast systems (agroforestry) relative to undisturbed forest,
97 and (2) trait-based responses should converge according to fragment-matrix contrast, being
98 stronger in more intensively disturbed matrices (pasture, cropland) due to a greater loss of
99 suitable foraging and roosting sites for bats. In contrast, for lower-contrast landscapes we
100 anticipated the functional composition in the matrix to mirror more closely that of well-
101 preserved primary forest.

102 **2. Material and methods**

103 We followed a systematic review methodology (Lortie, 2014) to synthesize information
104 about bat responses to type of habitat modification. Studies were identified based on Meyer
105 et al. (2016) and through a comprehensive search in SCOPUS and Google Scholar
106 (accessed in July 2018) using the keywords: “bat* AND Neotropic* AND (assemblage*
107 OR community* OR diversity* OR fragment* OR deforestation* OR disturbance* OR
108 pasture* OR cropland* OR secondary forest* OR agroforestry*)”. No restriction on date
109 was used. The publications retrieved were subsequently screened for suitability for
110 inclusion in the analysis based on the article’s title, abstract and text. This resulted in a total
111 of 30 studies conducted in eight countries throughout the Neotropics (Figure 1) which were
112 deemed relevant based on the following criteria: studies (1) were published in an indexed,

113 peer-reviewed scientific journal, (2) compared bat assemblages between well-preserved
114 primary forest plots and at least one type of terrestrial human-disturbed habitat, (3)
115 provided species abundance data for each habitat (see Supporting Information, Table S1),
116 and (4) provided information on sampling effort per habitat. Furthermore, to avoid biases in
117 the results that might be introduced by different sampling methods, we (5) included only
118 studies in which ground-level mist-nets were used, and consequently restricted our analysis
119 to phyllostomid bats as they can be well-sampled with this method (Kalko, Handley, &
120 Handley, 1996). As our purpose here was to review evidence for the effects of
121 *anthropogenic* habitat modification in unpopulated terrestrial systems on Neotropical bat
122 assemblages, we (6) excluded studies that were conducted in naturally fragmented
123 landscapes (e.g. forest patches embedded in grasslands or in a matrix dominated by
124 savannas, such as presented by Montiel, Estrada, & León, 2006 and Bernard & Fenton,
125 2007), islands (Meyer & Kalko, 2008), and urban landscapes (Jung & Threlfall, 2018). Our
126 review thus focuses on a range of human-modified habitats varying in structural complexity
127 and landscape contrast: (1) pasture, (2) cropland, (3) secondary forest, and (4) agroforestry.
128 We excluded “wood plantation” and “logged forest” because these habitats were only
129 represented by a small number of studies (four studies each).

130 Throughout all studies included, well-preserved forest represented primary, old-
131 growth forest with minimal or no anthropogenic disturbance. Secondary vegetation
132 included sites where, after forest removal, natural succession had occurred for between one
133 and 30 years. We analyzed early- and late-stage secondary forest jointly due to small
134 sample size for late succession (only one study assessed secondary forest with more than 20
135 years of regeneration). Approximately 65% of the studies were conducted in secondary
136 forest with less than 10 years of regeneration. In agroforestry systems, only the understory

137 had been removed, and large trees were kept to provide shade for mainly cocoa, coffee and
138 banana. In croplands, the forest had been completely cut and replaced by sun crop
139 monocultures, such as corn, citrus, coffee, palm and allspice. In pastures, the understory
140 had been removed to allow cattle grazing, although in some cases a few trees were
141 maintained.

142 **2.1 Species traits**

143 To calculate the various aspects of functional diversity, we used four species traits that
144 comprise important functional components of Neotropical bat diversity, and that are related
145 to species responses to human-modified tropical landscapes and ecosystem functioning
146 (Luck, Lavorel, McIntyre, & Lumb, 2012; Farneda et al., 2015): (1) body mass – based on
147 the average of each species, (2) trophic level – two broad trophic categories:
148 “animalivorous” or “phytophagous”, (3) diet – based on the main food item of each species,
149 and (4) habitat breadth – based on the number of habitat types in which a species occurs,
150 varying from 1 (more restricted distribution) to 6 (more widespread) (see Table S3 for trait
151 values of individual species). Trait information was obtained from the Ecological Register
152 database (ecoregister.org, accessed on 15 July 2018), a repository of published ecological
153 survey data from around the world (Alroy, 2019). Logarithmic transformations and
154 standardization to a mean of zero and a standard deviation of one were performed on body
155 mass to normalize values and to facilitate comparison of their relative effects.

