

1 **Constraints on avian seed dispersal reduce potential for resilience in degraded**  
2 **tropical forests**

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## 23 **Abstract**

- 24 1. Seed dispersal – one of the many services supplied by biodiversity – is a critical  
25 process underpinning the resilience of tropical forests. Forest loss or degradation  
26 typically leads to defaunation, altering seed transfer dynamics and impairing the  
27 ability of forested habitats to regenerate or recover from perturbation. However, the  
28 extent of defaunation, and its likely impacts on the seed dispersers needed to restore  
29 highly degraded or clear-felled areas, remains poorly understood, particularly in  
30 human-modified tropical forest landscapes.
- 31 2. To quantify defaunation of seed-dispersing birds, we used field survey data from  
32 more than 400 transects in three regions of Brazil, first comparing the recorded  
33 assemblages with those predicted by geographic range maps, and then assessing  
34 frugivore habitat associations across gradients of land cover modification at local  
35 scales.
- 36 3. We found that current bird assemblages have lower functional trait diversity than  
37 predicted by species range maps in Amazonia (4–6%), with a greater reduction  
38 (28%) for the Atlantic Forest region, which has been more heavily deforested for a  
39 longer period. These reductions are probably caused by local extinctions of forest-  
40 dependent bird species following land-use change.
- 41 4. Direct measures of seed dispersal are difficult to obtain, so we instead focused on  
42 the potential for seed transfer inferred from shared species occurrence between land  
43 cover types. Of 83 predominantly frugivorous bird species recorded in relatively intact  
44 forests, we show that 10% were absent from degraded forest, and 57% absent from  
45 the surrounding matrix of agricultural land covers, including many of the large-beaked  
46 species. Of 112 frugivorous species using degraded forest, 47% were absent from  
47 matrix habitats.
- 48 5. Our findings suggest that degraded forest can supply seed dispersal services to  
49 adjacent cleared lands, and that direct transfer of seeds from intact forest to cleared

50 areas may be limited, particularly for large-seeded trees. We conclude that resilience  
51 of tropical forest landscapes is best achieved by protecting a mosaic of forest types,  
52 including sufficient core areas of intact forest surrounded by buffer zones of  
53 degraded forest.

54 **Keywords:** Amazon, Atlantic Forest, defaunation, frugivory, land cover change, resilience,  
55 secondary forest, succession

## 56 **1 INTRODUCTION**

57 The degradation and fragmentation of tropical forests, along with their conversion to  
58 production landscapes, is driving widespread defaunation (Canale et al., 2012; Dirzo et al.,  
59 2014) with large frugivorous birds particularly affected (Bovo et al., 2018; Bregman et al.,  
60 2014). This loss of species can disrupt seed-dispersal networks (da Silva & Tabarelli, 2000),  
61 thereby limiting forest regeneration (Galetti et al., 2013; Gardner et al., 2019). Defaunation  
62 alters assemblages of frugivores in disturbed forests, with few species occurring in adjacent  
63 non-forest landscapes (Bregman et al., 2016). This potentially impedes recolonisation by  
64 tree species that have become extirpated, reducing ecosystem resilience and raising the  
65 cost of reforestation programmes (Chazdon & Uriarte, 2016). Few studies, however, have  
66 assessed how habitat degradation affects potential seed transfer from intact tropical forests  
67 to adjacent cleared areas by examining frugivore communities.

68 One possibility is that many seed-dispersers associated with intact forests rarely if ever visit  
69 non-forest habitats, such that species transferring seeds into matrix habitats are primarily  
70 those associated with degraded forests and forest edges. If this is the case, tree species  
71 recruitment will be adversely affected because these frugivorous birds are a non-random  
72 subset in terms of key ecological traits, such as beak or gape size (Bovo et al., 2018). In  
73 particular, the absence of species with larger beaks and wider gapes may constrain seed  
74 transfer because the ability of avian frugivores to disperse seeds is limited by gape width,  
75 which places an upper physiological constraint on the size of seeds they can ingest whole

76 and hence which tree species can be dispersed (Burns, 2013; Wheelwright, 1985). This trait-  
77 matching between avian frugivores and their food plants offers a useful tool for assessing  
78 the structure and function of mutualistic interaction networks (Dehling et al., 2014;  
79 McFadden et al., 2022) and their response to environmental change (Schleuning et al.,  
80 2020).

81 In accordance with the trait-matching hypothesis, the local extinction of large-gaped birds  
82 has been shown to impair dispersal of larger seeds (da Silva & Tabarelli, 2000; Galetti et al.,  
83 2013). These local extinctions of key seed dispersers may lead to declining plant  
84 populations, particularly for large-seeded tree species, resulting in changes to recruitment  
85 and composition (Sethi & Howe, 2009). Movement constraints on seed-dispersers may also  
86 cause the rewiring of interaction networks between seed dispersers and their food plants,  
87 with unpredictable outcomes driven by species-specific responses to different land covers  
88 (Habel et al., 2019; Rehm et al., 2017). In effect, the type of seeds dispersed between  
89 different land cover types will be governed by the traits of frugivores that can persist in or  
90 routinely disperse through both forest and non-forest landscapes. In addition, this process of  
91 seed transfer may involve an extra step from intact to degraded forest and then to matrix  
92 simply because intact forests are usually separated from the matrix by an intervening buffer  
93 of degraded or secondary forests (Mayhew et al., 2019; Nunes et al., 2022).

