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Large-bodied and wide-beaked avian frugivores show greater specialisation in tropical seed dispersal networks

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Frugivory_Networks_and_Traits_R1_track_changes.docx	Main Document - Tracked Changes	1.7 MB	Page 34
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1 **Large-bodied and wide-beaked avian frugivores show greater**
2 **specialisation in tropical seed dispersal networks**

3 **ABSTRACT**

4 **Aim:** Avian frugivores with large bodies and beaks are increasingly threatened due to smaller
5 population sizes, greater energy requirements, and higher vulnerability to hunting pressure and
6 illegal wildlife trade. However, it remains unclear whether birds with these traits adopt
7 consistent strategies in their interactions with fleshy-fruited plants and, therefore, hold specific
8 trait-driven roles in fruit-frugivore networks that are difficult to replace under extinction
9 scenarios.

10 **Location:** Worldwide.

11 **Time Period:** Contemporary.

12 **Major Taxa Studied:** Birds.

13 **Methods:** Here, we analyze 215 avian frugivory networks spanning diverse bioregions,
14 ecosystems, and habitats to examine whether body mass and beak width influence the functional
15 roles and position of avian frugivores in interaction networks. Specifically, we first examine
16 how these traits relate to species-level network metrics. In addition, we simulated the removal of
17 species with extreme (i.e., higher and lower) body mass and beak width values to study whether
18 relationships at the species level can scale up and affect overall network structure.

19 **Results:** Our findings indicate that larger species, as well as those with wider beaks, play more
20 specialized roles in tropical frugivory networks (higher d'), with wide-beaked species having
21 fewer interactions and larger species being involved in interactions of greater strength. The
22 potential extinction of a few of these species with extreme traits could scale up, modifying
23 network structure. The consistent pattern observed across different conditions suggests that
24 large-bodied frugivores, which in turn show stronger dependence on fruits, may have evolved to
25 fill niche-specific seed dispersal roles in highly diverse environments – roles whose functional
26 singularity is difficult to replace.

27 **Main Conclusions:** These results emphasize the importance of implementing targeted
28 conservation strategies to protect large-bodied and large-beaked avian frugivores. Such efforts
29 are crucial for maintaining the integrity of seed dispersal networks and, consequently,
30 supporting broader ecosystem functioning.

31

32 **Keywords:** Avian frugivory; Defaunation; Ecological networks; Endozoochory; Functional
33 traits; Mutualistic networks; Seed dispersal; Species extinction impacts; Trait-based ecology.

34 INTRODUCTION

35 Avian frugivores play a crucial role in seed dispersal, significantly contributing to forest
36 regeneration and maintaining landscape-scale connectivity (Schupp et al., 2010; Jordano, 2014;
37 González-Varo et al., 2017). This ecological function enables animal-dispersed plants to
38 colonize matrix habitats, which is crucial for plant community dynamics and ecosystem
39 resilience after land-use changes (Hatfield et al., 2024; Rey et al., 2021). Fragmentation and
40 habitat degradation not only threaten the viability and persistence of plant populations but also
41 put many avian frugivore species at risk, with body size emerging as a critical factor influencing
42 their vulnerability to extinction (Pimm et al., 1988). Large-bodied species may be more
43 vulnerable or prone to extinction due to several factors, including smaller population sizes,
44 lower reproductive rates, larger geographic or home range requirements, or being at higher
45 trophic levels than small-bodied species (Gaston & Blackburn, 1997; Woodward et al., 2005).
46 Additionally, they are particularly susceptible to defaunation due to size-selective hunting
47 practices (e.g., Donoso et al., 2020) and are highly sensitive to human pressures, often being
48 the first to vanish following habitat degradation (Galetti et al., 2013; Pigot et al., 2016). Large-
49 bodied species are fundamental to long-distance seed dispersal and maintaining metapopulation
50 connectivity as they can remove a greater number of seeds per visit, retain them for longer, and
51 deposit them farther from the parent plant than smaller birds (Wotton & Kelly, 2012; Fell et al.,
52 2023). Thus, the selective extinction of these species could have a disproportionately high
53 impact on ecosystems due to their unique roles and functions, which may not be readily
54 replaceable, as it has been shown in previous local studies (Wotton & Kelly, 2012; Vidal et al.,
55 2014). However, the consequences that the loss of these species may have on the structure of
56 seed dispersal networks have not yet been studied on a global scale.

57 Large-bodied species have higher absolute energy requirements than smaller species,
58 which strongly influences their foraging decisions. Given similar diets and food densities, larger
59 birds must consume greater amounts of food, yet they are often more energetically efficient per
60 unit body mass. As a result, they tend to target larger and/or more energy-rich food items and to
61 exploit environments that maximize the balance between energetic costs and benefits, as

predicted by “optimal foraging theory” (Pyke 1978). Beyond body size, beak characteristics also play a significant role in determining the foraging strategy and feeding habits of birds (e.g., Grant et al., 1985). Specifically, the ability of avian frugivores to disperse seeds from fleshing-fruit plants is limited by gape width (for which beak width is often used as a proxy), which imposes an upper physiological constraint on the size of seeds they can ingest whole (Wheelwright, 1985; Herrera, 1995; Burns, 2013). As a result, size-coupling frequently occurs in fruit-frugivore interactions, leading to positive relationships between disperser gape width and the average diameter of fruits they consume. This relationship may, however, follow a triangular pattern; species with wide gapes can theoretically consume and disperse fruits of a wide range of sizes, while species with narrower beaks are restricted to smaller fruits (Galetti et al., 2013; Pigot et al., 2016). Consequently, according to the ‘trait-matching’ hypothesis, plants producing large-seeded fruits could be negatively impacted by the local extinction of large-gaped birds (Galetti et al., 2013). Species with unique or prominent beak characteristics (colorful, large, and/or wide beaks) could be more susceptible to illegal trade due to their popularity, visual appeal, or perceived value. For example, some species of parrots or toucans, known for their large and colorful beaks, are likely to attract attention in illegal wildlife markets, a factor often linked to overexploitation and extinction risk (Tella & Hiraldo, 2014; Harris et al., 2015).

Thus, overexploitation resulting from the wild bird trade and size-selective hunting practices poses significant threats to large-bodied and large-gaped avian species. Although these species are vital for the recruitment and persistence of plant populations (Pires et al., 2018), it remains unclear whether they play a consistent, trait-driven role in mutualistic networks. Gaining insight into this could improve our understanding of frugivory dynamics and the potential consequences of losing these species, especially since large and/or broad-billed bird species may act as central or ‘keystone species’ (Wotton & Kelly, 2012). In this context, the role of species with extreme traits within seed dispersal networks is a matter of ongoing debate. For instance, while some studies have suggested that large avian frugivores play a central role in some plant-frugivore networks due to their potential to have a more generalist diet (i.e., larger fundamental niche)—consume fruits from a wider size spectrum (Palacio et al., 2016)—others

91 have found no correlation between body size and network centrality measures ([Naniwadekar et](#)
92 [al., 2019; Montoya-Arango et al., 2019](#)). This discrepancy may be due to the specific
93 characteristics (e.g., diversity of plant and bird clades) of each local network.

94 Additionally, the study of interaction networks could help elucidate the links between
95 species' functional traits and their ecological roles, as well as predict the response of plant-
96 disperser communities or analogous bipartite networks under different extinction scenarios
97 ([Moulatlet et al., 2023](#)). The stability and robustness of mutualistic networks to species
98 extinction depend on their modularity and nestedness; networks where a few species
99 monopolize most of the links are more likely to collapse than those with more evenly distributed
100 connections ([Bascompte & Jordano, 2007](#)). Although some authors have explored the
101 relationship between species' traits and their topological importance at a local scale ([Acevedo-](#)
102 [Quintero et al., 2020a](#)), there is a paucity of studies addressing this question at large scales
103 across multiple ecosystems (but see [Moulatlet et al., 2023](#)). This is paramount for determining
104 whether there is a universal pattern of the role of body size and gape width in mutualistic plant-
105 frugivore interactions.

106 Here, we used a large dataset of 215 bipartite interaction networks distributed from
107 around the world, linking avian frugivorous and plant species, to explore the universal role of
108 body mass and beak width in shaping species interactions. These traits directly influence seed-
109 dispersal function and may indicate specific roles in interaction networks. We hypothesized that
110 large-bodied species and those with wider beaks would consistently have more interactions
111 (higher degree), exhibit a lower specialization and occupy a more central position in the
112 network, given their potential to feed on a broader variety of fruits and exploit a greater
113 diversity of plant species. Alternatively, if the realized niche differs considerably from species'
114 fundamental or potential niche, and trait-matching processes predominate the ecology in these
115 networks, as predicted by the optimal foraging theory ([Pyke, 1978](#)), we might find the opposite
116 (i.e., higher specialization and lower centrality in larger and wider-beaked species).

117 Additionally, we expected that the removal of the largest species and those with the widest beak
118 sizes would significantly affect mean interaction diversity and links per species at the network
119 scale, highlighting their critical role in maintaining network structure.

120

121 **METHODS**

122 *Dataset*

123 This study utilized a dataset comprising 215 frugivory networks across the world (see [Fig. 1](#) and
124 [Table S1](#) in Supplementary Material for network details and references), including data on
125 frugivore avian species and fleshy fruits. This global dataset was compiled and used by [Fricke](#)
126 & [Svenning \(2020\)](#) to test the impact of alien species on networks of plant-frugivore
127 interactions. The original dataset comprised 403 interaction networks, but we filtered the dataset
128 to restrict our analysis to plant-bird interactions. Networks were filtered to exclude those with
129 fewer than two bird species or fewer than three plant species, as such small networks were
130 deemed incomplete and less representative. The resulting dataset consisted of 215 networks, of
131 which 113 were weighted (i.e., quantitative) and 102 were unweighted (i.e., qualitative binary
132 networks). For consistency, all networks were first transformed into qualitative networks (i.e.,
133 unweighted). However, analyses were also conducted using the original quantitative data from
134 the 113 weighted networks, yielding very similar results ([Table S2](#) and [Fig. S1](#) in
135 [Supplementary Material](#)).