156 **2.2 Data analysis**

157 We followed the methodological framework introduced by Ricotta et al., (2016) to quantify
158 functional and taxonomic diversity and community-level functional uniqueness of bat

159 assemblages. This approach takes into account relative species abundances, thus adequately
160 accommodating differences in sampling effort between studies. It does, however, not
161 control for potential variation in species detectability related to differences in habitat
162 complexity (Meyer et al. 2011). Relative species abundance was based on capture rate in
163 each assemblage, which was calculated by multiplying the area of each net by the time they
164 remained exposed in the field by the number of sampling repetitions by the number of nets
165 ($\text{m}^2\cdot\text{h}$; sensu Straube & Bianconi, 2002).

166 To quantify functional diversity, we calculated Rao's quadratic diversity index Q ,
167 which takes the differences (trait-based variance) between species pairs into account. For
168 taxonomic diversity, we computed the Simpson index D , which considers all species
169 maximally dissimilar (Botta-Dukát, 2005). Furthermore, we calculated community-level
170 functional uniqueness U (Q/D) (Ricotta et al., 2016). For all index values (Q , D and U),
171 pairwise comparisons between well-preserved primary forests (control group) and disturbed
172 habitat (treatment group) were performed using paired permutational tests with 9999
173 randomizations. The calculations of Q , D and U were performed with the 'uniqueness'
174 function provided by Ricotta et al., (2016).

175 To assess how habitat-level changes affect bat functional trait composition, we
176 calculated community-weighted mean trait values (CWM; Lavorel et al., 2008). This
177 method allows assessing shifts in mean trait values weighted by relative species abundances
178 (Lavorel et al., 2008), thus equalizing differences in capture effort between studies. We
179 calculated CWM traits using the 'functcomp' function of the R package FD (Laliberté &
180 Legendre, 2010). For each trait, pairwise comparisons between primary forests and matrix
181 type were performed using paired permutational tests with 9999 randomizations.

182 The functional pairwise dissimilarity matrices in all analyses were calculated using
183 Gower's distance since our trait matrix (see Table S3) included a mix of continuous and
184 categorical traits. Paired mean differences for Q , D , U and CWM were calculated using
185 bootstrap medians, i.e. difference between the median of the control group and of the
186 treatment group, as implemented in the R package dabestr (Ho et al. 2018). The result of
187 the bootstrap is 1000 difference values per habitat, which were used to determine the 95%
188 confidence intervals. All analyses were conducted using R software (R Development Core
189 Team, 2017).

190 **3. Results**

191 A total of 50,925 individuals of 103 bat species were used in the analysis. Species richness
192 was highest in primary forests, followed by agroforestry, early-stage secondary forest,
193 cropland, and pasture (Table 1). Primary forests were functionally and taxonomically more
194 diverse than modified habitats (Figure 2). Pasture, cropland and secondary forest had
195 significantly lower functional diversity than primary forest ($p < 0.05$). In contrast,
196 differences for agroforestry were not significant ($p = 0.434$) (Figure 3; Table 2). Secondary
197 forest and cropland had significantly lower taxonomic diversity and community-level
198 functional uniqueness U than primary forest ($p < 0.032$) (Figure 3; Table 2), reflecting a
199 substantial loss of species that perform different ecological functions in these habitats.

