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2 **Using avian functional traits to assess the impact of land-**
3 **cover change on ecosystem processes linked to resilience in**
4 **tropical forests**

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7 **Authors:** Tom P. Bregman^{1,2*}, Alexander C. Lees^{3,4,5}, Hannah E. A. MacGregor^{1,6},
8 Bianca Darski^{7,8}, Nárgila G. de Moura^{4,5}, Alexandre Aleixo⁵, Jos Barlow^{5,9}, Joseph A.
9 Tobias^{1,10*}

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11

12 **Affiliations:**

13 ¹ Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1
14 3PS, UK.

15 ²Global Canopy Programme, 23 Park End Street, Oxford, OX1 1HU, UK.

16 ³Division of Biology & Conservation Ecology, School of Science & the Environment,
17 Manchester Metropolitan University, Manchester, M1 5GD, UK.

18 ⁴Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca
19 NY 14850, USA.

20 ⁵Departamento de Zoologia, Museu Paraense Emílio Goeldi, Caixa Postal 399,
21 Belém, Pará, CEP 66040-170, Brazil.

22 ⁶School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart,
23 Tasmania, 7001, Australia.

24 ⁷Curso de Pós-graduação de Zoologia, Universidade Federal do Pará/Museu Paraense

25 Emílio Goeldi, Caixa Postal 399, Belém, Pará, CEP 66040-170, Brazil.

26 ⁸Programa de Pós-graduação em Ecologia, Universidade Federal do Rio Grande do

27 Sul, Porto Alegre, RS, Brazil.

28 ⁹Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK.

29 ¹⁰Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst

30 Road, Ascot, Berkshire, SL5 7PY.

31 *To whom correspondence should be addressed. E-mail:

32 tpbregman@gmail.com; j.tobias@imperial.ac.uk

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36

37 **Abstract**

38 Vertebrates perform key roles in ecosystem processes via trophic interactions with
39 plants and insects, but the response of these interactions to environmental change is
40 difficult to quantify in complex systems, such as tropical forests. Here we use the
41 functional trait structure of Amazonian forest bird assemblages to explore the impacts
42 of land-cover change on two ecosystem processes: seed dispersal and insect
43 predation. We show that trait structure in assemblages of frugivorous and
44 insectivorous birds remained stable after primary forests were subjected to logging
45 and fire events, but that further intensification of human land-use substantially
46 reduced the functional diversity and dispersion of traits, and resulted in communities
47 which occupied a different region of trait space. These effects were only partially
48 reversed in regenerating secondary forests. Our findings suggest that local extinctions
49 caused by the loss and degradation of tropical forest are non-random with respect to
50 functional traits, thus disrupting the network of trophic interactions regulating seed
51 dispersal by forest birds and herbivory by insects, with important implications for the
52 structure and resilience of human-modified tropical forests. Furthermore, our results
53 illustrate how quantitative functional traits for specific guilds can provide a range of
54 metrics for estimating the contribution of biodiversity to ecosystem processes, and the
55 response of such processes to land-cover change.

56

57 **1. Introduction**

58 Tropical forests supply a wide array of goods and services to humanity, and are
59 integral to the long-term stability of global air quality, climate and biogeochemical
60 cycles [1]. In turn, the health of tropical forests is underpinned by biodiversity,
61 particularly because more than 90% of tropical woody plant species depend on
62 animals to disperse their seeds [2], a classic case of a ‘biodiversity service’ vital for
63 the long-term delivery of core ecosystem services [3]. Thus, sustainable management
64 of tropical forests should not be solely restricted to preserving tracts of habitat, but
65 must also target the interactions among animal and plant species that are key to
66 ecosystem function and resilience.

67 The dominant threat to the world’s tropical forests and their biodiversity is
68 land-cover change [4], with negative impacts likely to escalate rapidly over the next
69 century, driven by the projected growth of human populations and rising demand for
70 energy, timber, food and other agricultural products [5, 6]. The resulting loss and
71 degradation of primary forests typically reduces species richness, and increases
72 biological homogenization, across a wide range of taxonomic groups [7-11].
73 However, it is becoming increasingly clear that the raw number and even
74 heterogeneity of species surviving in communities may be poor indices of functional
75 aspects of biodiversity [12, 13], including the trophic interactions needed to maintain
76 recruitment and gene flow in rainforest trees [14, 15]. Consequently, the implication
77 of land-cover change for the health and stability of tropical forest ecosystems, and
78 their ability to recover from human-driven perturbations, is still largely unclear [16-
79 18].