94 To determine the effects of disturbance on seed dispersal, two key questions must be  
95 answered. First, given that the potential to disperse different seeds is dependent on species  
96 traits, it is important to examine the functional diversity (FD) of the bird species assemblage.  
97 FD metrics use traits to quantify the potential roles played by species in a given community  
98 (Cadotte et al., 2011; Petchey & Gaston, 2002). One way to examine FD is with a volume-  
99 based measure (Mason et al., 2005) with morphological traits providing a representation of  
100 ecological niche space (Pigot et al., 2020; Tobias et al. 2020). If functionally unique species  
101 are lost, the functional volume is reduced, indicating the likely impairment of seed dispersal  
102 services for certain plant species. If, however, the species lost are not functionally unique,

103 this can still result in reduced functional redundancy, i.e., where different species perform  
104 similar roles, species loss does not necessarily reduce FD but nonetheless leads to an  
105 increase in future risk by leaving seed dispersal service reliant on fewer species (Biggs et  
106 al., 2020). Second, it is important to understand how frugivores use the modified landscape.  
107 If certain species or traits are restricted to a single land cover type, seed dispersal between  
108 different land covers will also be restricted, as birds are not able to act as “mobile links”  
109 (Sekercioglu, 2006), which will in turn reduce the potential for forest regeneration.

110 In this study, we aim to investigate how land-use change and habitat degradation affects the  
111 potential for natural seed dispersal by assessing changes in key traits and FD in  
112 assemblages of fruit-eating birds. To investigate the potential functional impacts of  
113 defaunation at a regional scale, we compare the species assemblages predicted by  
114 geographical range maps to those recorded by intensive field surveys using the distribution  
115 of individual traits and measures of functional volumes (which account for trait  
116 combinations). Previous research shows local declines of larger-beaked seed-dispersers in  
117 tropical forests (Galetti et al. 2013; Dirzo et al., 2014; Pérez-Méndez et al., 2016; Bovo et al.  
118 2018) because of a range of factors, including slower reproductive output, larger spatial  
119 requirements and sensitivity to hunting. We therefore predict that assemblages recorded by  
120 recent surveys will have fewer large species than predicted by range maps, contributing to a  
121 reduction in FD.

122 To examine different seed-dispersal scenarios, we subdivide land cover into three broad  
123 classes – intact forest, degraded forest and the agricultural/silvicultural matrix. Previous work  
124 has identified high levels of species turnover across land cover types in the same  
125 assemblages (Hatfield et al., 2020; Moura et al., 2013; Solar et al., 2015) and elsewhere  
126 (González-Varo et al., 2017), suggesting that direct transfer of seeds between very different  
127 habitats is reduced. Because of this and the pattern of extirpation of larger species we  
128 predict that movements between intact forest and the matrix are potentially limited to a  
129 reduced shared species pool representing a narrower range of traits, whereas there is a

130 higher potential for seed dispersal between intact and degraded forests, or between  
131 degraded forests and matrix (Figure 1).

## 132 **2 MATERIALS AND METHODS**

### 133 **2.1 Bird surveys and comparison with historical avifauna**

134 We analysed avifaunal data collected from the state of São Paulo (Brazilian Atlantic Forest;  
135 23°S 45°W) and two areas in the state of Pará (Brazilian Amazonia): Santarém (03°S 55°W)  
136 and Paragominas (03°S 48°W). These three survey sites are each in a different  
137 biogeographic province and differ in their disturbance histories, providing a useful  
138 comparison. All datasets used three 15-minute point counts spaced along a transect to  
139 sample bird assemblages but differed slightly in overall study design (owing to different  
140 habitat extent and configuration). Amazonian sampling was conducted in 2010–2011 at 352  
141 transects (300 m, 75 m radius points 150 m apart, surveyed twice; Supplementary Methods;  
142 Lees et al., 2012, 2013). Atlantic Forest sampling was conducted in 2015–2017 at 147  
143 transects (150 m, 25 m radius points 75 m apart, surveyed four times; Supplementary  
144 Methods; Hatfield et al., 2020).

145 All study regions have undergone dramatic forest loss and fragmentation (Figure S1;  
146 Gardner et al., 2013; Joly et al., 2014), leading to the local extinction of bird species, and  
147 even – in the case of the Atlantic Forest – global extinctions (Brooks et al., 1999; Lees &  
148 Pimm, 2015). To compare current bird assemblages with that expected in each region prior  
149 to large scale impacts, we compiled a list of species historically present according to  
150 published range maps for each region (BirdLife International and Handbook of the Birds of  
151 the World, 2020). We determined which native, introduced and (locally) extinct bird species  
152 had geographical distributions overlapping the sampling sites, independently for the three  
153 regions. Thus, providing a full potential species list for each after taxonomic alignment and  
154 exclusions based on finer scale biogeographic factors (Supplementary Methods).

### 155 **2.2. Trait data and ecological classifications**

156 We restricted our sample of study species to those with diets composed  $\geq 50\%$  of fruit  
157 according to a previous scoring system (Wilman et al., 2014). By omitting species with a  
158 smaller proportion of fruit in their diet we may exclude some generalist taxa that play  
159 important roles in dispersing seeds into matrix areas. However, our approach means that we  
160 focus primarily on obligate and near obligate frugivores which form the core of seed  
161 dispersal networks (de Assis Bomfim et al., 2018), due to their higher consumption and  
162 visitation rates (Pigot et al., 2016). We did not exclude species that are often classed as  
163 seed predators (e.g., parrots), as those with a large percentage of fruit in their diet ( $\geq 50\%$ )  
164 have been shown to provide some seed dispersal services (Heleno et al., 2011; Tella et al.,  
165 2015).