200 The most pronounced differences in functional trait composition between primary
201 forest and modified habitats were found for secondary forest, for which paired permutation
202 tests comparing CWM trait values revealed significant changes for body mass, trophic
203 level, diet and habitat breadth ($p < 0.05$) (Figure 4; Table 2). While phytophagous species

204 represented by nectarivores with a more widespread geographic distribution increased
205 significantly in secondary forest relative to undisturbed forest, animalivorous species
206 represented by carnivores, insectivores and sanguinivores, were markedly underrepresented
207 (Figure 4). Furthermore, bats in secondary forest had slightly, but significantly lower body
208 mass than those in primary forest ($p = 0.026$) (Table 2). For pastures, we found
209 significantly lower CWM trait values for bats with an insectivorous diet ($p = 0.049$), while
210 croplands were characterized by a significant increase in habitat breadth associated to wide-
211 ranged species ($p = 0.030$) (Figure 4; Table 2). Statistical support for changes in functional
212 trait composition in agroforestry system was limited (Figure 4; Table 2).

213 **4. Discussion**

214 The global terrestrial human footprint continues to expand towards the remaining pristine
215 habitats, threatening biodiversity, ecosystem services and human well-being (Ehrlich &
216 Ehrlich, 2013; Ceballos et al., 2015). Across the Neotropics, conversion of native
217 vegetation to cattle pasture and crop monoculture constitute one of the main causes of
218 biodiversity decline, leading to frequent and pervasive large-scale changes in biological
219 communities (Phalan et al., 2013; Poore & Nemecek, 2018). Our findings indicate that the
220 direction of these effects on Neotropical bat assemblages is fundamentally influenced by
221 the type of matrix surrounding primary forest patches in human-modified ecosystems.
222 Matrix habitats which are less similar to primary forest in terms of vegetation structure and
223 composition (pasture, cropland, early-stage secondary forest) displayed significant
224 decreases in bat functional and taxonomic diversity, community-level functional

225 uniqueness, and stronger shifts in functional trait composition compared to lower-contrast
226 systems (agroforestry).

227 The importance of matrix quality in sustaining biodiversity and ecosystem
228 functioning in fragmented landscapes has widely been documented in the literature (e.g.
229 Laurance et al., 2017; Kupfer et al., 2006; Watling et al., 2011; Driscoll et al., 2013;
230 Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Our results confirm previous findings
231 that matrix quality can intensify (in the case of cropland, pasture and early-stage secondary
232 forest) or mitigate (as observed for agroforestry systems) the negative impacts of
233 deforestation on multiple dimensions of bat biodiversity. Conceptually, the matrix is a
234 habitat structurally and compositionally different from primary forest (Driscoll et al., 2013),
235 and this has implications for the occurrence and abundance patterns of its bat assemblages
236 (Avila-Cabadilla, Stoner, Henry, & Añorve, 2009; Farneda et al., 2015; Gonçalves, Fischer,
237 & Dirzo, 2017), which in turn may significantly affect their taxonomic and functional
238 diversity.

239 Our results indicate that bat responses in pasture, cropland and secondary forest are
240 linked to species-specific differences in terms of foraging requirements. Despite some
241 studies suggesting that these habitats harbor considerable bat taxonomic diversity and
242 provide important foraging habitats for some phytophagous bat species (Medellín, Equihua,
243 & Amin, 2000; Moreno & Halffter, 2001; Avila-Cabadilla et al., 2009), they host
244 assemblages that significantly differ in richness and composition from those in primary
245 forest (Faria, 2006; Barlow et al., 2007; Meyer et al., 2016; Farneda et al., 2018a). The
246 conservation value of pasture, cropland and secondary forest for bats critically depends on
247 landscape context, generally being greater in mosaic landscapes where patches of residual
248 tree cover (e.g. riparian vegetation, live fences) are located close to old-growth forest

249 (Estrada, Coates-Estrada, & Meritt, 1993; Vleut, Levy-Tacher, Galindo-González, de Boer,
250 & Ramírez-Marcial, 2012). For secondary forest in particular, their long-term protection
251 against human land-use changes is pivotal to achieving significant taxonomic and
252 functional recovery of Neotropical bat assemblages in fragmented landscapes (Farneda et
253 al., 2018a, b; Rocha et al., 2018).