80 One way of addressing this problem is to focus on ecological traits associated
81 with ecosystem processes. The standard approach uses dendrogram-based metrics,

82 such as functional diversity [19], to capture the range of ecological traits present in a
83 community of species. This technique has revealed that increasing habitat disturbance
84 may cause declines in functional diversity by eliminating species with distinct
85 ecological traits [20-22], or else reduces functional redundancy by lowering the
86 number of species performing similar roles within the ecosystem [23, 24].

87 While these findings highlight the effects of environmental change on
88 biodiversity and the functional trait structure of ecological communities, there is
89 currently a limit to what can be inferred about ecosystem processes. For instance,
90 most previous studies of functional diversity pool all functional groups (e.g. dietary
91 groups) together within total communities, making it difficult to draw conclusions
92 about any specific process [20, 25], particularly as the impacts of land-cover change
93 vary across such groups [26, 27]. Likewise, most previous studies are unidimensional
94 in that they pool together multiple functional traits despite contrasting functions (e.g.
95 diet, dispersal, etc.), making it difficult to tease apart the effects of land-cover change
96 on different processes [28, 29]. Finally, the interpretation of previous studies is
97 hampered by their use of functional trait categories, which are often relatively crude
98 (e.g. broad dietary guilds) [30]. This approach potentially over-simplifies variation in
99 function [20], largely because species within categories are not equivalent, but instead
100 tend to perform an array of different ecological roles [31, 32]. Thus, standard methods
101 may conceal the effects of land-cover change on ecosystem function, particularly with
102 regard to non-linearity in underlying processes (e.g. tipping points).

103 To address these issues, we sampled rainforest bird communities across a
104 gradient of land-use intensity in Amazonia and then estimated the effect of land-cover
105 change on community structure. Specifically, we quantified structure using
106 continuous functional traits for all members of two dietary guilds—frugivores and

107 insectivores—which account for (77%) of species in our sample (see the electronic
108 supplementary material). We focused separately on these two avian guilds because
109 they perform important but non-overlapping functional roles through their trophic
110 interactions with plants and insects [33].

111 The interaction between frugivorous birds and plants has a major influence on
112 plant dispersal and recruitment, and is critical to the long-term resilience of forests
113 undergoing anthropogenic change [34-36]. The loss of avian frugivores from
114 rainforest systems can alter the structure of tree communities and impede
115 regeneration, particularly in fragmented landscapes where birds are a key vector of
116 seed dispersal among forest patches [37-39]. Rates of forest regeneration can also be
117 influenced by the fate of insectivorous forest birds because they regulate the top-down
118 control of herbivory by phytophagous insects [40, 41]. Specifically, a loss of
119 insectivores can lead to increased leaf damage, and hence both increased seedling
120 mortality and reduced plant growth in degraded and secondary forests [42, 43].

121 Quantifying the full network of interactions between birds, insects and plants
122 is a monumental—perhaps even impossible—task, even in simple ecosystems [2].
123 Instead, to provide an index of the type and diversity of interactions involved, we
124 quantified biometric variables from museum specimens of all study species, and then
125 partitioned these variables into separate niche axes, including overall size, trophic
126 traits (beak shape), locomotory traits (tarsus:tail/wing ratio) and dispersal traits (wing
127 shape). Although such trait axes are not direct measures of seed dispersal and insect
128 predation, they are nonetheless informative about key aspects of the ecological niche
129 related to such processes (see electronic supplementary material). Thus, contractions
130 or shifts in the variety of beak shapes and locomotory traits occurring in a community
131 reflect changes in the filling of ecological niche space across the community as a

132 whole, and the types, sizes or locations of the seeds and insects consumed by birds
133 [28, 44]. Moreover, similar shifts in wing shapes are relevant to seed dispersal
134 dynamics, particularly in patchy or human-modified landscapes [37, 45, 46]. By
135 focusing on specific avian trophic groups, and partitioning their functional
136 morphology into separate niche axes, we can begin to examine the influence of land-
137 cover on multiple dimensions of biodiversity with relevance to ecosystem function
138 and resilience [25, 29].