166 Following disturbance and clearance of forests, the likelihood that a species is lost from an  
167 assemblage is related to its forest dependency. We therefore classified species as being  
168 forest and non-forest associated for the FD analyses, with all species initially analysed,  
169 followed by the forest species subset alone. Classification used the primary habitat category  
170 in AVONET (Tobias et al., 2022); in addition, we re-ran the analyses based on an  
171 independent classification, focusing on species listed as having medium or high forest  
172 dependency by BirdLife International (BirdLife International, 2022; Buchanan et al., 2011)  
173 with clear discrepancies reviewed (Supplementary Methods).

174 To calculate FD, we used a set of morphological traits (Table S3) associated with diet (beak  
175 length, width and depth), locomotion (tarsus and tail length) and dispersal (wing length and  
176 hand-wing index). Species averages for these traits were based on published measurements  
177 of museum specimens and live-caught birds (Sheard et al., 2020; Tobias et al., 2022; mean  
178 sample per species = 16.6 individuals). Hand-wing index (HWI) is a metric of wing shape  
179 associated with flight efficiency and dispersal distance (Sheard et al. 2020). We also added  
180 average gape size for all species (McFadden et al. 2022; mean sample per species = 17.7  
181 individuals). For eight species not included, we used previously unpublished gape size  
182 values measured following the same methodology (Supplementary Methods).

### 183 **2.3 Assemblage functional diversity**

184 We estimated FD using the convex hull volume of the functional space occupied by an  
185 assemblage (Villéger et al., 2008). The functional space was constructed in three  
186 dimensions using axes based on the total range of traits across all avian frugivores in each  
187 region independently (combining the species lists from transects and geographical range  
188 maps).

189 Functional axes were generated using a two-step PCA process designed to partition the  
190 effects of body size from morphological trait variation associated with foraging and  
191 locomotion (Trisos et al., 2014). Specifically, two PCAs were initially conducted – a PCA  
192 based on foraging traits (gape size, beak length along the culmen, beak length to the  
193 anterior edge of the nares, beak width and beak depth) and a second based on locomotion  
194 traits (tarsus length, tail length, wing length and HWI). The first axis from both the foraging  
195 and locomotion trait PCAs were then combined in a second PCA that reflects variation in  
196 body size. This provided the three axes to construct the functional space, one from the  
197 second step PCA reflecting variation in body size, the second axis from the foraging PCA  
198 reflecting variation in trophic niche and the second axis from the locomotion PCA reflecting  
199 variation in locomotion (Figure S2). FD calculations were conducted in the R package  
200 'betapart' (Baselga et al., 2021).

201 This analysis of FD allowed us to compare species assemblages predicted by range maps  
202 and those recorded by surveys. The list derived from range maps provides an approximation  
203 of the expected species assemblage. The proportion of the functional volume of the  
204 expected species assemblage (inferred from range maps) that was retained (shared) and  
205 lost by the observed assemblage (inferred from site transects) was calculated. The  
206 percentage retained was then also compared to that retained by randomly generated  
207 assemblages (with richness held constant; Supplementary Methods). This allowed us to  
208 examine whether the species losses estimated from the survey data reduced FD retention to



209 a greater extent than a trait-independent process of loss whereby species are lost at random  
210 with respect to their traits as opposed to a trait-based filter (e.g., loss of the largest species).  
211 All estimates were conducted for the full avian frugivore assemblage and then for a restricted  
212 sample of forest species.

#### 213 **2.4 Assessing the potential for seed transfer among land cover types**

214 When assessing the potential for seed transfer among land cover types we chose to focus  
215 primarily on frugivore gape width as this provides the best measure of seed dispersal  
216 limitation with regards to size. The land cover classifications provided in the original studies  
217 (Hatfield et al., 2020; Moura et al., 2013) were aggregated into three categories: intact forest,  
218 degraded forest and matrix (Table S1 and S2). Intact forest is used as a relative term as  
219 these landscapes are still likely affected by historic and ongoing disturbance.

220 First, we compiled frugivore lists for each land cover type (each region independently). Next,  
221 we produced lists of species common to both intact forest and degraded forest then, intact  
222 forest and the matrix. We also produced a list of species common to both degraded forest  
223 and the matrix. This allowed us to calculate the percentages of species in common and to  
224 evaluate possible seed dispersal pathways in the context of gape width, with the overlap lists  
225 corresponding to the potential steps in Figure 1. Species overlaps were also calculated when  
226 sampling effort across land cover types was fixed (Supplementary Methods). To include  
227 estimates of dispersal ability, we also repeated the overlap comparison with HWI and with  
228 body mass (AVONET; as an indication of body size). The proportion of functional diversity  
229 not retained by the species shared between land cover types was also estimated by applying  
230 the above methods (2.3) to lists of species occurring in multiple habitat combinations  
231 (Supplementary Methods). For both gape width and FD, we compared the observed species  
232 overlaps to random selections to test for trait-based filters (such as an increased likelihood of  
233 extirpation for species with large body size; Supplementary Methods).

234 In addition to the percentage overlaps for each region, overall figures were calculated by  
235 combining the species by land cover lists from the three regions, then calculating overlaps.  
236 This approach differs from averaging values across regions as some species are found in  
237 multiple regions and each region has a different species richness. Land cover associations  
238 may also differ between regions as sensitivity to forest degradation is not uniform across a  
239 species' geographic range (Moura et al., 2016; Orme et al., 2019). This means that across-  
240 region pooling may not accurately reflect the associations of individual species in a particular  
241 region. On the other hand, many of these species have few detections even with the large  
242 sampling effort considered, so the pooled figures represent an increased sampling effort for  
243 species found in multiple regions.