136 Our dataset comprised 2,150 plant species and 1,031 bird species belonging to 167 and
137 102 families, respectively. For each bird species included in the dataset, we obtained their
138 average body mass (used as a proxy for body size) and beak width from AVONET ([Tobias et](#)
139 [al., 2022](#)). Body size constitutes a multifaceted trait that influences a wide range of biological
140 functions, including dispersal capacity and foraging behavior. It plays a key role in shaping
141 ecological interactions and can affect an individual's ability to access resources and compete
142 with others. On the other hand, beak width (frequently used as a proxy for gape width)
143 constitutes an effect trait and predicts the size of food to be handled and consumed
144 ([Wheelwright, 1985](#)).

145

146 *Network completeness*

147 To evaluate the sampling quality and reliability of the interaction networks included in this
148 study, we assessed their network completeness, which estimates how thoroughly each network
149 captures the full set of potential interactions of each species. This is essential to ensure that
150 derived metrics are not biased by under-sampling, and that network-level comparisons are based
151 on robust and representative data (Chacoff et al., 2012). Because our dataset included both
152 quantitative (weighted) and qualitative (unweighted) networks, we applied different approaches
153 to optimize the estimate of completeness depending on network type. For weighted networks,
154 sample coverage was calculated using the ‘iNEXT’ R package (Hsieh et al., 2016), which
155 estimates coverage of interactions based on interaction frequency data. In contrast, for
156 unweighted networks, we employed Chao’s estimator of species richness (Chao & Jost, 2012).
157 Completeness in this case was calculated as the ratio between the observed interaction richness
158 and the estimated richness from Chao’s estimator (Martínez-Núñez et al., 2020). This analysis
159 revealed that the majority of networks exhibited moderate to high levels of completeness.
160 Specifically, only three networks showed completeness values below 40%, nine networks fell
161 below 50%, and 16 networks out of 215 had values below 60% (Fig. S2). Thus, based on these
162 results, we conclude that most networks were adequately sampled and provide reliable estimates
163 of interaction patterns. In addition, we employed appropriate null models in most analyses to
164 account for the potential effect of network completeness and network size on the results.

165

166 *Effect of body mass and beak width on network metrics*

167 To test the role of avian body mass and beak width on frugivory networks, two types of
168 analyses were conducted: one at the species level and another at the network level. These
169 analyses were designed to detect a broad yet significant signal across a diverse range of
170 environmental conditions, species compositions, and networks. Their low specificity allows for
171 the identification of universal patterns and generalization, suggesting that any significant
172 differences observed may point to fundamental ecological principles despite the inherent
173 variability in local environmental conditions, network sampling specifics, or phylogenetic
174 idiosyncrasies.

175

176 *Species-level analyses*

177 Species-level metrics (degree, strength, closeness centrality, and specialization, d') ([Table 1a](#))
 178 were calculated directly from the original interaction networks for every avian species in every
 179 network using the *specieslevel* function from the ‘bipartite’ package ([Dormann, 2009](#)).
 180 Subsequently, generalized linear mixed models (GLMMs) were employed to investigate the
 181 relationship between both (log-transformed) body mass and beak width on each of these four
 182 network metrics. GLMMs were implemented using a Poisson error distribution with a *log* link
 183 function (species degree), a gamma error distribution with a *log* link function (interaction
 184 strength and closeness), or a beta family with *logit* link function (d'). For each response variable
 185 (degree, interaction strength, closeness, and d'), we fitted two models: one with body mass as
 186 the explanatory fixed effect and another with beak width. GLMMs were built using ‘lme4’
 187 ([Bates et al., 2015](#)) and ‘glmmTMB’ ([Brooks et al., 2017](#)). Separate models were fitted to avoid
 188 collinearity, given that body mass and beak width were correlated (Spearman’s $\rho = 0.61, p < 0.001$). Network ID was included as a random intercept and random slope to account for
 189 variability across different frugivory networks and allow for different relationships (i.e., slopes)
 190 between traits and species-level metrics in different networks.

192 Lastly, we fitted additional models accounting for phylogenetic relatedness, which may
 193 underlie, for example, the tendency of larger species to occupy specific network roles, and for
 194 interspecific variation in frugivory. We used a consensus tree generated from a sample of 1,000
 195 trees obtained from BirdTree (www.birdtree.org) and data on the proportional contribution (%)
 196 of fruits to each species’ diet from AVONICHE ([Sayol et al. 2026](#)). Using these data, we
 197 examined the relationship between morphological traits (body mass and beak width) and
 198 species-level interaction specialization (d') using Phylogenetic Generalized Least Squares
 199 (PGLS) models implemented in the R package *caper* ([Orme et al. 2025](#)). Additionally, we
 200 investigated whether species traits (body mass and beak width) were associated with their
 201 degree of frugivory, while controlling for phylogenetic relatedness.

202 *Differences across bioregions*

203

204 Our dataset comprised interaction networks from different biogeographic contexts (19 networks
 205 from the Austral bioregion, 24 from Oceanic Islands, 53 from Temperate bioregions, and 119
 206 from Tropical bioregions). To assess whether the trait–network role relationships are consistent
 207 across broad biogeographic contexts, we refitted the same generalized linear mixed models
 208 described above, but including an interaction between each focal trait and biogeographic
 209 category (see [Appendix S1 in Supplementary Material](#) for further details).

210

211 *Network-level analyses*

212 To explore whether these relationships at the species level are strong enough to scale and affect
 213 network-level properties, we tested the effect of species removal on network metrics. For this
 214 purpose, we simulated five distinct scenarios. In the first, named the “*Largest species removed*”
 215 scenario, we removed the largest bird species from the metanetwork. In the “*Smallest species*
 216 *removed*” scenario, the smallest species were eliminated. In the “*Widest beaks removed*”
 217 scenario”, we removed species with the widest beaks, while in the “*Narrowest beaks removed*”
 218 scenario, we removed species with the narrowest beaks. Lastly, in the “*Random species*
 219 *removed*” scenario, species were removed randomly. For this last scenario, the process was
 220 repeated 1,000 times to obtain average metric values following random extirpations. For each of
 221 the five simulated scenarios, we removed 10% (~103 species), 20% (~206 species), and 30%
 222 (~309 species) of the total pool of species (1,031 species); following different criteria according
 223 to each scenario. The exact numbers varied slightly due to ties in species values, with these
 224 species retained as a group to avoid arbitrary selection. The removal process followed a
 225 deterministic approach, where species were selected and removed based directly on their body
 226 mass and beak measurements. Networks where at least one species was removed were then
 227 selected and compared with the networks from the random scenario (the percentage of networks
 228 affected in each scenario is shown in [Table S3](#)).

229 Next, for each network and scenario, we estimated four network-level metrics (namely,
 230 connectance, nestedness, links per species, and Shannon diversity) ([Table 1b](#)) using the
 231 *networklevel* function from ‘bipartite’. To examine the effect of different scenarios on these

232 network metrics, we fitted linear mixed-effects models (one for each response variable, namely
 233 network metric) using the *lmer* function of the ‘lme4’ package. Each model included scenario as
 234 a fixed effect to evaluate its impact on the network metrics, while variability between networks
 235 was accounted for by including network ID as a random factor. The residuals of the models met
 236 the assumptions of independence and normality.

237

238 *Sensitivity analysis*

239 Although the interaction networks employed in this study exhibit high completeness, we
 240 conducted a sensitivity analysis to assess whether the observed roles and positions in the
 241 network of large-bodied, wide-beaked species might be influenced by sampling bias.
 242 Specifically, we sought to rule out the possibility that their inferred level of specialization is an
 243 artifact of species low abundance and, consequently, fewer recorded interactions. Such species
 244 may appear more specialized due to limited sampling rather than reflecting true ecological
 245 patterns. For this analysis, we used a subset of 113 quantitative (weighted) networks that
 246 included interaction frequencies ([see Appendix S1 in Supplementary Material for further](#)
 247 [details](#)).

248

249 **RESULTS**

250 *Relationship between morphological traits and species-level metrics*

251 We found a positive relationship between body mass and specialization ($\beta = 0.090 \pm 0.026$; $z =$
 252 3.513 , $p < 0.001$) indicating that larger species tend to be more specialized and interact with a
 253 particular subset of species ([Fig. 2](#)). On the contrary, body mass was negatively associated with
 254 closeness centrality indicating that larger species are more peripheral in the network ($\beta = -0.012$
 255 ± 0.003 ; $z = -4.091$, $p < 0.001$) ([Fig. 2](#)). Additionally, a positive relationship between body mass
 256 and species interaction strength was observed, meaning that larger species depend on few
 257 species ($\beta = 0.073 \pm 0.027$; $z = 2.673$, $p = 0.008$). This relationship remained significant when
 258 weighted networks were used ([Table S2](#), [Fig. S1](#)). No significant relationship was found
 259 between body mass and interaction degree ($\beta = -0.002 \pm 0.022$; $z = -0.072$, $p = 0.943$).