254 Our findings are also consistent with the assertion that higher-quality matrix
255 habitats, such as agroforestry systems are biodiversity-friendly with the potential to be of
256 considerable conservation value for bats. Traditional agroforestry systems provide refuge
257 and food resources for different bat ensembles under a stratified canopy that resemble
258 primary forest habitats (Bhagwat, Willis, Birks, & Whittaker 2008; Garcia-Morales,
259 Badano, & Moreno, 2013). Similar canopy structure to old-growth forest and an understory
260 that is often comprised of native shrubs can mitigate edge effects and create corridors or
261 stepping stones for bats to forage and shelter (Meyer et al., 2016).

262 Different bat ensembles respond in different ways to spatiotemporal variation in
263 resource distribution associated with changes in landscape structure and composition (e.g.
264 degree of fragment-matrix structural contrast, size and isolation of primary forest patches)
265 due to their ecological differences (e.g. diet, movement ability, foraging behavior)
266 (Cisneros et al., 2015; Marciente, Bobrowiec, & Magnusson, 2015; Voss, Fleck, Strauss,
267 Velazco, & Simmons, 2016; Farneda et al., 2018a). Our results regarding functional
268 composition (CWM trait values) reveal that certain gleaning insectivorous bats are
269 adversely affected by pasture intensification. This finding probably reflects the scarcity of
270 food and roost resources provided by these habitats as well as elevated predation pressure.
271 A similar pattern was found in a recent meta-analysis (Gonçalves et al., 2017), with
272 livestock ranching affecting mainly carnivorous and gleaning insectivorous Neotropical bat

273 species. Species with a greater habitat breadth (e.g. *Carollia* spp., *Sturnira* spp.) responded
274 positively to habitat conversion, reaching highest abundances in cropland. The simplified
275 vegetation structure of agricultural fields strongly affects and limits the distribution of
276 many forest-dependent bat species (Medellín et al., 2000; Willig et al., 2007).
277 Phytophagous bats (represented here mainly by nectarivores as they showed a significant
278 response, see Figure 4) tend to increase in abundance in secondary forest matrices due to
279 additional food resources (Delaval & Charles-Dominique, 2006; Muscarella & Fleming,
280 2007; Farneda et al., 2015), whereas the abundance of animalivorous bats with larger body
281 mass, such as many carnivores, insectivores and sanguinivores, tends to decrease in
282 response to insufficient roosting and prey resources (Gorresen & Willig, 2004; Meyer &
283 Kalko, 2008; Farneda et al., 2015).

284 The elevated number of significant traits supported by the functional trait
285 composition analysis in secondary forests can be associated with the high vegetation
286 heterogeneity of this habitat across the Neotropics. Secondary forests, as analyzed here,
287 show greater variation in vegetation physiognomy and structure (regeneration ranging
288 between one to 30 years) compared to more homogeneous habitats such as cropland, which
289 could explain the larger variation in bat responses. However, although different countryside
290 habitats noticeably accommodate interior-forest dwellers in different ways, the increase and
291 the long-term persistence of bat species that perform different ecological functions in
292 human-dominated landscapes fundamentally depends on the conservation of vast areas of
293 primary forest. This finding may be generalizable to all human-dominated complex
294 landscapes here studied regardless of matrix type. Our results emphasizing the conservation
295 value of primary forests as important functional and taxonomic repositories of bat diversity
296 are in line with findings obtained for large and small terrestrial mammals, birds,

297 amphibians, lizards, butterflies, dung beetles and other tropical animal assemblages
298 (Barlow et al., 2007; Gardner et al., 2009; Watson et al., 2018).