## 244 **3 RESULTS**

### 245 **3.1 Functional diversity of frugivore assemblages**

246 Field surveys of frugivorous birds detected 73 species in Santarém, compared with 104  
247 predicted by geographical range maps for the region. Similarly, surveys detected 76 species  
248 compared to 87 species predicted in Paragominas, and 46 species compared to 81 species  
249 predicted in São Paulo. The species assemblages recorded by field surveys in both  
250 Amazonian study regions suggested a loss of  $\leq 6\%$  of FD compared to original levels of FD  
251 calculated for the same regions based on range maps. The equivalent reduction in FD for  
252 São Paulo was much higher, with an estimated decline of 28% compared with expected FD  
253 calculated from range maps. Similar results were found when the assemblage was limited to  
254 only forest species (Table 1 and Figures 2, S3-4). When comparing observed assemblages  
255 to those randomly generated from the species pool, we found no strong evidence of losses  
256 being clustered in relation to traits (Table 1).

257 Considering individual traits (Table S4–S6; Figure S5–S7), the Santarém survey  
258 assemblage had lower maximum values for beak length and HWI compared to that predicted  
259 from range maps. The mean ( $\pm$  sd) gape size was similar for the field survey (15 mm  $\pm$  7.8

260 mm) and range map ( $14.7 \text{ mm} \pm 7.7 \text{ mm}$ ) assemblages. For Paragominas, only HWI differed  
261 in maximum values, with a lower maximum in the field survey assemblage. The mean gape  
262 size was similar for the field survey ( $14.7 \text{ mm} \pm 7.0 \text{ mm}$ ) and range map ( $14.5 \text{ mm} \pm 6.8 \text{ mm}$ )  
263 assemblages. In São Paulo, observed maximum values for tarsus length, wing length and  
264 HWI were lower, and most traits showed reduced maximum values for the forest species  
265 assemblage comparisons. For this region there was a slight reduction in the mean gape size  
266 when comparing the field survey ( $11.6 \text{ mm} \pm 6.8 \text{ mm}$ ) to the range map ( $12.5 \text{ mm} \pm 6.9 \text{ mm}$ )  
267 assemblage.

### 268 **3.2 Potential for seed dispersal**

269 Across study regions, we found that 57% of species found in intact forest were not detected  
270 in the matrix, and are therefore highly unlikely to disperse seeds between the two (Figure  
271 1a). Regionally the number of species found in intact forest but not in the matrix was 28  
272 (62% of intact forest assemblage) in Santarém, 30 (79%) in Paragominas and 12 (46%) in  
273 São Paulo. In all three regions, only a few species present in intact forest were absent from  
274 nearby degraded forest (Figure 1b; 10% of frugivore species richness in intact forest across  
275 all sites): 1 species (2%) in Santarém; 4 species (11%) in Paragominas; 6 species (23%) in  
276 São Paulo. Roughly half (47% overall) of frugivore species were found in degraded forest  
277 but not in the nearby matrix (Figure 1c): 38 species (54% of the degraded forest  
278 assemblage) in Santarém; 48 species (70%) in Paragominas; 12 species (32%) in São  
279 Paulo.

280 The FD represented by the species shared between land covers did not correspond exactly  
281 with species richness. The species shared between intact forest and matrix did not retain  
282 59%, 90% and 60% of the intact forest FD in Santarém, Paragominas and São Paulo,  
283 respectively (Table S7). The high species overlap between intact and degraded forest  
284 translated into lower FD losses with 16%, 28% and 1% (Santarém, Paragominas and São  
285 Paulo; Table S7) of intact forest assemblage FD not retained by the species shared between

286 intact and degraded forest. When considering the species shared between degraded forest  
287 and matrix, 52%, 62% and 33% (Santarém, Paragominas and São Paulo; Table S7) of  
288 degraded forest assemblage FD was not retained. When considering specific traits, very few  
289 large-gaped frugivore species occurred across the full land cover gradient (Figure 3), with  
290 similar patterns observed for HWI and body mass (Figures S8 and S9).

291 Given that the intensity of surveys differed across land cover types (Table S2), comparisons  
292 among bird assemblages may be influenced by sampling biases. However, when we ran the  
293 analyses with sampling effort fixed across land cover types, we found that overlap  
294 percentages were qualitatively similar (Figure S10). In addition, given that in many cases few  
295 species were shared between land cover types, we tested whether any reductions in  
296 maximum gape width and FD could be attributed to trait-based filtering or were  
297 indistinguishable from random nestedness. Evidence for trait-based filtering was only found  
298 when considering FD in both Amazonian regions (Table S7) and also for the gape width of  
299 species shared between intact and degraded forest in Santarém (Table S8).

#### 300 **4 DISCUSSION**

301 Our results suggest that seed dispersal between intact tropical forest and matrix landscapes  
302 will proceed through a combination of direct and stepwise processes (scenarios a–c; Figure  
303 1). Given the high species turnover observed across land cover gradients, we conclude that  
304 relatively few frugivore species are involved in direct seed dispersal from remaining patches  
305 of intact forest into the surrounding matrix, with these events likely to be rare. Moreover, we  
306 can infer that direct dispersal is mainly restricted to smaller seeds, because a relatively low  
307 number of large-gaped frugivorous bird species are shared between both habitats. This  
308 finding implies that large-seeded tree species are more likely to require a stepwise process,  
309 potentially delaying natural forest regeneration by decades if the distance to intact forest is  
310 too large.