260 Beak width was positively associated with specialization ($\beta = 0.087 \pm 0.026$; $z = 3.361$, $p < 0.001$) and negatively with degree ($\beta = -0.112 \pm 0.024$, $z = -4.597$, $p < 0.001$), indicating that
 261 species with wider beaks are more specialized and has fewer interactions (Fig. 2). In addition, a
 262 wider beak was associated with a decrease in closeness, meaning that species with wider beaks
 263 occupy a less central position in the network ($\beta = -0.011 \pm 0.003$, $z = -3.762$, $p < 0.001$). No
 264 significant relationship was found between beak width and species interaction strength (estimate
 265 = -0.006 ± 0.018 ; $z = -0.350$, $p = 0.726$) (Fig. 2). The relationship between species traits and
 266 their specialization was still significant after accounting for phylogenetic relatedness and degree
 267 of frugivory (Table S4).

269 Results at the bioregional scale showed that these relationships were not universal and
 270 were mainly driven by patterns in the tropical bioregion (Fig. 3), with similar trends in the
 271 Austral and Oceanic Islands bioregions. In temperate bioregions, however, larger and wide-
 272 beaked species were not significantly more specialized (d') (see Appendix S1 and Fig. 3).

273

274 *Trait-based scenarios on network-level metrics*

275 Trait-based removal scenarios targeted species occupying the lower and upper extremes of the
 276 body mass and beak width distributions (Fig. 4). The removal of the top 10% largest species
 277 (Table S5) had a positive impact on both the average number of links that each species has
 278 within the network and Shannon diversity (“*Largest species removed*” scenarios in Table 2).
 279 Specifically, the estimates for links per species and Shannon diversity were 0.044 ± 0.006 ($t_{187} = 7.722$,
 280 $p < 0.001$) and 0.047 ± 0.008 ($t_{187} = 5.623$, $p < 0.001$), respectively. This effect remained
 281 when a higher percentage of the largest species was removed (Table 2). Conversely, removing
 282 the top 10% and 20% of the largest species negatively affected nestedness, with estimates of -
 283 0.586 ± 0.181 ($t_{187} = -3.235$, $p < 0.001$) and -0.802 ± 0.274 ($t_{190} = -2.924$, $p = 0.004$) for the 10%
 284 and 20%, respectively. No significant effects were observed for the removal of the top 30% of
 285 species (Table 2).

286 When excluding the smallest 10% (Table S6) and 20% of species (“*Smallest species*
 287 *removed*” scenarios), we observed it positively impacted the number of links per species and
 288 Shannon diversity, with estimates of 0.068 ± 0.005 ($t_{196} = 15.120$, $p < 0.001$) and 0.078 ± 0.004

289 ($t_{196} = 19.640, p < 0.001$), respectively, for the 10% level (Table 2). Additionally, no significant
 290 effects on nestedness were found when removing the smallest species (Table 2).

291 Regarding beak width, the removal of species with the widest beaks consistently
 292 increased the average number of links that each species has within the network ($\beta = 0.042 \pm$
 293 $0.008; t_{192} = 5.404, p < 0.001$) and Shannon diversity ($\beta = 0.049 \pm 0.010; t_{192} = 4.492, p < 0.001$)
 294 at the 10% level of the “*Widest beaks removed scenario*” compared to the null scenario.
 295 Excluding these species also affected links per species and Shannon diversity at the higher
 296 levels (Table 2). In contrast, the removal of the top 10% of species with the widest beaks
 297 negatively affected nestedness, with an estimate of $-0.389 \pm 0.145 (t_{192} = -2.683, p < 0.008)$
 298 (Table S7). No significant effects were found for the 20% and 30% levels (Table 2).

299 When removing the species with the narrowest beaks (Table S8) (“*Narrowest beaks*
 300 *removed*” scenario), we found it negatively impacted the average number of links ($\beta = -0.066 \pm$
 301 $0.016; t_{196} = -4.242, p < 0.001$) and Shannon diversity ($\beta = -0.106 \pm 0.021; t_{196} = -4.956, p$
 302 < 0.001) at the 10% level. These effects persisted at the 20% and 30% levels for Shannon
 303 diversity (Table 2). Removing species with the narrowest beaks did not have a significant effect
 304 on nestedness (Table 2). Network connectance was also tested for all scenarios and levels, but
 305 this metric was not significantly affected in any case.

306 Finally, the observed network metrics for larger-bodied and wider-beaked species
 307 differed significantly from those expected under a random interaction structure, given the same
 308 number of interactions (Fig. 5).

309

310 *Relationship between morphological traits and frugivory*

311 We found a significant relationship between both morphological traits and the species’ degree
 312 of frugivory (Fig. S3); the level of dependence on this food resource increases with body mass
 313 (PGLS; lambda: 0.924 [CI: 0.903-0.942], $\beta = 11.93 \pm 2.75, t = 4.33, p < 0.001$) and beak width
 314 (lambda: 0.928 [CI: 0.907-0.945], $\beta = 14.86 \pm 5.65, t = 2.63, p < 0.01$).

315

316 **DISCUSSION**

317 Understanding how functional traits shape the strategies and roles of avian species in seed
318 dispersal networks offers valuable ecological insights with important implications for
319 conservation. Our study demonstrates that body size and beak width are key predictors of the
320 roles that birds play in frugivory networks. At the species level, we found that large-bodied
321 birds and those with wider beaks tend to occupy more specialized positions, engaging in fewer
322 but stronger interactions and exhibiting lower network centrality. At the community level, our
323 simulations revealed that removing these species significantly alters network structure:
324 nestedness increases, as do both the number of interactions and mean interaction diversity.
325 These findings highlight the unique and specialized roles of large-bodied, wide-beaked
326 frugivores and their importance in maintaining network integrity. More broadly, our results
327 reinforce the idea that downsizing in ecological networks can have far-reaching consequences
328 for ecosystem functioning, particularly in mutualistic systems structured by trait-matching, as
329 predicted by previous theoretical work ([Donoso et al., 2017](#)).

330

331 *Relationship between species traits and network roles*

332 Contrary to our initial hypothesis, we found that larger species tend to occupy more peripheral
333 positions in frugivory networks, as evidenced by the negative relationship between body mass
334 and closeness centrality. This pattern suggests that, although these species form strong
335 interactions, they do so selectively. Our findings align with several local-scale studies. For
336 example, [Naniwadekar et al. \(2019\)](#) reported that large frugivores, such as hornbills and
337 imperial pigeons, were less connected than intermediate-sized species like barbets and bulbuls
338 in Indian forests (see also [Montoya-Arango et al., 2019](#)). In contrast, [Palacio et al. \(2016\)](#)
339 observed that large frugivores such as cotingas and toucans held more central roles in networks
340 from a nearby, more pristine region in the Colombian Andes. These contrasting results may
341 reflect variation in network properties across ecosystems, elevations, and bioregions (e.g.,
342 differences in trait distributions; [Acevedo-Quintero et al., 2020b](#)), as well as the effects of
343 anthropogenic disturbance ([Martins et al., 2022](#); [Emer et al., 2018](#)). Despite this environmental
344 variability, our findings indicate that the peripheral role of the largest species in frugivory
345 networks is consistent and generalizable at a global scale ([Moulatlet et al., 2023](#)).

346 In line with these findings, we observed that large-bodied species tend to adopt a
347 foraging strategy characterized by fewer but stronger and more specialized interactions. The
348 positive association between body mass, species strength, and specialization suggests that these
349 birds typically occupy more specialized roles within frugivory networks. This pattern may be
350 shaped in part by energetic constraints: large-bodied frugivores require higher caloric intake and
351 are likely to selectively target energy-rich fruits while avoiding those with lower nutritional
352 value (Sebastián-González, 2017; Quintero et al., 2020). Such behavior aligns with predictions
353 from optimal foraging theory, which proposes that animals maximize energy gain per unit effort
354 (Pyke, 1978). In addition to energetic demands, trait-matching mechanisms may further
355 reinforce specialization (Martins et al., 2024). Species with extreme morphological traits, such
356 as large body size or wide beaks, tend to fill distinct functional niches, interacting preferentially
357 with plants whose fruit traits align closely with their morphology (Dehling et al., 2016; Pigot et
358 al., 2016; Bender et al., 2018). For example, large-bodied birds often favor heavier fruits
359 (Buitrón-Jurado & Sanz, 2021), and their limited number of interactions may result from
360 morphological mismatches that restrict their ability to interact with smaller-fruited species
361 (Dehling et al., 2014). The relationship between specialization and morphological traits does not
362 constitute an artefact of phylogenetic inertia; there was a significant relationship between the
363 species' average specialization (d') and their body mass (and beak width) after accounting for
364 phylogenetic relatedness (Table S4). The existence of a moderate phylogenetic signal for this
365 metric ($\lambda = 0.67$) suggests that high specialization values are not heavily concentrated on a few
366 clades. Taken together, these results suggest that evolutionary pressures have contributed to the
367 specialization of large-bodied frugivores, increasing their vulnerability by tying them to a
368 narrower range of functionally distinctive fruiting plants. This pattern highlights the importance
369 of trait-matching and optimal foraging in frugivores' ecology, and might partly explain why
370 bird assemblages in more productive regions tend to be more specialized globally (Malmagro et
371 al., 2025).