299 **4.1 Conservation implications**

300 The future of biodiversity and associated ecosystem services will critically depend on our
301 ability to increase the quality and permeability of matrix habitats that are strongly impacted
302 by humans (Pereira & Daily, 2006; Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, &
303 Tabarelli, 2013; Mendenhall et al., 2014). Our findings suggest that ecological functions
304 provided by bats in human-modified tropical landscapes depend on a heterogeneous mosaic
305 of different land cover types that provide specific resources for the species. This finding
306 provides an important tool for a more effective land management in countryside ecosystems
307 to conserve the full set of key ecological functions that bats provide. Conservation
308 strategies for maximizing bat functional diversity and composition in human-modified
309 landscapes should, in addition to ensuring the preservation of large (> 100 ha) areas of
310 primary forest (see Farneda et al., 2015), manage the matrix by promoting natural corridors
311 and stepping stones through spontaneous natural regeneration and active regeneration.
312 Residual vegetation, such as strips of riparian forest and scattered trees may enhance
313 functional connectivity between forest patches, favoring bat movements across human-
314 modified landscapes. These measures to increase the number of favorable habitats for
315 foraging and roosting may sustain species-rich bat assemblages and key ecological
316 functions in human-dominated landscapes. Moreover, our findings corroborate earlier
317 studies by Perfecto and Vandermeer (2010) and Watson et al. (2018) in highlighting the
318 fundamental importance of dynamic agroecological matrices (e.g. syntropic farming) as an

319 alternative to the current monoculture intensification model, and the exceptional value of
320 intact forest ecosystems for supporting biodiversity in the Anthropocene.

321 **Acknowledgments**

322 We are grateful to Eduardo Arcoverde de Mattos, Vinicius Farjalla, Marco Mello, Marcos
323 Figueiredo, the associate editor, and two anonymous reviewers for comments on earlier
324 drafts. FZF was supported by a fellowship from Coordenação de Aperfeiçoamento de
325 Pessoal de Nível Superior (CAPES), CFJM by Fundação para a Ciência e a Tecnologia
326 (FCT; PTDC/BIA-BIC/111184/2009), and CEVG by Conselho Nacional de
327 Desenvolvimento Científico e Tecnológico (CNPq) and by INCT in Ecology, Evolution and
328 Biodiversity Conservation (MCTIC/CNPq/FAPEG).

329 **Data availability statement**

330 The data used in this study were uploaded as online Supporting Information.

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514 **Table 1.** Number of Neotropical bat studies, number of species observed and sampling
 515 effort for each habitat category considered in the analysis.

Habitat	Number of studies	Species	Effort (m ² .h)
Cropland	7	44	340,924
Pasture	8	30	285,784
Agroforestry system	14	85	770,781
Secondary forest	17	78	600,845
Primary forest	30	100	2,088,575

516 **Table 2.** Statistical significance for (a) functional (Rao's Q) and taxonomic (Simpson D)
 517 diversity, and community-level functional uniqueness U , and (b) community-weighted
 518 mean (CWM) trait values between primary forest (PF) and pasture (PA), cropland (CL),
 519 secondary forest (SF), and agroforestry (AF). Pairwise comparisons of differences between
 520 primary forest and the human-modified habitat were performed with a paired permutational
 521 test using 9999 permutations. Significant differences are in bold ($p < 0.05$).

Indices/Traits	Habitat category			
	PF-PA	PF-CL	PF-SF	PF-AF
(a)				
Rao's Q	0.045	0.031	0.001	0.434
Simpson D	0.141	0.031	0.003	0.399
Functional uniqueness U	0.066	0.031	0.001	0.426
(b)				
Body mass	0.399	0.831	0.026	0.062
Trophic level: animalivorous	0.599	0.597	0.001	0.690
Trophic level: phytophagous	0.579	0.592	0.001	0.692
Diet: carnivore	0.254	0.255	0.001	0.230
Diet: frugivore	0.854	0.781	0.748	0.827
Diet: insectivore	0.049	0.078	0.004	0.113
Diet: nectarivore	0.414	0.761	0.036	0.999
Diet: omnivore	0.365	0.842	0.137	0.207
Diet: sanguinivore	0.557	0.841	0.019	0.215
Habitat breadth	0.444	0.030	0.045	0.106

522 **Figure 1.** Geographic distribution of the 30 Neotropical bat studies in human-modified
523 landscapes used in the analysis. Different green colours represent the number of studies per
524 country and sizes of orange circles represent the number of studies per site, where a site is
525 defined as a particular study location.