311 The number of avian frugivores shared between more structurally similar habitats (that is,  
312 shared between intact and degraded forests; or between degraded forests and the matrix) is  
313 relatively high. Additional seed dispersal between intact forest and matrix may therefore  
314 follow a stepwise pathway through degraded intermediaries, such as secondary forests. This  
315 stepwise dispersal pattern is much less efficient, however, as it requires seeds deposited in  
316 intermediate habitats to develop into seed-bearing trees before they can be transferred to  
317 the surrounding matrix. These results also indicate that transport of larger seeds by birds is  
318 reliant on a relatively small number of large-gaped species (Burns, 2013; Wheelwright,  
319 1985), providing an important insight into likely challenges for natural regeneration in human-  
320 modified tropical forest landscapes.

321 Reliance on few large-gaped species as potential dispersal vectors between intact forest and  
322 matrix is clearest for the sites in São Paulo and Paragominas but can still be seen to a lesser  
323 extent in Santarém (Figure 3). In São Paulo and Paragominas, it is not only that there are  
324 few large-gaped species shared between intact forest and matrix, very few large-gaped  
325 species are recorded in the matrix at all (Figure S11). These findings align with previous  
326 studies reporting that relatively few bird species use both intact and cleared land-cover types  
327 (Rehm et al., 2017) and that these ecologically flexible species with the greatest potential to  
328 act as mobile links for seed dispersal tend to be smaller bodied with smaller gapes (Pizo &  
329 dos Santos, 2011).

330 In our Amazonian landscapes, the dispersal of very large seeds between intact forest and  
331 the cleared matrix relies on species like *Pteroglossus aracari* and other toucans  
332 (*Ramphastidae*). In the Atlantic Forest landscapes, birds with larger gape sizes detected in  
333 both intact forest and cleared matrix included toucans (*Ramphastos dicolorus*) and cotingas  
334 (*Pyroderus scutatus*). While the importance of large-gaped frugivorous birds for the  
335 recruitment of large seeds is well known (Beltrán & Howe, 2020; Reid et al., 2021), reliance  
336 on very few species reduces resilience to future perturbations, particularly if population size

337 is also low. Our results show that, especially for São Paulo, most large-gaped species are  
338 either rare visitors to matrix areas or missing from these landscapes altogether.

339 All our surveys detected fewer bird species than predicted by range maps, resulting in  
340 slightly lower estimates of FD than anticipated from geographical ranges. In contrast with  
341 some previous studies (e.g., Bovo et al, 2018), we found no evidence that larger-gaped  
342 species were more likely to drop out from current assemblages. Nonetheless, their loss has  
343 a disproportionate impact on FD because redundancy declines towards the extremes of the  
344 trait distribution. The absence of one large-gaped species therefore represents a greater  
345 decline in ecological function and resilience than the loss of a different species more  
346 centrally placed on the gape-size gradient, where redundancy is high (Ali et al. 2023).

#### 347 **4.1 Methodological limitations**

348 It is worth emphasising that distribution maps can provide misleading information about  
349 historical assemblages. Mapping exercises tend to overestimate species richness at finer  
350 scales (Hurlbert & Jetz, 2007), and are unlikely to account for habitat specialisation (Jetz et  
351 al., 2008). In addition, field surveys are subject to imperfect detection of species with cryptic  
352 behaviours or spatiotemporally patchy distributions. Even with intensive sampling effort, the  
353 diversity of rare or inconspicuous species in tropical bird communities makes detection  
354 challenging (Banks-Leite et al., 2014; Robinson et al., 2018). Nonetheless, the number of  
355 species overlooked by our field surveys is likely to be very low, particularly for large-gaped  
356 species which tend to be highly conspicuous when present. Almost all the losses we detect  
357 are therefore likely to represent true losses of function or declines in functional redundancy  
358 (Figure 2). In addition, even the frugivorous species detected in our study landscapes may  
359 be greatly reduced in population size by habitat loss and hunting, meaning that the volume  
360 and distance of seed dispersal may be substantially reduced in comparison with historical  
361 landscapes.

362 Our analyses focus exclusively on specialist avian frugivores, potentially overlooking the  
363 contribution of bird species for which fruit is not a major part of their diet, such as omnivores  
364 (Carlo & Morales, 2016; Rehm et al., 2017) or invertivores that supplement their diet with  
365 some fruit (Camargo et al., 2020). Migratory tyrant-flycatchers, for instance, may consume  
366 large quantities of berries in degraded Amazonian and Atlantic forests during the non-  
367 breeding season, with potentially large impact on early successional stages (Athiê & Dias  
368 2016). Other taxa such as fish, reptiles and mammals can disperse seeds but again may  
369 perform different roles in the dispersal system (de la Peña-Domene et al., 2014; Donatti et  
370 al., 2011). Moreover, they face similar pressures from habitat loss and direct exploitation in  
371 human-modified landscapes (Costa-Pereira & Galetti, 2015). Although birds cannot provide  
372 a complete picture of seed dispersal on land cover gradients, they appear to play a major  
373 role, especially for later successional species (de la Peña-Domene et al. 2014).

374 We have argued that patterns of species occurrence across land cover gradients can  
375 provide insights into the likely transfer of seeds between habitat types (Sekercioglu, 2006).  
376 This is based on the reasoning that the locations in our study represent adjacent portions of  
377 a gradient and previous evidence suggests that individual birds will move between adjacent  
378 land cover types (Mayhew et al. 2019) with widespread spillover effects (Hatfield et al.  
379 2020). However, this type of information is sparse and species may vary in how often they  
380 move between land cover classes. Our approach also makes assumptions about the food  
381 plants of frugivorous birds, despite relatively limited knowledge of diets and trophic  
382 interactions, particularly in the context of tropical forest birds.

383 To address these issues, further work is required to clarify rates of movement between land  
384 covers by tracking individual birds, and to provide more detailed information about avian  
385 diets through techniques such as metabarcoding (Hoenig et al., 2022). This improvement in  
386 dietary information would allow for a more comprehensive treatment of species, including  
387 abundant generalists, for which fruit is not the main component of their diet but which may  
388 nonetheless function as important seed dispersers for particular plant species (Pizo, 2004).