139 One advantage of quantifying multiple functional traits as continuous
140 variables, rather than the categories adopted by many studies (e.g. [13, 18]), is that we
141 can visualise the effects of land-cover change on the structure of communities. We
142 plotted species in multivariate trait space (hereafter termed ‘morphospace’) to assess
143 the volume and density of functional traits in different land-cover categories. Using
144 the same niche axes, we then assessed changes in the structure and function of bird
145 communities across the same gradient by applying two standard metrics: Functional
146 Diversity, FD [19], and Functional Dispersion, F_{DIS} [47]. These metrics offer
147 complementary perspectives on variation in functional diversity, with F_{DIS} being more
148 sensitive to the overall spread of traits in morphospace and less sensitive to species
149 richness (see electronic supplementary material).

150 By combining detailed datasets of species occurrence, morphological traits
151 and land-cover, we assess the impacts of anthropogenic change on two functionally
152 important avian guilds in Amazonian rainforests. Specifically, for each niche axis in
153 frugivorous and insectivorous birds, we ask (1) how FD varies with land-cover, (2)
154 whether this variation exceeds that predicted by purely random processes, and (3)
155 how F_{DIS} varies across the same land-cover categories. In addition, we use linear

156 mixed models to ask (4) how the community mean value for each niche axis varies
157 across a land-cover gradient, with disturbance treated as a continuous variable.

158

159 **2. Materials and methods**

160 (a) Study site and species

161 We collected data during intensive field surveys (July 2010–May 2011) across two
162 study regions in eastern Amazonian Brazil as part of the Sustainable Amazon
163 Network [48]. One area (1.9 million ha) was located in the municipality of
164 Paragominas, another (~1 million ha) in the municipalities of Santarém, Belterra and
165 Mojuí dos Campos (hereafter, Santarém), both in Pará state. The two regions differ in
166 their history of human occupation, but encompass broadly similar land uses, with a
167 mix of primary and secondary forest habitats interspersed with agricultural and
168 silvicultural production areas. Both these mosaic landscapes are typical of recently
169 cleared and developed regions of Amazonia, providing an ideal replicated framework
170 for investigating the impacts of land-cover change on biodiversity and ecosystem
171 function.

172 Sampling within the two regions was based on a hierarchical stratified-random
173 design with proportional sampling of forest and non-forest areas [48]. We focused on
174 36 hydrological catchments, 18 per study region, each covering ~5000 ha. Within
175 these catchments, we collected detailed environmental information in 300-m long
176 transects (n = 377). Bird surveys consisted of two repetitions of three 15-minute point
177 count surveys at three points evenly spaced every 150 m along each transect, with a
178 single observer identifying species seen and heard within a fixed 75 m radius. We
179 excluded from the analysis 47 transects in ‘rare’ habitat types (e.g. smallholder
180 agriculture, plantations, fruticulture) that were not easily placed along a gradient of

181 land-use intensity, leaving a total sample of 330 transects (sites). The distribution of
182 transects among the remaining land-cover categories is given in figure 1. In total, 472
183 bird species were recorded across the two regions, with an average of 154 (range =
184 97–208) species per catchment, and 39 (range = 2–79) species per transect. For more
185 details of survey methods and results see the electronic supplementary material.

186

187 (b) Habitat and trophic niche

188 We assigned all bird species into two categories of habitat choice depending on
189 whether they were primarily detected in (i) forest or (ii) non-forested habitats,
190 following [49]. These categories are referred to hereafter as forest and non-forest
191 species, respectively (see the electronic supplementary material). We ran analyses
192 pooling forest and non-forest bird species, and then treating these groups in isolation
193 since they are likely to show contrasting responses to forest extent and quality [50].
194 Moreover, non-forest species play little role in the functioning of forest ecosystems
195 [33].

196 We classified species into trophic niches (dietary guilds) based on a recent
197 assessment of diets for the world's birds [51]. Guilds were defined by the food that
198 made up the majority (>50%) of their diet, such that species were classified as
199 insectivores, for example, if they were largely insectivorous but also consumed
200 smaller quantities of nectar and fruit. Species were categorized as omnivores if no
201 primary diet was apparent (all dietary components <50% of intake). Nine major guilds
202 were represented in our sample: Omnivore, Insectivore, Frugivore, Granivore,
203 Nectarivore, Herbivore, Carnivore, Piscivore, and Scavengers (see electronic
204 supplementary material). Of these, insectivores were the most frequent guild with 206
205 species in Santarém and 188 species in Paragominas, and frugivores were the second

206 most speciose guild with 67 species in Santarém and 72 species in Paragominas. We
207 conducted all analyses separately on insectivores and frugivores because they respond
208 differently to land-cover change and forest disturbance [49, 52]. Full species lists and
209 classifications are provided in the electronic supplementary material (dataset S1).