526 **Figure 2.** Functional diversity (Rao's index Q), taxonomic diversity (Simpson index D),
527 and community-level functional uniqueness U for the control group (primary forest) and the
528 respective treatment group (pasture, cropland, secondary forest and agroforestry).
529 Individual studies are represented by circles, and the mean difference of each habitat is
530 indicated by the vertical bar.

531 **Figure 3.** The paired mean differences between primary forest and the human-modified
532 habitats (pasture, cropland, secondary forest and agroforestry) are shown for functional
533 (Rao's index Q) and taxonomic (Simpson index D) diversity, and community-level
534 functional uniqueness U . Paired mean difference (delta value) is plotted as a bootstrap
535 sampling distribution based on 1000 randomizations. Mean differences are depicted as dots,
536 and 95% confidence intervals are indicated by horizontal lines. Habitats for which
537 significant differences ($p < 0.05$) were found are highlighted in red. Positive and negative
538 values indicate delta values that are greater and smaller, respectively, than for primary
539 forest (zero line).

540 **Figure 4.** Comparison of community-weighted mean (CWM) trait values between primary
541 forests and human-modified habitats: pasture, cropland, secondary forest and agroforestry.
542 Paired mean difference (delta value) between the respective human-modified habitat and

543 primary forest is plotted as a bootstrap sampling distribution based on 1000
544 randomizations. Mean differences are depicted as dots, and 95% confidence intervals are
545 indicated by horizontal lines. Statistically significant traits ($p < 0.05$) are highlighted in red.
546 Positive and negative values indicate delta values that are greater and smaller, respectively,
547 than for primary forest (zero line).