389 Nonetheless, the addition of these species is unlikely to alter our main conclusions because  
390 generalist species tend to be more important in degraded forests and are unlikely to provide  
391 dispersal services for larger seeds.

392 Along with more detail on movements and diet, we also require robust data on abundance.  
393 Without a better grasp on the number of individual birds involved, it is challenging to  
394 evaluate the implications of presence-absence data, as functions are often effectively lost  
395 even when particular frugivore species are still present but reduced to such low numbers  
396 that they are essentially not delivering any effective seed dispersal function. Future analyses  
397 should also encompass the role of seed-dispersing mammals such as primates and bats,  
398 which may play a vital role in mediating regeneration potential of human-modified tropical  
399 forests (Stoner et al., 2007).

#### 400 **4.2 Pathways to resilience in tropical forests**

401 With tropical deforestation continuing at a rapid pace, maintaining the potential for forest  
402 regeneration is a critical concern. Logged and disturbed rainforests contain tree species with  
403 lower average wood density and smaller seeds (Bello et al., 2015; Hawes et al., 2020) while  
404 cleared areas have greatly reduced value for biodiversity. The relevance of strategies  
405 promoting rapid and affordable forest regeneration is brought into sharp focus by policy  
406 targets, including the Brazilian government's Nationally Determined Contributions under the  
407 Paris Agreement, which represent a binding commitment to achieve carbon neutrality and  
408 mitigate climate change impacts, partly through forest restoration. For example, the state of  
409 Pará has committed to restore c.5 Mha of Amazonian rainforest by 2030 (Plano Estadual  
410 Amazônia Agora, 2020). Such targets can be achieved through direct interventions such as  
411 tree-planting programmes. However, the passive restoration of tropical forests via natural  
412 processes has a number of benefits over active restoration, including increased diversity  
413 (Chazdon & Guariguata, 2016) and greater potential to track climate change (Fricke et al.,



414 2022). In addition, natural regeneration is the only financially viable solution over extensive  
415 degraded areas because it can be delivered at minimal cost (Chazdon & Guariguata, 2016).

416 Where forest restoration is a key objective, our results suggest that dispersal from natural  
417 seed sources would require close proximity to intact native forest, supporting earlier work  
418 (e.g., Cardoso da Silva et al., 1996). Cleared areas further away from native forests may  
419 require alternative approaches, such as applied nucleation and nurse trees, to help  
420 encourage seed dispersers to use more of the landscape (Pizo & dos Santos, 2011;  
421 Freeman et al., 2021). The likelihood of recruitment will often be low, however, as many  
422 matrix environments provide unsuitable terrain for seed germination and sapling growth  
423 (Reid & Holl, 2013). Our results also suggest that degraded forest plays a critical role in  
424 supplying seeds and seed-dispersal agents. These disturbed habitats not only hold more  
425 biodiversity than fully cleared landscapes, they also support landscape-level resilience by  
426 providing a vital source and conduit for seed transfer into the non-forest matrix. Thus,  
427 prioritising the conservation and management of substantial areas of logged and secondary  
428 forests is not only beneficial in terms of their efficient nutrient cycling and carbon uptake  
429 (Malhi et al. 2022), but also vital for promoting the healthy seed-dispersal dynamics required  
430 for rapid and economical reforestation programmes.

431 While secondary and disturbed forests can play a key role, our findings highlight the  
432 importance of preserving extensive intact forests to promote seed transfer from large-seeded  
433 trees, including commercially important hardwoods and other species with tall stature crucial  
434 to achieving the vegetation structure and microhabitat complexity of old growth forests  
435 (Hawes et al., 2020). In effect, the potential for forest resilience and regeneration will best be  
436 delivered by mosaic landscapes with degraded-forest buffers around core areas of intact  
437 forest that are not too distant. This tallies with proposals to focus restoration efforts on  
438 landscapes with intermediate forest cover levels and good connectivity with intact forest  
439 (Tambosi et al., 2014; Mayhew et al., 2019).

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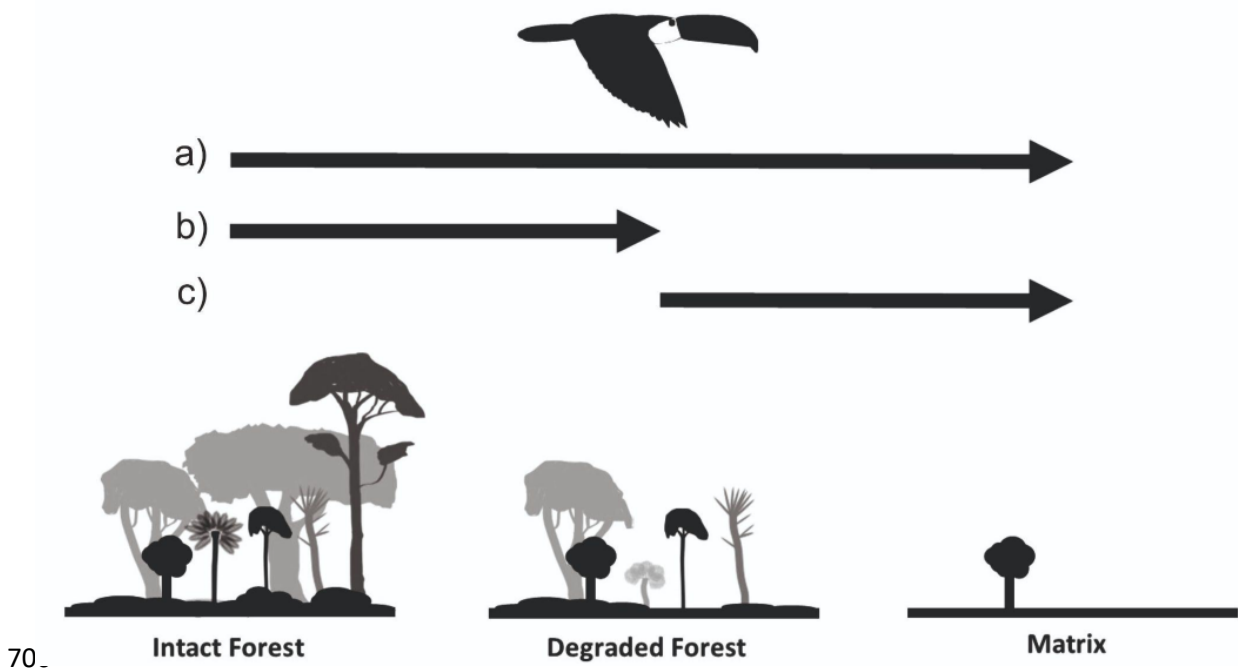
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707 **FIGURE 1** Schematic of possible seed dispersal scenarios from intact forest to matrix.