372 Dietary preferences for large, energy-rich fruits (consistent with optimal foraging
373 theory) may also explain why wide-beaked birds occupy less central positions in frugivory
374 networks and display a high degree of specialization. Despite their potential to handle a broad

375 range of fruit sizes due to reduced gape limitations (Dehling et al., 2014), these species interact
 376 with only a narrow subset of plants, showcasing the key difference between potential or
 377 fundamental dietary niche and the actual realized niche. Fruit profitability often increases with
 378 size, likely shaping birds' foraging decisions. Trait-matching mechanisms, especially under
 379 stressful conditions, may further reinforce this specialization, as birds tend to select fruits that
 380 align with their beak size (Wheelwright, 1985; Martins et al., 2024). In this context, our findings
 381 suggest that both large-bodied and wide-beaked frugivores specialize in interacting with a
 382 limited group of plants producing large, high-reward fruits, which may be driven by energetic
 383 demands and cost-benefit trade-offs.

384

385 *Effects of trait-based species loss on network-level metrics*

386 Notably, the effects of body mass and beak width scale up to the network level even when only
 387 10% of species at trait extremes are removed. This highlights the disproportionate structural role
 388 of a few species with extreme morphologies. Contrary to our second hypothesis, removing the
 389 largest species led to increases in Shannon diversity and links per species, but decreased
 390 nestedness—indicating that these species (e.g., toucans, hornbills, wood pigeons, curassows,
 391 and crows) engage in fewer interactions than expected by chance. These results support the idea
 392 that peripheral generalists can enhance nestedness and contribute to network stability (see also
 393 Moulatlet et al., 2023). Our findings are consistent with previous studies at smaller scales
 394 showing that large-bodied birds tend to engage in stronger, but fewer, interactions (Saavedra et
 395 al., 2014). Similarly, the removal of the smallest species (e.g., flowerpeckers, sunbirds, finches,
 396 New World flycatchers) increased interaction diversity without significantly affecting
 397 nestedness, suggesting that they also interact with a limited number of plants—likely due to
 398 morphological constraints and mixed diets (Pigot et al., 2016; Galetti et al., 2013; Wheelwright,
 399 1985). As facultative frugivorous, smaller species seem to rely less on fruits and more on
 400 alternative resources such as nectar, insects, or non-fruiting plants, which could explain their
 401 lower number of links in frugivory networks (Fig. S3).

402 Although many species with the widest beaks were not among the top-10 largest species
 403 (e.g., barbets, trogons, tityras, and parakeets), the removal of these species still increased the

404 average number of links that each species has within the network and reduced network
405 nestedness. This means that wide-beaked species also exhibit a high level of specialization,
406 interacting with a small subset of flesh-fruit plants. In contrast, the removal of narrow-beaked
407 species (mostly canopy-gleaners, including doves, tree warblers, Sylviid warblers, and white-
408 eyes, among others) showed that they interact with a wider range of species than the average.
409 This suggests that while a wide beak imposes major constraints and leads to specialization,
410 narrow-beaked species do not seem morphologically constrained in their ability to interact with
411 a broad range of plant species within their habitats. These results were unexpected, as previous
412 studies have shown that species with wider beaks can consume a broader range of fruits while
413 narrow-beaked species are usually restricted to smaller fruits (Wheelwright, 1985; Burns, 2013;
414 Galetti et al., 2013; Pigot et al., 2016). This could be related to the existence of intraspecific
415 variability in fruit sizes, resulting from phenotypic plasticity and local adaptations of ecotypes
416 (Sultan, 1995). Such variability may result in small-beaked frugivores interacting with an
417 ecotype of a plant species that typically produces large fruits, but in this case, bears smaller
418 fruits. In addition, unlike species at the other end of the spectrum, most narrow-beaked species
419 are small passerines whose energy needs are generally lower. Our findings thus suggest that
420 plant-disperser interactions are only minimally constrained by beak-size limitations. Instead, the
421 energy requirements of each species might play a more significant role in determining foraging
422 behavior and food selection. It is likely that as a result of the higher energy demands, large-
423 bodied species may be forced to be semi-obligate specialists despite their potential to exploit a
424 broad spectrum of food items. These findings align with previous research that points to a more
425 important role of the energy content of fruits, rather than morphological constraints, in shaping
426 frugivory interactions (Sebastián-González, 2017). This study challenges the assumption that
427 beak width directly correlates with broader realized feeding interactions, highlighting a more
428 complex relationship between beak morphology and ecological roles in frugivory networks, and
429 reinforcing the view that beak shape is far from being an ideal feeding adaptation (e.g., Navalón
430 et al., 2019).
431 When analyzing our results across bioregions, we found that the positive relationship between
432 both traits (body mass and beak size) and specialization largely reflects the pattern observed in

433 the bioregion that constitutes the bulk of the dataset, namely the tropical region. A similar trend
434 was detected in the Austral and Oceanic island regions, whereas the temperate region exhibited
435 an opposite relationship. This discrepancy between the temperate region and the other
436 bioregions may be explained by several factors. First, unlike in the tropics, frugivory networks
437 in temperate regions are dominated by songbirds, most of which are considered facultative
438 frugivores, as they rely on fruits mainly during the autumn period, and large non-passeriform
439 birds are comparatively scarce (Kissling et al., 2009; Fleming & Kress, 2011). Second,
440 temperate forests are smaller, more fragmented, and less productive, and, unlike rainforests in
441 South America or Australasia, fleshy fruits are typically produced by woody plants only
442 seasonally (Kissling et al., 2009). Consequently, the overall pattern emerging from this study is
443 largely driven by frugivory networks dominated by large, forest-specialist species. Finally, it
444 should be noted that most available data come from South America and southern Europe
445 (Mediterranean region), whereas regions such as northern Asia, North America, and Africa are
446 strongly underrepresented, potentially limiting the generalizability of our findings. Expanding
447 the dataset to include networks from these understudied regions would allow a more
448 comprehensive assessment of the observed patterns.

449

450 *Conclusions*

451 This study provides critical insights into the role of bird species with extreme traits, offering a
452 deeper understanding of the importance of functional traits in shaping mutualistic interactions
453 on a global scale. This is especially challenging given the variability of foraging strategies and
454 niche breadths in avian frugivores (Hargreaves & Alexander, 2024). Results shown here contest
455 previous studies and reveal an even higher-than-expected vulnerability of large avian species
456 due to their reliance on a narrower range of fruiting plants, which could threaten important
457 ecosystem services such as seed dispersal (Wotton & Kelly, 2012). Additionally, our study
458 uncovers a complex relationship between beak morphology and species' ecological roles in
459 frugivory networks, so that wide-beaked species, despite their potential to exploit a greater
460 diversity of fruits, interact with fewer plants than species with narrower beaks, possibly due to
461 their physiological requirements. The topological importance of large-bodied and wide-beaked

462 species, coupled with the pressure they face from habitat loss, selective hunting, and/or illegal
 463 trade, highlights the need for targeted conservation strategies in order to preserve key ecological
 464 functions crucial for maintaining ecosystems' health.

465

466 **Data and Code Availability Statement**

467 All the data and the R code used in this study are publicly available in Figshare, following the
 468 link: <https://figshare.com/s/79662e7682d7b186f0e2>.

469

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669 **Table 1.** Description of the species-level and network-level metrics used in the present study.

Metric	Description	Reference
(a) Species-level		
<i>Species degree</i>	Sum of links per species and constitutes the most intuitive measure of centrality.	Bascompte et al. (2006)
<i>Species strength</i>	Sum of dependencies of each species, quantifying its relevance of a species across all its partners.	Bascompte et al. (2006)
<i>Closeness centrality</i>	Proximity of a species (node) to all other species (nodes) in the network, indicating how rapidly one node can affect other nodes in a network.	Moulatlet et al., (2023)
<i>Specialization (d')</i>	Degree of interaction specialization at the species level, based on its discrimination from random selection of partners.	Blüthgen et al., (2006)
(b) Network-level		
<i>Network connectance</i>	Proportion of all possible links that are realized in a network. It can be interpreted biologically as the average of species-specific links and thus provides a measure of how “dense” or “connected” the ecological network is.	Dunne et al. (2002)
<i>Nestedness</i>	Hierarchical organization of interactions within ecological networks. It constitutes an important metric for understanding the stability, resilience, and functionality of ecological networks.	Bascompte et al. (2003)
<i>Links per species</i>	Mean number of links per species in a network. A higher value of this metric indicates that species are highly involved in ecological interactions, often implying a more complex and interdependent ecological network.	(Blüthgen et al., 2006).
<i>Shannon diversity</i>	Diversity of interactions in a network. A higher score of this metric indicates a more diverse network, where interactions are more evenly distributed among species, contributing to the overall complexity and stability of the ecological system	Bersier et al. (2002)