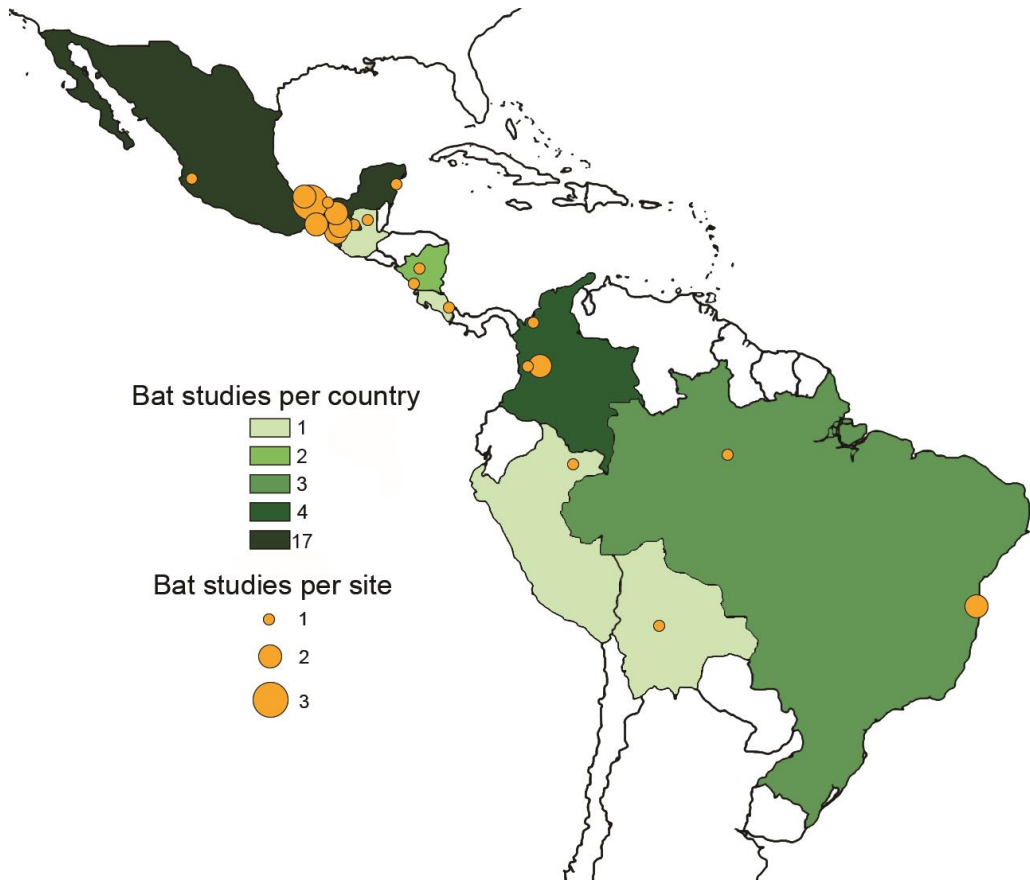


Figure 1.

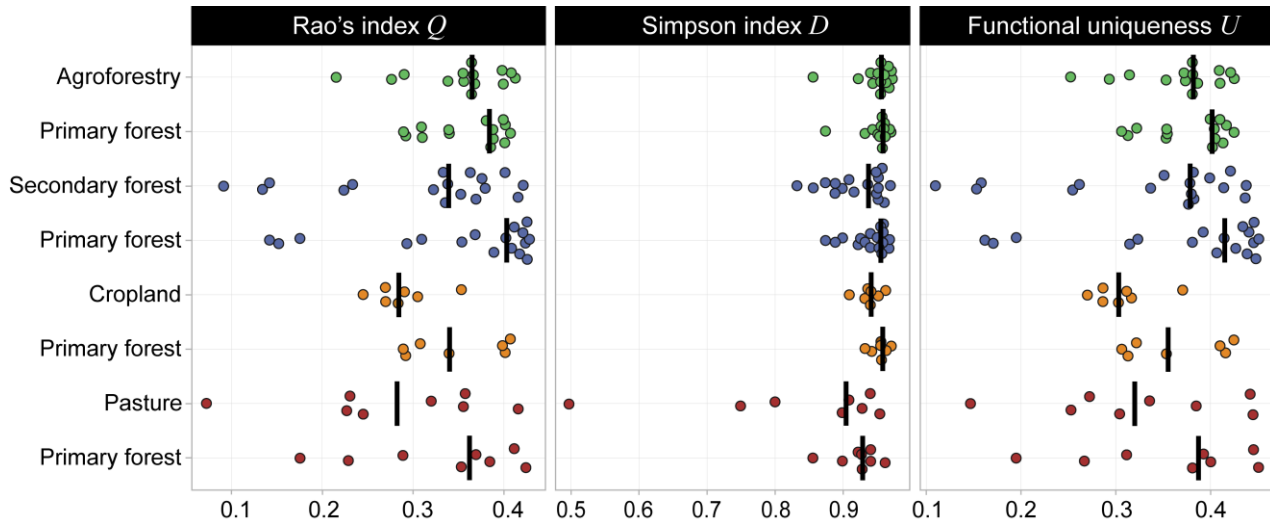


Figure 2.