708 Seeds could be transferred directly from intact forest into the matrix (Scenario a); transferred

709 only from intact forest to degraded forest without subsequent seed dispersal into the matrix

710 (Scenario b); or only transferred from degraded forest to the matrix without any prior seed

711 dispersal from intact to degraded forest (Scenario c). Alternatively, seeds can be transferred

712 from intact forest to surrounding matrix via a stepwise pathway (b then c), although this

713 involves a major rate-limiting step – that is, it can take many years before seeds deposited in

714 degraded forest develop into trees mature enough to bear fruit that can be consumed and

715 subsequently transferred into the matrix.

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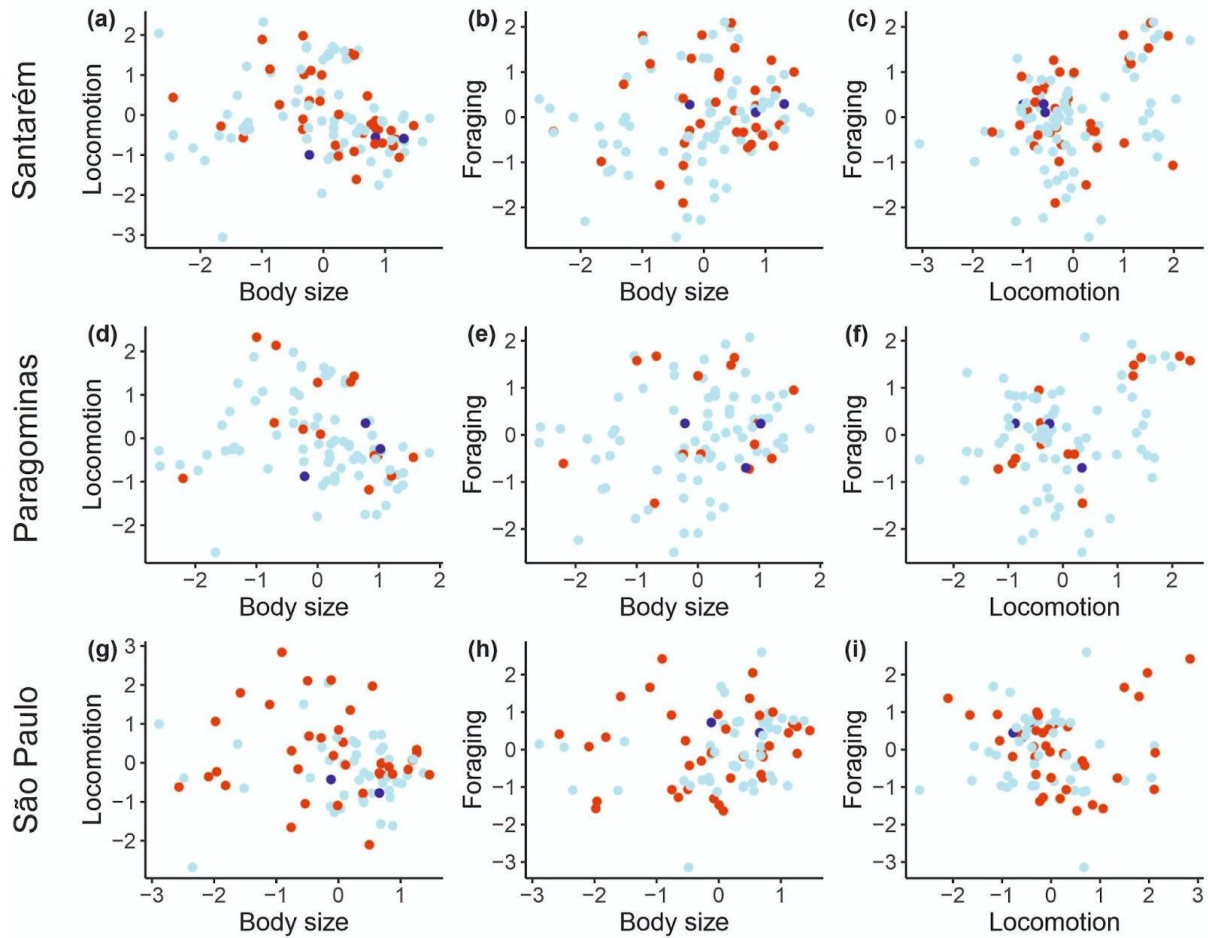
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724 **FIGURE 2** Distribution of species along trait axes for all frugivores in Santarém (a, b and c),