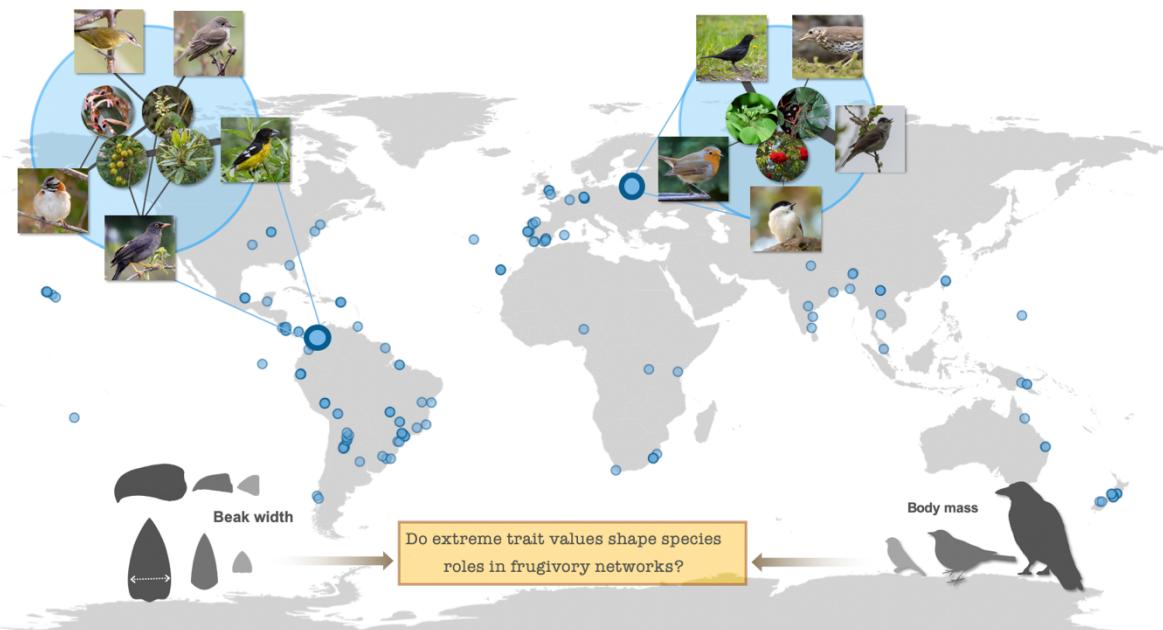
670

671 **Table 2. Impact of trait-based species removal on network-level metrics across scenarios**
 672 **and levels.** Results from linear mixed-effects models assessing how species removal based on
 673 body mass (high, low) and beak width (wide, narrow) at three removal levels (10%, 20%, 30%)
 674 affects four network metrics: connectance, nestedness, links per species, and Shannon diversity.
 675 The table reports fixed-effect estimates (\pm SE), degrees of freedom, *t*-statistics, and *p*-values for
 676 each scenario and removal intensity.

Scenarios effects on network-level metrics

		Connectance				Links per species				
		Estimate \pm SE	df	<i>t</i>	<i>p</i> -value	Estimate \pm SE	df	<i>t</i>	<i>p</i> -value	
MASS SCENARIOS	HIGH MASS-FREE SCENARIOS	10%	0.004 \pm 0.004	187	1.067	0.287	0.044 \pm 0.006	187	7.722	<0.001
		20%	-0.003 \pm 0.003	190	-1.203	0.230	0.093 \pm 0.012	190	7.629	<0.001
		30%	0.000 \pm 0.004	196	-0.052	0.959	0.063 \pm 0.016	196	3.899	<0.001
	LOW MASS-FREE SCENARIOS	10%	-0.002 \pm 0.002	196	-1.555	0.122	0.068 \pm 0.005	196	15.120	<0.001
		20%	0.001 \pm 0.003	207	0.177	0.859	0.079 \pm 0.010	207	8.187	<0.001
		30%	-0.002 \pm 0.004	197	-0.372	0.710	0.014 \pm 0.018	197	0.764	0.446
	WIDE BEAK-FREE SCENARIOS	10%	-0.005 \pm 0.002	192	-2.532	0.012	0.042 \pm 0.008	192	5.404	<0.001
		20%	0.000 \pm 0.003	198	-0.100	0.921	0.086 \pm 0.012	198	8.019	<0.001
		30%	-0.004 \pm 0.004	199	-1.002	0.317	0.116 \pm 0.017	199	6.860	<0.001
BEAK WIDTH SCENARIOS	NARROW BEAK-FREE SCENARIOS	10%	0.006 \pm 0.004	196	1.714	0.088	-0.066 \pm 0.016	196	-4.242	<0.001
		20%	0.006 \pm 0.004	198	1.722	0.087	-0.034 \pm 0.018	198	-1.836	0.068
		30%	0.002 \pm 0.004	192	0.461	0.645	-0.036 \pm 0.018	192	-1.955	0.052
			Nestedness				Shannon diversity			
			Estimate \pm SE	df	<i>t</i>	<i>p</i> -value	Estimate \pm SE	df	<i>t</i>	<i>p</i> -value
	HIGH MASS-FREE SCENARIOS	10%	-0.586 \pm 0.181	187	-3.235	<0.001	0.047 \pm 0.008	187	5.623	<0.001
		20%	-0.802 \pm 0.274	190	-2.924	0.004	0.108 \pm 0.015	190	7.432	<0.001
		30%	-0.248 \pm 0.441	196	-0.563	0.574	0.071 \pm 0.022	196	3.200	0.002
	LOW MASS-FREE SCENARIOS	10%	-0.324 \pm 0.135	196	-2.407	0.017	0.078 \pm 0.004	196	19.640	<0.001
		20%	0.002 \pm 0.368	207	0.004	0.997	0.081 \pm 0.011	207	7.177	<0.001
		30%	-0.182 \pm 0.447	197	-0.408	0.683	0.007 \pm 0.024	197	0.273	0.785
	WIDE BEAK-FREE SCENARIOS	10%	-0.389 \pm 0.145	192	-2.683	0.008	0.049 \pm 0.010	192	4.492	<0.001
		20%	0.001 \pm 0.268	198	0.003	0.998	0.084 \pm 0.014	198	6.157	<0.001
		30%	-0.201 \pm 0.330	199	-0.609	0.543	0.112 \pm 0.024	199	4.772	<0.001
	NARROW BEAK-FREE SCENARIOS	10%	0.324 \pm 0.391	196	0.826	0.410	-0.106 \pm 0.021	196	-4.956	<0.001
		20%	0.126 \pm 0.444	198	0.284	0.777	-0.076 \pm 0.025	198	-3.006	0.003
		30%	-0.456 \pm 0.422	192	-1.077	0.283	-0.060 \pm 0.024	192	-2.507	0.013

677

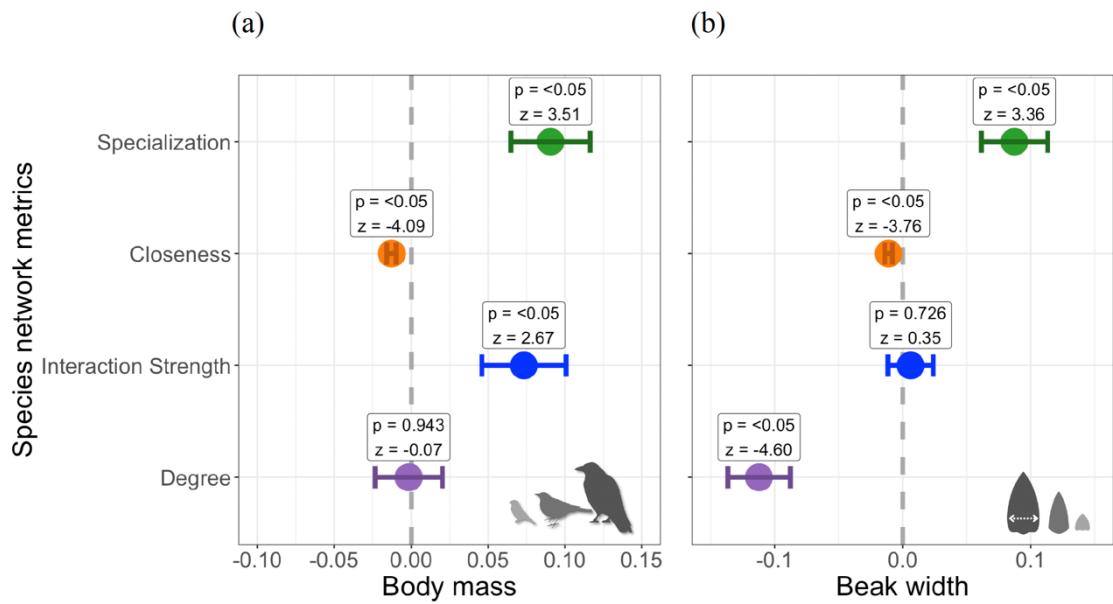


678

679 **Fig. 1. Geographic distribution of frugivory networks in the dataset and trait-based**
 680 **framework.** Networks' locations and the theoretical framework of the study. The 215 networks
 681 of study are represented on the map, distributed in 6 continents, 7 biogeographical regions and
 682 several subregions (see Table S1). In this study, we explore the role of avian frugivores' body
 683 mass and beak width in shaping their roles in frugivory networks.