210

211 (c) Environmental conditions

212 We used a 22-year time-series of Landsat images combined with ground-truthed
213 vegetation mapping to classify transects into one of five land-cover classes:
214 undisturbed primary forest, disturbed primary forest (forests affected by logging and
215 fire events), secondary forest (6–22+ years old), arable agriculture and pasture (see
216 electronic supplementary material). Undisturbed forests in these landscapes typically
217 have lower mean canopy openness and higher basal area (area covered by trees and
218 woody palms ≥ 10 cm) than forests subject to disturbance events [53]. Thus, we also
219 used mean canopy openness and basal area to provide a continuous assessment of
220 land-use intensity. Bird survey sampling was distributed proportionally among habitat
221 categories by area (for a detailed breakdown of sampling see [54]). Within each land-
222 cover class, we excluded all species with fewer than three observations across all
223 transects within that habitat, as these are likely to be transient or low-density
224 populations with minimal contribution to ecosystem functioning; that is, they are
225 likely to be ‘functionally extinct’ within that land-cover class [32, 55].

226

227 (d) Trait sampling

228 We measured bird specimens in museum collections to generate biometric trait data
229 for all frugivore and insectivore species ($n = 365$) recorded in our study. Where
230 possible, we selected four specimens (two males; two females) from which we took

231 seven morphometric measurements: beak length, width and depth, wing length,
232 Kipp's distance, tarsus length, and tail length. See electronic supplementary material
233 for further details of data sampling and sources, methods, and rationale for selecting
234 traits. Functional trait data are given in dataset S1.

235 Functional traits in birds are often strongly correlated, largely through their
236 association with overall body size. To prevent these correlations biasing analyses
237 towards detecting only processes associated with body size, we used ordination
238 techniques to derive independent trait axes. Specifically, we generated three trait axes
239 related to different ecological characteristics by applying a two-step principal
240 component analysis (PCA) on morphological trait data, following previous studies
241 [25, 28]. Initially, separate PCAs were undertaken on locomotory (tarsus:tail/wing
242 ratio) and trophic traits (beak shape). In both cases, the first components correlated
243 strongly with body size, and thus we combined them in a second PCA to produce a
244 single size-related axis (see [28]). The second components of the locomotory and
245 trophic PCA were both correlated with niche trait variation independent from body
246 size. Thus, these scores were used as the locomotory and trophic trait axes,
247 respectively (see electronic supplementary material, table S1, S2). A fourth axis
248 (dispersal traits) consisted of the log-transformed Hand-wing index, a standard
249 measure of flight ability computed from wing length and Kipp's distance (see
250 electronic supplementary material).

251

252 (e) Variation in functional diversity

253 We calculated FD on the basis of presence-absence data for all communities (with
254 each transect classed as a community). To test whether disturbed habitats are capable
255 of maintaining ecosystem function, we first (Analysis 1) assessed how raw *FD* of

256 communities varied with land-cover. Then (Analysis 2) we assessed whether this
257 variation deviated from random using an independent swap algorithm, which controls
258 for underlying variation in species richness[56]; see electronic supplementary
259 material. Specifically, the *FD* values derived for each community in the five land-
260 cover categories were compared to a null expectation drawn from 999 random
261 communities with species richness equal to the observed community, and the
262 probability of presence for each particular species determined by its overall
263 occurrence frequency across all communities [56]. Finally (Analysis 3), we assessed
264 whether raw *F_{DIS}* varied across different land-cover categories. Observed values of
265 standardised *FD* and *F_{DIS}* were pooled for each land-cover category.

266 In analyses 1–3, we used two-tailed Wilcoxon signed-rank tests to compare
267 among categories. We completed analyses 2–3 in two different ways regarding the
268 treatment of trait data. First, we combined all measured traits into a single PCA, and,
269 second, we conducted the two-step PCA described above to generate derived trait
270 axes linked to specific ecological functions. We ran null model simulations (analysis
271 2) separately for both regions because the two study regions lie in different
272 biogeographical provinces and there are pre-existing differences in species
273 composition. However, because Santarém and Paragominas were similar in their
274 history of forest loss and disturbance and community structure [48, 54], we combined
275 data from both regions before running Wilcoxon analyses (that is, communities were
276 partitioned by land-cover category, but pooled across regions).