725 Paragominas (d, e and f) and São Paulo (g, h and i). Data points are coloured to indicate

726 whether species in the frugivore assemblages are predicted to occur based on geographic

727 distributions but not detected by surveys (red), found in surveys but not predicted to occur by

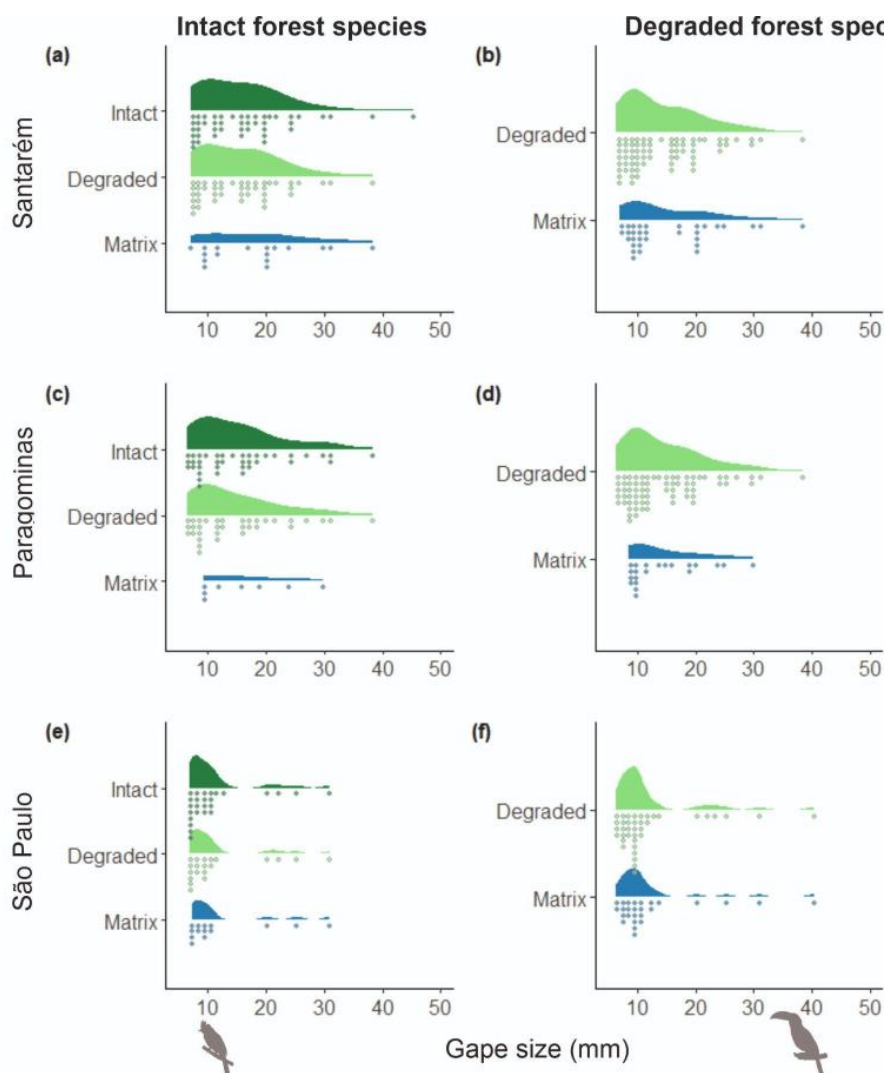
728 geographic range distributions (dark blue), or both detected by empirical surveys and

729 predicted by geographic distribution (pale blue).

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734 **FIGURE 3** Gape sizes of frugivorous birds across different land cover types for Santarém (a,  
735 b), Paragominas (c, d) and São Paulo (e, f). Gape size (a horizontal linear measurement  
736 across the base of the mandibles where they join) is an index of maximum fruit size that can  
737 be consumed by each species. Each dot represents a single species, grouped into 1 mm  
738 bins. Left-hand panels (a, c, e) show species recorded in intact forest, and indicate whether  
739 they also occur in degraded and matrix habitats; right-hand panels (b, d, f) show species  
740 recorded in degraded forest, and indicate whether they also occur in the matrix. Bird species  
741 with larger gape sizes (>20 mm) are most frequent in intact forest and rarer in degraded or  
742 matrix habitats. Silhouettes of a small-gaped *Myiarchus* flycatcher and a large-gaped toucan  
743 (*Ramphastidae*) were obtained from phylopic.org.

744 **TABLE 1** – Historical declines in functional diversity (FD) for study assemblages. Declines  
745 were estimated as a percentage of the expected FD calculated from the projected historical  
746 avifauna determined by geographical range maps. Values are given for each of the three  
747 regions (Santarém, Paragominas and São Paulo) for all frugivores and for forest frugivores  
748 (i.e., frugivores largely restricted to forest vegetation). Results for forest frugivores are shown  
749 for two different classifications: main values are based on species with primary habitat  
750 classified as forest in AVONET (Tobias et al. 2022); values in brackets are based on BirdLife  
751 International’s forest dependency categories (BirdLife International, 2022; Buchanan et al.,  
752 2011).

Region	All frugivores		Forest frugivores	
	Percentage FD reduction	Randomly generated FD reduction $\leq$ observed loss (%)	Percentage FD reduction	Randomly generated FD reduction $\leq$ observed (%)
Santarém	6	6	7 (8)	12 (17)
Paragominas	4	35	2 (1)	19 (22)
São Paulo	28	32	33 (33)	48 (29)

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