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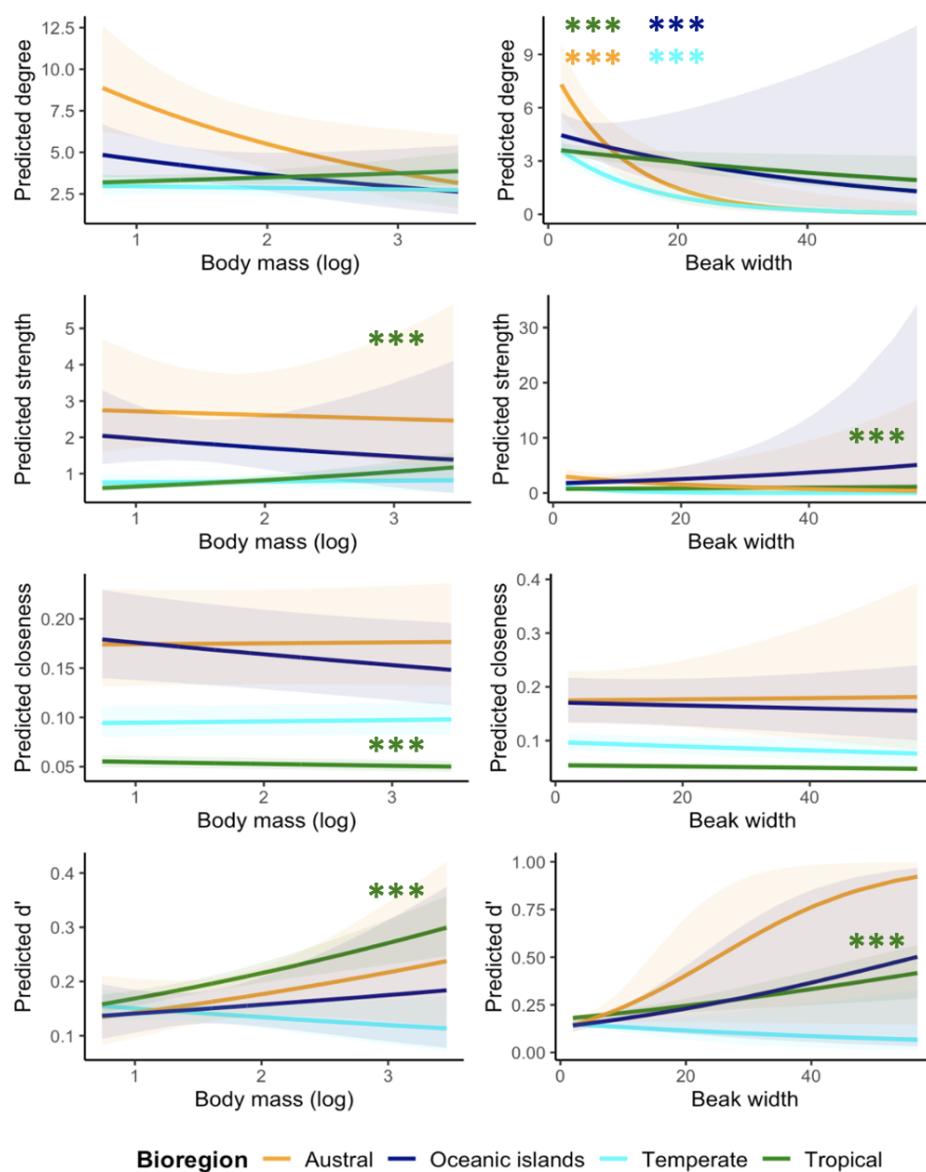
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686

687 **Fig. 2. Effects of body mass and beak width on species-level network roles.** Effects of (A)
 688 body mass (log-transformed) and (B) beak width on four species-level metrics (specialization,
 689 closeness, interaction strength, and degree). The colored dots represent the estimates of the
 690 models (β , slope), p -values and z -statistics are represented inside squares.

691

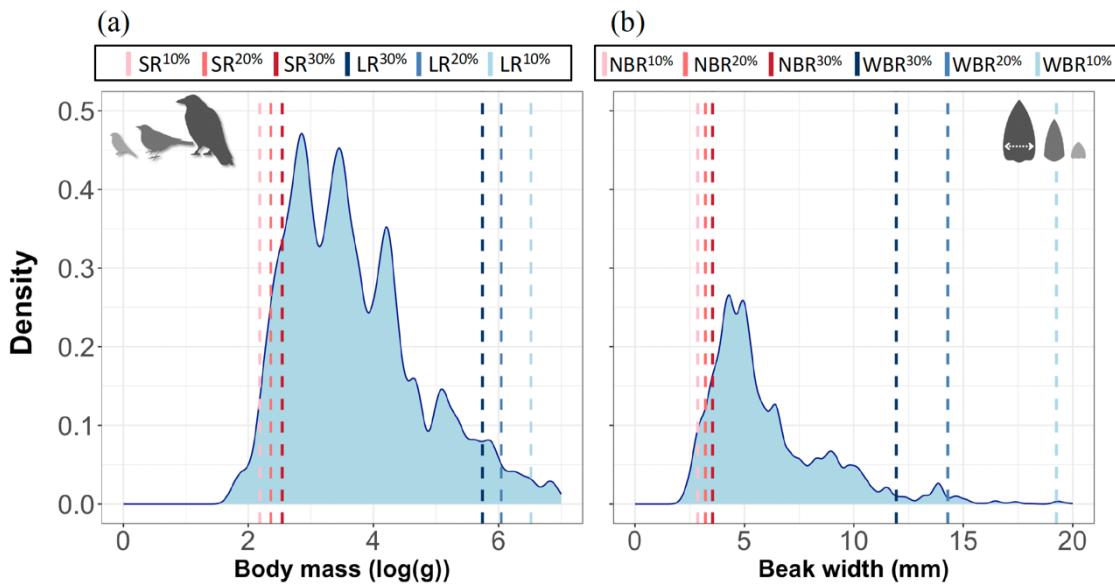


692

693 **Fig. 3. Relationship between bird traits and network roles in different bioregional**
 694 **categories.** Predicted species degree, interaction strength, closeness, and specialization d' as a
 695 function of their body mass (log) and beak width in Austral, Oceanic Islands, Temperate, and
 696 Tropical bioregional categories. Solid lines show marginal effects with 95% CI. Asterisks (***)
 697 show significantly positive or negative slopes.

698

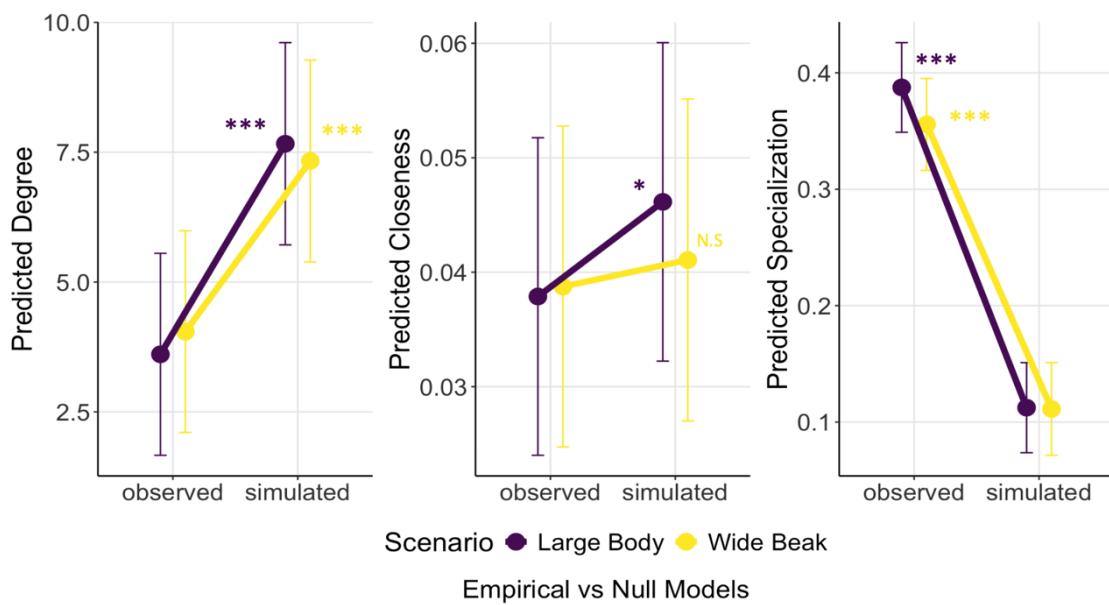
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700

701 **Fig. 4. Trait distributions and selection thresholds for body mass and beak width.**
 702 **Distribution of (A) body mass (log-transformed) and (B) beak width.** Mean values of the
 703 species eliminated on different levels of each scenario are represented with dotted lines (SR:
 704 Smaller species removed; LR: Larger species removed; NBR: narrowest beaks removed, and
 705 WBR: widest beaks removed).

706



707

708 **Fig. 5. Differences between observed and null metrics for large-bodied and wide-beaked**
 709 **species.** Predicted values of degree, closeness, and specialization for empirical and null-model
 710 (Patefield algorithm) networks, considering only quantitative networks and focusing on the 10%
 711 largest-bodied species (“Large Body”) and the 10% widest-beaked species (“Wide Beak”).
 712 Simulated values are based on null models that randomize interactions while preserving the
 713 interaction frequency of each species. Dots represent model-predicted means with 95%
 714 confidence intervals. Asterisks indicate statistically significant differences between observed and
 715 simulated values within each scenario (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; N.S., not significant).

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719

1 **Large-bodied and wide-beaked avian frugivores show greater**
2 **specialisation in global-tropical seed dispersal networks**

3 **ABSTRACT**

4 **Aim:** Avian frugivores with large bodies and beaks are increasingly threatened due to smaller
5 population sizes, greater energy requirements, and higher vulnerability to hunting pressure and
6 illegal wildlife trade. However, it remains unclear whether birds with these traits adopt
7 consistent strategies in their interactions with fleshy-fruited plants and, therefore, hold specific
8 trait-driven roles in fruit-frugivore networks that are difficult to replace under extinction
9 scenarios.

10 **Location:** Worldwide.

11 **Time Period:** Contemporary.

12 **Major Taxa Studied:** Birds.

13 **Methods:** Here, we analyze 215 avian frugivory networks spanning diverse bioregions,
14 ecosystems, and habitats to examine whether body mass and beak width influence the functional
15 roles and position of avian frugivores in interaction networks. Specifically, we first examine
16 how these traits relate to species-level network metrics. In addition, we simulated the removal of
17 species with extreme (i.e., higher and lower) body mass and beak width values to study whether
18 relationships at the species level can scale up and affect overall network structure.

19 **Results:** Our findings indicate that larger species, as well as those with wider beaks, tend to
20 play more specialized roles in the tropical frugivory networks (higher d'), characterized with
21 wide-beaked species having by fewer interactions and larger species being involved in
22 interactions of greater strength but stronger interactions. This specialization leads to lower
23 overall network connectivity. The potential extinction of a few of these species with extreme
24 traits could scale up, modifying network structure. The consistent pattern observed across
25 different conditions suggests that large-bodied frugivores, which in turn show stronger
26 dependence on fruits, may have evolved to fill niche-specific seed dispersal roles in highly

27 diverse environments—roles, whose functional singularity is are functionally difficult to
28 replace.