277

278 (f) Variation in the trait structure of communities

279 Given the high level of variation of habitat condition within land cover classes,
280 relating to the timing, frequency and intensity of human disturbance, we also used a

281 Generalised Linear Mixed Model (GLMM) to examine how mean values for each
282 trait axis varied across a continuous gradient of ecological condition (Analysis 4).
283 Ecological condition was based on the first principal component scores from a PCA
284 of canopy openness and basal area, which explained 92% of the variation (see the
285 electronic supplementary material, table S3, for eigenvalues). We allowed the
286 relationship between the environmental PC score and functional traits to be both
287 linear and non-linear (i.e. quadratic). We accounted for potential spatial
288 autocorrelation by including catchment number (1–36) nested within region
289 (Santarém or Paragominas) as random effects in models. Adequate model
290 specification was confirmed by visual inspection of the residuals. The best models
291 were then selected using the Akaike information criterion, AIC [57], with smaller
292 values indicating a closer fit to the observed data.

293

294 **3. Results**

295 (a) Species richness and functional traits

296 Species richness of frugivores and forest insectivores was high in primary forest but
297 declines to very low levels wherever human land-use reaches the highest intensity
298 (pastures, arable agriculture). This effect was not simply a reflection of reduced
299 sampling in human land-uses, as confirmed by species accumulation curves [54]. The
300 pattern was reflected in a dramatic contraction and thinning of the functional trait
301 structure of communities across the land-cover gradient, as visualised by plotting all
302 species in multivariate morphospace (figure 1). Both the species richness of
303 communities, and the volume of morphospace they occupied, were intermediate in
304 secondary forests.

305

306 (b) Functional diversity

307 Raw FD for insectivore and frugivore communities was lower in secondary forest and
308 non-forest habitats than in primary forest (Analysis 1, figure 2, table S4). This effect
309 was strong both when forest and non-forest species were combined, and when forest
310 species were analysed in isolation. However, observed FD of non-forest insectivores
311 remained similar across the disturbance gradient, apart from in pastures where there
312 was a significant increase in FD compared to primary forest communities (figure 2).
313 Similarly, the FD of non-forest frugivores remained relatively constant across the
314 land-use gradient, except in arable agricultural habitats where the frugivore
315 component of avian communities was removed almost entirely. We note that these
316 patterns in raw FD are likely to be strongly driven by variation in species richness.

317 Using a null-model approach, and pooling forest and non-forest species, we
318 found that FD in insectivore communities was neither more nor less than expected by
319 chance, regardless of position across the land-use gradient (Analysis 2, figure 3a,
320 table S5). Although observed F_{DIS} of insectivore communities changed with land-
321 cover, the relationship was non-linear because F_{DIS} decreased from primary to
322 secondary forest, and then increased again in pastures (Analysis 3, figure 3c, table
323 S6). These patterns were substantially altered when we focused exclusively on forest
324 insectivores, with FD significantly lower in pastures than predicted by our null model
325 (figure 3e), and F_{DIS} significantly reduced in pastures in comparison to primary forest
326 (figure 3g).

327 Regardless of whether forest and non-forest species were pooled or not,
328 increased intensity of human land-use was associated with declining FD and F_{DIS} in
329 frugivores. In secondary forests, pastures and arable land, FD was significantly lower

330 than null expectations (Analysis 2, figure 3, table S5), and F_{DIS} was lower than in
331 primary forests (Analysis 3, figure 3, table S6).

332 When we focused on individual traits, we found that overall trends concealed
333 idiosyncratic patterns (figure S1, tables S7–S9). For example, body size and
334 locomotory traits contributed disproportionately to the low FD of forest insectivore
335 and frugivore communities in pasture, while trophic traits were neither over- nor
336 under-dispersed. In contrast, dispersal traits had higher FD than expected under our
337 null expectation (figure S1). Changes in the F_{DIS} of individual traits mirrored the
338 collapse of FD . Specifically, the F_{DIS} of all traits, apart from dispersal traits in
339 insectivores, declined in secondary forests and/or pastures from highs in primary
340 forests (figure S1, tables S10–S12). In contrast, the F_{DIS} of dispersal traits was similar
341 in primary and secondary forest communities, and increased in pastures (figure S11,
342 table S10).