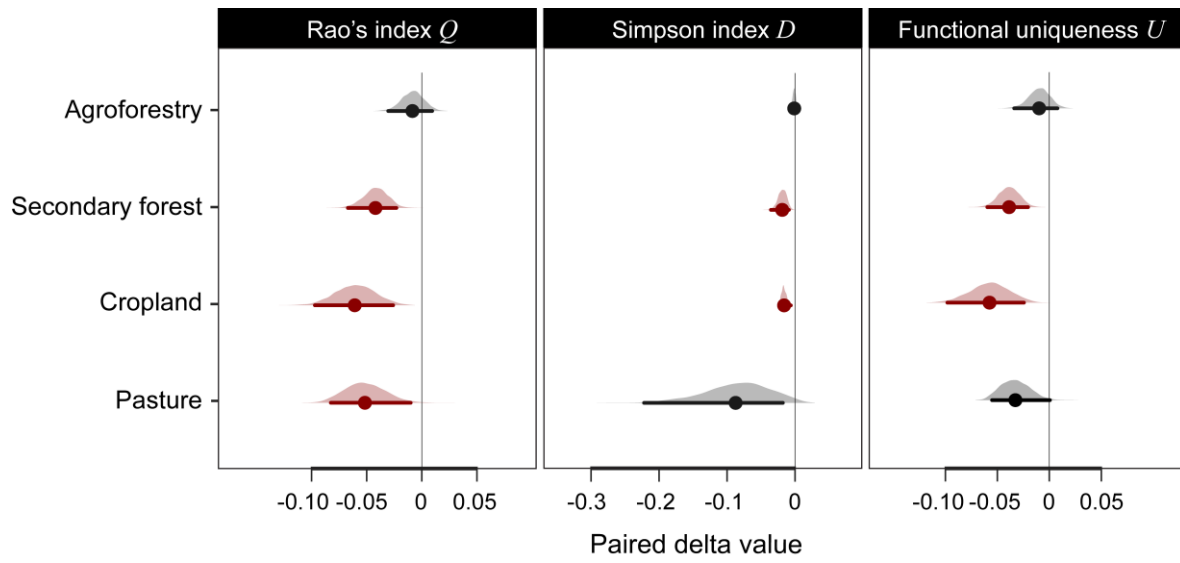


Figure 3.

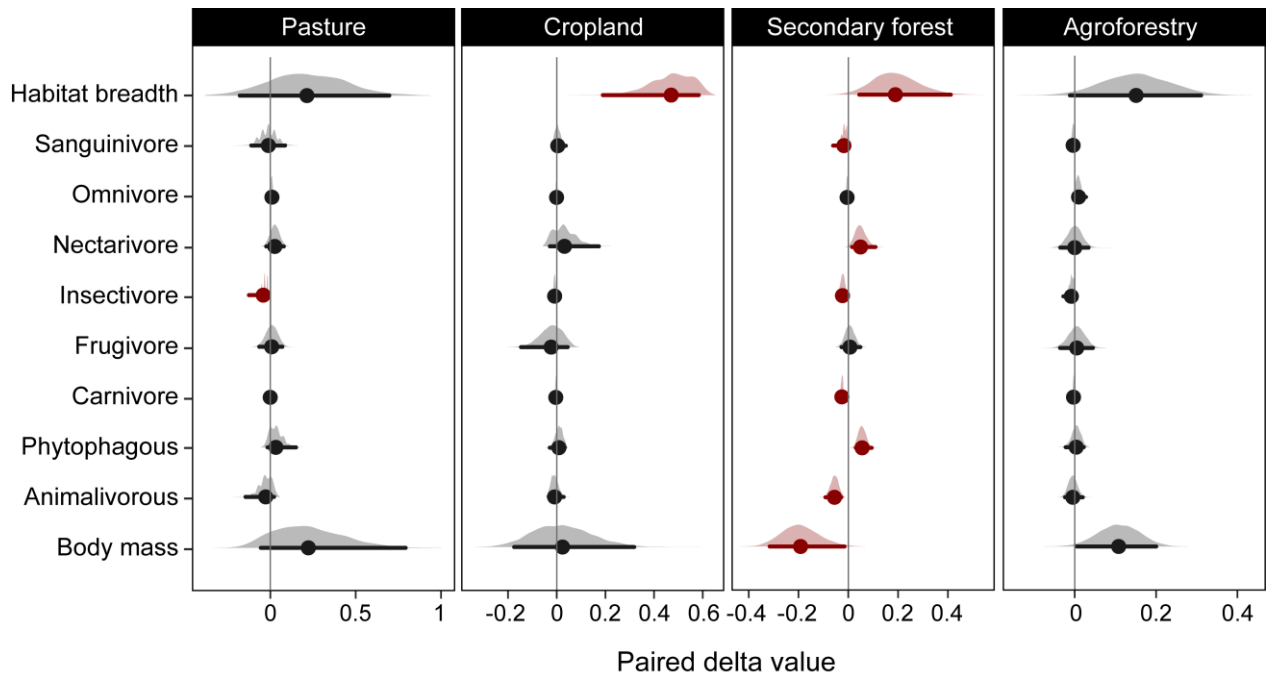


Figure 4.