29 **Main Conclusions:** These results emphasize the importance of implementing targeted
30 conservation strategies to protect large-bodied and large-beaked avian frugivores. Such efforts
31 are crucial for maintaining the integrity of seed dispersal networks and, consequently,
32 supporting broader ecosystem functioning.

33

34 **Keywords:** Avian frugivory; Defaunation; Ecological networks; Endozoochory; Functional
35 traits; Mutualistic networks; Seed dispersal; Species extinction impacts; Trait-based ecology.

36 **INTRODUCTION**

37 Avian frugivores play a crucial role in seed dispersal, significantly contributing to forest
 38 regeneration and the maintenance of maintaining landscape-scale connectivity (Schupp et al.,
 39 2010; Jordano, 2014; González-Varo et al., 2017). This ecological function enables animal-
 40 dispersed plants to colonize matrix habitats, which is crucial for plant community dynamics and
 41 ecosystem resilience after land-use changes (Hatfield et al., 2024; Rey et al., 2021).
 42 Fragmentation and habitat degradation not only threaten the viability and persistence of plant
 43 populations but also put many avian frugivore species at risk, with body size emerging as a
 44 critical factor influencing their vulnerability to extinction (Pimm et al., 1988). Large-bodied
 45 species may be more vulnerable or prone to extinction due to several factors, including smaller
 46 population sizes, lower reproductive rates, larger geographic or home range requirements, or
 47 being at higher trophic levels than small-bodied species (Gaston & Blackburn, 1997; Woodward
 48 et al., 2005). Additionally, they are particularly susceptible to defaunation due to size-selective
 49 hunting practices (Carvalho et al., 2016; e.g., Donoso et al., 2020) and are highly sensitive to
 50 human pressures, often being the first to vanish following habitat degradation (Galetti et al.,
 51 2013; Pigot et al., 2016). Large-bodied species are fundamental to long-distance seed dispersal
 52 and maintaining metapopulation connectivity as they can remove a greater number of seeds per
 53 visit, retain them for longer, and deposit them farther from the parent plant than smaller birds
 54 (e.g., Wotton & Kelly, 2012; Fell et al., 2023). Thus, the selective extinction of these species
 55 could have a disproportionately high impact on ecosystems due to their unique roles and
 56 functions, which may not be readily replaceable, as it has been shown in previous local studies
 57 (Wotton & Kelly, 2012; Vidal et al., 2014). However, the consequences that the loss of these
 58 species may have on the structure of seed dispersal networks have not yet been studied on a
 59 global scale.

60 Large-bodied species have higher absolute energy requirements than smaller species,
 61 which strongly influences their foraging decisions. Given similar diets and food densities, larger
 62 birds must consume greater amounts of food, yet they are often more energetically efficient per
 63 unit body mass. As a result, they tend to target larger and/or more energy-rich food items and to

64 exploit environments that maximize the balance between energetic costs and benefits, as
65 predicted by “optimal foraging theory” (Pyke 1978). Beyond body size, beak characteristics also
66 play a significant role in determining the foraging strategy and feeding habits of birds (e.g.,
67 Grant et al., 1985). Specifically, the ability of avian frugivores to disperse seeds from fleshing-
68 fruit plants is limited by gape width (for which beak width is often used as a proxy), which
69 imposes an upper physiological constraint on the size of seeds they can ingest whole
70 (Wheelwright, 1985; Herrera, 1995; Burns, 2013). As a result, size-coupling frequently occurs
71 in fruit-frugivore interactions, leading to positive relationships between disperser gape width
72 and the average diameter of fruits they consume. This relationship may, however, follow a
73 triangular pattern; species with wide gapes can theoretically consume and disperse fruits of a
74 wide range of sizes, while species with narrower beaks are restricted to smaller fruits (Galetti et
75 al., 2013; Pigot et al., 2016). Consequently, according to the ‘trait-matching’ hypothesis, plants
76 producing large-seeded fruits could be negatively impacted by the local extinction of large-
77 gaped birds (da-Silva & Tabarelli, 2000; Galetti et al., 2013). Species with unique or prominent
78 beak characteristics (colorful, large, and/or wide beaks) could be more susceptible to illegal
79 trade due to their popularity, visual appeal, or perceived value. For example, some species of
80 parrots or toucans, known for their large and colorful beaks, are likely to attract attention in
81 illegal wildlife markets, a factor often linked to overexploitation and extinction risk (e.g., Tella
82 & Hiraldo, 2014; Harris et al., 2015).

83 Thus, overexploitation resulting from the wild bird trade and size-selective hunting
84 practices pose significant threats to large-bodied and large-gaped avian species. Although these
85 species are vital for the recruitment and persistence of plant populations (Jordano et al., 2016;
86 Pires et al., 2018), it remains unclear whether they play a consistent, trait-driven role in
87 mutualistic networks. Gaining insight into this could improve our understanding of frugivory
88 dynamics and the potential consequences of losing these species, especially since large and/or
89 broad-billed bird species may act as central or ‘keystone species’ (Wotton & Kelly, 2012;
90 Windsor et al., 2023). In this context, the role of species with extreme traits within seed
91 dispersal networks is a matter of ongoing debate. For instance, while some studies have
92 suggested that large avian frugivores play a central role in some plant-frugivore networks due to

93 their potential to have a more generalist diet (i.e., larger fundamental niche)—consume fruits
 94 from a wider size spectrum (Palacio et al., 2016)—others have found no correlation between
 95 body size and network centrality measures (Ruggera et al., 2016; Naniwadekar et al., 2019;
 96 Montoya-Arango et al., 2019). This discrepancy may be due to the specific characteristics (e.g.,
 97 diversity of plant and bird clades) of each local network.

98 Additionally, the study of interaction networks could help elucidate the links between
 99 species' functional traits and their ecological roles, as well as predict the response of plant-
 100 disperser communities or analogous bipartite networks under different extinction scenarios
 101 (Carlucci et al., 2020; Moulatlet et al., 2023). The stability and robustness of mutualistic
 102 networks to species extinction depend on their modularity and nestedness; networks where a
 103 few species monopolize most of the links are more likely to collapse than those with more
 104 evenly distributed connections (Proulx et al., 2005; Bascompte & Jordano, 2007). Although
 105 some authors have explored the relationship between species' traits and their topological
 106 importance at a local scale (e.g., Acevedo-Quintero et al., 2020a), there is a paucity of studies
 107 addressing this question at large scales across multiple ecosystems (but see Moulatlet et al.,
 108 2023). This is paramount for determining whether there is a universal pattern of the role of body
 109 size and gape width in mutualistic plant-frugivore interactions.

110 Here, we used a large dataset of 215 bipartite interaction networks distributed from
 111 around the world, linking avian frugivorous and plant species, to explore the universal role of
 112 body mass and beak width in shaping species interactions. These traits directly influence seed-
 113 dispersal function and may indicate specific roles in interaction networks. We hypothesized that
 114 large-bodied species and those with wider beaks would consistently have more interactions
 115 (higher degree), exhibit a lower specialization and occupy a more central position in the
 116 network, given their potential to feed on a broader variety of fruits and exploit a greater
 117 diversity of plant species. Alternatively, if the realized niche differs considerably from species'
 118 fundamental or potential niche, and trait-matching processes predominate the ecology in these
 119 networks, as predicted by the optimal foraging theory (Pyke, 1978), we might find the opposite
 120 (i.e., higher specialization and lower centrality in larger and wider-beaked species).
 121 Additionally, we expected that the removal of the largest species and those with the widest beak

122 sizes would significantly affect mean interaction diversity and links per species at the network
123 scale, highlighting their critical role in maintaining network structure.

124

125 **METHODS**

126 *Dataset*

127 This study utilized a dataset comprising 215 frugivory networks across the world (see [Fig. 1](#) and
128 [Table S1](#) in Supplementary Material for network details and references), including data on
129 frugivore avian species and fleshy fruits. This global dataset was compiled and used by [Fricke](#)
130 & [Svenning \(2020\)](#) to test the impact of alien species on networks of plant-frugivore
131 interactions. The original dataset comprised 403 interaction networks, but we filtered the dataset
132 to restrict our analysis to plant-bird interactions. Networks were filtered to exclude those with
133 fewer than two bird species or fewer than three plant species, as such small networks were
134 deemed incomplete and less representative. The resulting dataset consisted of 215 networks, of
135 which 113 were weighted (i.e., quantitative) and 102 were unweighted (i.e., qualitative binary
136 networks). For consistency, all networks were first transformed into qualitative networks (i.e.,
137 unweighted). However, analyses were also conducted using the original quantitative data from
138 the 113 weighted networks, yielding very similar results ([Table S2](#) and [Fig. S1](#) in
139 [Supplementary Material](#)).

140 Our dataset comprised 2,150 plant species and 1,031 bird species belonging to 167 and
141 102 families, respectively. For each bird species included in the dataset, we obtained their
142 average body mass (used as a proxy for body size) and beak width from AVONET ([Tobias et](#)
143 [al., 2022](#)). Body size constitutes a multifaceted trait that influences a wide range of biological
144 functions, including dispersal capacity and foraging behavior. It plays a key role in shaping
145 ecological interactions and can affect an individual's ability to access resources and compete
146 with others. On the other hand, beak width ([frequently](#) used as a proxy for gape width)
147 constitutes an effect trait and predicts the size of food to be handled and consumed
148 ([Wheelwright, 1985](#)).