343

344 (c) Community structure in relation to functional traits

345 GLMM analyses revealed systematic shifts in mean trait values for both forest (8
346 models) and non-forest species (8 models) across the land-use gradient (figure S2,
347 table S13). In some (5 of 16) cases, four of which (80%) were restricted to insectivore
348 communities, the best fitting models included disturbance as a quadratic term (figure
349 S2, table S13) suggesting that the rate of change in mean community traits varied
350 across the gradient. The only model for frugivores that retained the quadratic
351 explanatory variable was for body size in non-forest species, but in this case the linear
352 explanatory variable was not significant, suggesting a v-shaped relationship with a
353 minimum at intermediate levels of disturbance (figure S2e, table S13). This may
354 reflect the presence of large toucans and terrestrial species in forested areas, and the

355 ability of some large frugivores (e.g. pigeons) to disperse through sparsely vegetated
356 agricultural landscapes. However, in most (11 of 16) cases, the best fitting models
357 included only the linear term, suggesting that the rate of change in mean community
358 traits remained similar across the disturbance gradient (figure S2). Of these 11 cases
359 in which a linear model was supported, 10 (91%) involved frugivores and non-forest
360 insectivores.

361

362 **4. Discussion**

363

364 To assess the impact of land-cover change on key trophic interactions, we focused on
365 discrete ecological and functional groups (forest and non-forest bird species;
366 frugivores and insectivores), and partitioned the functional traits of each species into
367 four dimensions of the ecological niche (size, diet, locomotion, dispersal). Our
368 findings reveal that defaunation associated with land-cover change has different
369 implications for insectivore and frugivore communities, and for different ecological
370 niche axes within those communities, providing insight into the relationship between
371 land-cover and the ecosystem processes regulated by birds.

372

373 (a) Impacts of land-cover change on functional diversity

374 When grouping all forest and non-forest species together, disturbed primary forests
375 supported similar levels of *FD* relative to undisturbed primary forests. In addition, the
376 trait structure of communities in disturbed primary forests was similarly dispersed
377 around mean trait values (F_{DIS}). However, the impact of further increases in land-use
378 intensity was stronger in frugivores, with significant declines in *FD* in secondary
379 forest, and diversity dropping to almost zero in the intensively farmed agricultural

380 areas (figure 1). Our results suggest that the FD and F_{DIS} of frugivores collapses in
381 highly disturbed habitats, presumably reflecting the removal of fruiting trees.

382 The impacts of land-cover change on forest-dependent insectivores were
383 generally similar, with the total volume of trait space collapsing in agricultural
384 habitats and only partially recovering in secondary forests (figure 1). Accordingly, the
385 overall raw FD for insectivores (forest and non-forest species combined) declined
386 with increasing habitat disturbance (figure 2a). These findings agree with previous
387 studies concluding that rainforest insectivores are highly sensitive to land-cover
388 change, with many species dropping out of fragmented habitat because of their poor
389 dispersal abilities and adaptation to the forest interior [49, 58].

390 Nonetheless, both FD and F_{DIS} of insectivores were more resilient to land-
391 cover change (figure 3), largely because non-forest insectivores occurred widely with
392 their FD remaining consistent (figure 2e) and their F_{DIS} increasing in disturbed
393 habitats (figure 3k). Focusing on forest species, and breaking functional variation
394 down into individual traits, provides further insights. For example, both the
395 standardised FD (figure S1d) and F_{DIS} (figure S1l) of dispersal traits in forest
396 insectivores increases with land-use intensification, presumably because disturbed
397 habitats retain some taxa with low-dispersal traits yet also receive an influx of highly
398 dispersive taxa. In contrast, standardised FD for overall size and locomotory traits in
399 forest insectivores, as well as the F_{DIS} for all other traits, showed a strong decline in
400 disturbed landscapes (figure S1). Overall, these results reveal that the effects of land-
401 cover change on functional diversity are (i) concealed when including non-forest
402 species in analyses [30], and (ii) idiosyncratic across different functional groups, and
403 ecological niche axes.

404

405 (b) Variation in trait distribution

406 We detected numerous shifts in the mean traits of both insectivore and frugivore
407 communities indicating that bird communities occupied a different region of trait
408 space after changes in human land-use (see electronic supplementary material). When
409 plotted across a continuous gradient in land-cover, this variation in trait structure
410 fitted both linear and quadratic models, but was best described by a quadratic fit. In
411 all cases, and particularly in forest insectivores, the rate of change in the mean
412 position of traits occurred most rapidly at high levels of disturbance. Such fluctuations
413 suggest that disturbed landscapes are especially sensitive to further small increases in
414 disturbance events (such as recurrent fires), as these have the potential to cause major
415 changes in the position of trait diversity. This finding indicates that the turnover of
416 species in repeatedly disturbed communities, although rapid [59], is nonetheless
417 outpaced by changes in trait structure related to key ecosystem processes.

418 Focusing on individual traits, we found that large species were particularly
419 sensitive to habitat disturbance and increasing land-use intensity, in agreement with
420 previous studies in tropical systems [15]. Specifically, for insectivores and forest
421 frugivores there was a decline in the overall mean size of species persisting in
422 disturbed habitats (figure S2, table S13). We attribute these shifts to a suite of factors
423 well known to increase the susceptibility of large species to local extinction in
424 degraded or fragmented environments, including increased hunting [60, 61].

425 In general, the functional trait structure of insectivore communities shifts with
426 increasing intensity of human land-use towards smaller tarsus to tail/wing ratio,
427 increased dispersal, and short, wide beaks. Based on the reported link between form
428 and function in birds [28], these findings suggest that the insectivore community is
429 increasingly dominated by species that capture prey in flight or from canopy foliage.

430 The pattern also reflects the addition of mobile, opportunistic, non-forest species, in
431 conjunction with the removal of dispersal-limited, forest-dependent species [58].
432 Changes in the functional trait structure of frugivore communities are less complex,
433 and more closely related to body size. It is possible that some large frugivore species
434 are hunted out from highly disturbed landscapes, and also that taxa persisting in these
435 environments tend to be smaller-bodied vagile species with lower nutritional
436 requirements.

437

438 (c) Implications for ecosystem function and landscape management

439 Our results suggest that ‘biodiversity services’ [3] supplied by birds and related to
440 tropical forest resilience are more effectively retained in disturbed primary (i.e.
441 logged or burnt) rainforests than in secondary forests, and that—unsurprisingly—such
442 services collapse in agricultural land-uses. These findings are consistent with the view
443 that disturbed (logged and burnt) primary forests are important in both maximising
444 species richness and maintaining ecosystem function in landscape mosaics [45, 54].
445 Although we found that secondary forests (6–22+ years old) are significantly less
446 complex than disturbed primary forests from a functional perspective, we note that
447 this result is likely to be age-dependent, with the trait structure of secondary forest
448 bird communities becoming progressively more like those of primary forests over
449 time. Moreover, even young secondary forests may increase matrix permeability and
450 dampen edge effects, thereby acting as an important buffer against the loss of
451 functional diversity through land-use change, and increasing the potential for
452 abandoned agricultural landscapes to regenerate rainforest [62].

453 Although the FD and F_{DIS} of frugivores declines precipitously in agricultural
454 landscapes, it is worth considering whether this matters. It could be argued, for

455 example, that declines in *FD* with habitat disturbance are simply a response to the
456 lower range of fruits available, in which case frugivores may continue to provide the
457 dispersal function in full. While this is undoubtedly true to an extent, frugivore
458 species often disappear before their food plants [32], particularly when large-bodied
459 species are hunted to extinction [37], meaning that demand for seed dispersal outstrips
460 supply [63]. Moreover, as many rainforest mammals, including primates, are unlikely
461 to disperse through non-forest habitats, birds may be the main vector of dispersal for
462 animal-dispersed trees in degraded or secondary forests [33]. From this perspective,
463 the ability of forests to regenerate fully relies on the presence or proximity of avian
464 seed dispersal agents, and is therefore impaired by shifts in the functional trait
465 structure of avian communities away from the state encountered in intact forest. Once
466 components of functional diversity in frugivores are lost, the chances of
467 recolonisation by associated food plants are theoretically reduced.

468 The loss of forest insectivores in agricultural habitats is almost as extreme, but
469 potentially offset by an influx of non-forest species. However, whether these species
470 help to maintain the top-down control of herbivory in forest remains to be
471 demonstrated [64], and is perhaps unlikely because non-forest insectivores tend to be
472 generalists with different foraging strategies and a preference for more open
473 microhabitats [65]. Thus, they may fail to capture many types of cryptic herbivorous
474 insects in patches of forested habitat embedded in agricultural landscapes.

475 One drawback of our analyses is that they do not account for species
476 abundance. Changes in abundance following disturbance often vary across species in
477 unpredictable ways [66], potentially leading to some species becoming ‘functionally
478 extinct’ when their abundance drops so low that they contribute little to ecological
479 processes [32, 55]. Moreover, *FD* can be a misleading surrogate for species

480 contributions to ecological processes because phenotypically distinct taxa tend to be
481 rarer and thus interact with fewer species across the network [67]. We partly address
482 this issue by excluding species that are either transient or rare from our analyses,
483 but—in common with most previous functional trait studies—we do not explicitly
484 account for changes in abundance. Further work should incorporate more informative
485 measures of abundance or interaction strength [30, 67].

486 Standard approaches to understanding environmental change based solely on
487 species richness and composition may overlook important implications for ecosystem
488 processes, leading to calls for functional diversity to be more explicitly considered in
489 biodiversity conservation strategies [13, 68, 69]. Our results support this view, yet
490 also highlight how treatment of functional diversity can be improved to provide
491 greater insight. In particular, we have shown contrasting effects of land-cover change
492 on functional traits in different avian dietary guilds, and even across different
493 dimensions of functional trait space. Given that these idiosyncratic patterns are
494 largely obscured by standard approaches, we propose that functional traits should,
495 where possible, be considered in the context of specific trophic interactions or their
496 constituent niche axes when exploring the implications of anthropogenic change on
497 biodiversity and ecosystem resilience.

498

499 Data accessibility. All data are provided (electronic supplementary material, S2).

500 Authors' contributions. J.A.T., T.B. and J.B. conceived and designed the study.

501 A.C.L. and N.G.M. designed and carried out field surveys. T.B., H.E.A.M., B.D. and

502 A.A. collected functional trait data. T.B. carried out analyses. T.B. and J.A.T. drafted

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751 **Figure 1.** Functional trait distribution for forest-dependent (a) insectivorous and (b)
752 frugivorous bird species across a land-use gradient in Amazonian forest. Sample sizes
753 are the number of species recorded in each land-use category. Each point shows data
754 from a single species; colours denote the density of species in a multivariate trait
755 space ('morphospace') described by three trait axes (dispersal traits, trophic traits, and
756 overall size); isopleths denote the areas of morphospace containing 75%, 50% and
757 25% of species occurring in each land-use. Arrows in (a) indicate the direction of
758 increasing values for each principal component axes (described in electronic
759 supplementary material, tables S3, S4). Data shown are exclusively from the
760 Santarem landscape to avoid pooling data from different study sites, which
761 overestimates the volume of morphospace within land-use categories.

762

763 **Figure 2.** Observed Functional Diversity (*FD*) for insectivores and frugivores in 330
764 avian communities across five land uses: primary forest (PF), disturbed primary forest
765 (DF), secondary forest (SF), pasture (PA) and arable agriculture (AG). (a) and (b)
766 show data for all species; (c) and (d) show data for forest species; (e) and (f) show
767 data for non-forest species. Data from Santarém and Paragominas are pooled.
768 Asterisks indicate that observed *FD* was significantly different from the null
769 expectation (* <0.05, ** <0.01, *** <0.001). All statistical results are from two-tailed
770 Wilcoxon signed-ranks tests. Full results and sample sizes in each land use category
771 are provided in electronic supplementary material, table S5.

772

773 **Figure 3.** Standardized effect size of Functional Diversity (*FD*) and Functional
774 Dispersion (*F_{DIS}*) for insectivores and frugivores in 330 avian communities across five
775 land uses: primary forest (PF), disturbed primary forest (DF), secondary forest (SF),
776 pasture (PA) and arable agriculture (AG). Data from Santarém and Paragominas are
777 pooled. Metrics were not calculated for subsets where sample size was too low.
778 Asterisks indicate that observed *FD* was significantly different from null expectations,
779 or that observed *F_{DIS}* was significantly different from *F_{DIS}* in primary forest (* <0.05,
780 ** <0.01, *** <0.001). All statistical results are from two-tailed Wilcoxon signed-
781 ranks tests. Full results and sample sizes in each land-cover category are provided in
782 electronic supplementary material, tables S5, S6.