149

150 *Network completeness*

151 To evaluate the sampling quality and reliability of the interaction networks included in this
152 study, we assessed their network completeness, which estimates how thoroughly each network
153 captures the full set of potential interactions of each species. This is essential to ensure that
154 derived metrics are not biased by under-sampling, and that network-level comparisons are based
155 on robust and representative data (Chacoff et al., 2012; Jordano, 2016). Because our dataset
156 included both quantitative (weighted) and qualitative (unweighted) networks, we applied
157 different approaches to optimize the estimate of completeness depending on network type. For
158 weighted networks, sample coverage was calculated using the ‘iNEXT’ R package (Hsieh et al.,
159 2016), which estimates coverage of interactions based on interaction frequency data. In contrast,
160 for unweighted networks, we employed Chao’s estimator of species richness (Chao & Jost,
161 2012). Completeness in this case was calculated as the ratio between the observed interaction
162 richness and the estimated richness from Chao’s estimator (e.g., Martínez-Núñez et al., 2020).
163 This analysis revealed that the majority of networks exhibited moderate to high levels of
164 completeness. Specifically, only three networks showed completeness values below 40%, nine
165 networks fell below 50%, and 16 networks out of 215 had values below 60% (Fig. S2). Thus,
166 based on these results, we conclude that most networks were adequately sampled and provide
167 reliable estimates of interaction patterns. In addition, we employed appropriate null models in
168 most analyses to account for the potential effect of network completeness and network size on
169 the results.

170

171 *Effect of body mass and beak width on network metrics*

172 To test the role of avian body mass and beak width on frugivory networks, two types of
173 analyses were conducted: one at the species level and another at the network level. These
174 analyses were designed to detect a broad yet significant signal across a diverse range of
175 environmental conditions, species compositions, and networks. Their low specificity allows for
176 the identification of universal patterns and generalization, suggesting that any significant
177 differences observed may point to fundamental ecological principles despite the inherent

178 variability in local environmental conditions, network sampling specifics, or phylogenetic
 179 idiosyncrasies.

180

181 *Species-level analyses*

182 Species-level metrics (degree, strength, closeness centrality, and specialization, d') ([Table 1a](#))
 183 [were calculated using the *specieslevel* function from the ‘bipartite’ R package \(Dormann, 2009\).](#)
 184 [Species degree represents the sum of links per species and constitutes the most intuitive](#)
 185 [measure of centrality \(Bascompte et al., 2006\). Species strength is the sum of dependencies of](#)
 186 [each species, quantifying its relevance of a species across all its partners \(Bascompte et al.,](#)
 187 [2006\). Closeness centrality measures the proximity of a species \(node\) to all other species](#)
 188 [\(nodes\) in the network, indicating how rapidly one node can affect other nodes in a network](#)
 189 [\(e.g., Moulatlet et al., 2023\). Lastly, specialization \(\$d'\$ \) describes the degree of interaction](#)
 190 [specialization at the species level, based on its discrimination from random selection of partners](#)
 191 [\(Blüthgen et al., 2006\). These metries](#) were calculated directly from the original interaction
 192 networks for every avian species in every network [using the *specieslevel* function from the](#)
 193 [‘bipartite’ package \(Dormann, 2009\).](#) Subsequently, generalized linear mixed models
 194 (GLMMs) were employed to investigate the relationship between both (log-transformed) body
 195 mass and beak width on each of these four network metrics. GLMMs were implemented using a
 196 Poisson error distribution with a *log* link function (species degree), a gamma error distribution
 197 with a *log* link function (interaction strength and closeness), or a beta family with *logit* link
 198 function (d'). For each response variable (degree, interaction strength, closeness, and d'), we
 199 fitted two models: one with body mass as the explanatory fixed effect and another with beak
 200 width. GLMMs were built using [the ‘lme4’ \(Bates et al., 2015\) and ‘glmmTMB’ \(Brooks et al.,](#)
 201 [2017\) packages in R.](#) Separate models were fitted to avoid collinearity, given that body mass
 202 and beak width were correlated (Spearman’s $\rho = 0.61, p < 0.001$). Network ID was included as a
 203 random intercept and random slope to account for variability across different frugivory
 204 networks and allow for different relationships (i.e., slopes) between traits and species-level
 205 metrics in different networks.

206 Lastly, we fitted additional models accounting for phylogenetic relatedness, which may
 207 underlie, for example, the tendency of larger species to occupy specific network roles, and for
 208 interspecific variation in frugivory. We used a consensus tree generated from a sample of 1,000
 209 trees obtained from BirdTree (www.birdtree.org) and data on the proportional contribution (%)
 210 of fruits to each species' diet from AVONICHE (Sayol et al. 2026). Using these data, we
 211 examined the relationship between morphological traits (body mass and beak width) and
 212 species-level interaction specialization (d') using Phylogenetic Generalized Least Squares
 213 (PGLS) models implemented in the R package *caper* (Orme et al. 2025). Additionally, we
 214 investigated whether species traits (body mass and beak width) were associated with their
 215 degree of frugivory, while controlling for phylogenetic relatedness.

216 *Differences across bioregions*

217 Our dataset comprised interaction networks from different biogeographic contexts (19 networks
 218 from the Austral bioregion, 24 from Oceanic Islands, 53 from Temperate bioregions, and 119
 219 from Tropical bioregions). To assess whether the trait–network role relationships are consistent
 220 across broad biogeographic contexts, we refitted the same generalized linear mixed models
 221 described above, but including an interaction between each focal trait and biogeographic
 222 category (see Appendix S1 in Supplementary Material for further details).

223

224 *Network-level analyses*

225 To explore whether these relationships at the species level are strong enough to scale and affect
 226 network-level properties, we tested the effect of species removal on network metrics. For this
 227 purpose, we simulated five distinct scenarios. In the first, named the “*High-Largest species*
removed” *Mass-free*-scenario²², we removed the largest bird species from the metanetwork. In
 228 the “*Low Mass-free Smallest species removed*” scenario²², the smallest species were eliminated.
 229 In the “*Wide Beak-free Widest beaks removed*” scenario²², we removed species with the widest
 230 beaks, while in the “*Narrowest beaks removed*” *Beak-free*-scenario²², we removed species with
 231 the narrowest beaks. Lastly, in the “*Stochastic Random species removed*” scenario²², species
 232 were removed randomly. For this last scenario, the process was repeated 1,000 times to obtain
 233

234 average metric values following random extirpations. For each of the five simulated scenarios,
 235 we removed 10% (~103 species), 20% (~206 species), and 30% (~309 species) of the total pool
 236 of species (1,031 species); following different criteria according to each scenario. The exact
 237 numbers varied slightly due to ties in species values, with these species retained as a group to
 238 avoid arbitrary selection. The removal process followed a deterministic approach, where species
 239 were selected and removed based directly on their body mass and beak measurements.
 240 Networks where at least one species was removed were then selected and compared with the
 241 networks from the random scenario (the percentage of networks affected in each scenario is
 242 shown in [Table S3](#)).

243 Next, for each network and scenario, we estimated four network-level metrics (namely,
 244 connectance, nestedness, links per species, and Shannon diversity) ([Table 1b](#)) using the
 245 *networklevel* function from ‘*bipartite*’ ([Dormann, 2009](#)). To examine the effect of different
 246 scenarios on these network metrics, we fitted linear mixed-effects models (one for each
 247 response variable, namely network metric) using the *lmer* function of the ‘*lme4*’ package ([Bates
 et al., 2015](#)). Each model included scenario as a fixed effect to evaluate its impact on the
 248 network metrics, while variability between networks was accounted for by including network
 249 ID as a random factor. The residuals of the models met the assumptions of independence and
 250 normality.

252

253 *Sensitivity analysis*

254 Although the interaction networks employed in this study exhibit high completeness, we
 255 conducted a sensitivity analysis to assess whether the observed roles and positions in the
 256 network of large-bodied, wide-beaked species might be influenced by sampling bias.
 257 Specifically, we sought to rule out the possibility that their inferred level of specialization is an
 258 artifact of species low abundance and, consequently, fewer recorded interactions. Such species
 259 may appear more specialized due to limited sampling rather than reflecting true ecological
 260 patterns. For this analysis, we used a subset of 113 quantitative (weighted) networks that
 261 included interaction frequencies ([see Appendix S1 in Supplementary Material for further
 details](#)
[see Appendix for further details](#)). Within each network, frugivorous bird species were

263 ranked by body mass and beak width, and two groups were identified: (i) the top 10% in body
 264 mass and (ii) the top 10% in beak width. For each species in these groups, we calculated three
 265 species-level network metrics (degree, closeness, and specialization, d^*) using the *specieslevel*
 266 function from the ‘*bipartite*’ R package (Dormann, 2009). To test whether these observed values
 267 could result from sampling limitations alone, we implemented a null model that randomized the
 268 identity of each species’ interaction partners within each network, while preserving the observed
 269 number of interactions per species. This procedure was repeated 1,000 times per species and
 270 network, recalculating the same three metrics after each iteration. Finally, we fitted a linear
 271 mixed model to compare the observed metric values for the top 10% largest-bodied and widest-
 272 beaked species with their distributions under the null model. The models included Network ID
 273 and species as random intercepts. This allowed us to assess whether their observed roles and
 274 position in the network differed significantly from expectations under random interaction
 275 structure, given their observed interaction frequencies.
 276

277 RESULTS

278 Relationship between morphological traits and species-level metrics

279 We found a positive relationship between body mass and specialization ($\beta_{estimate} = 0.090 \pm$
 280 $0.026; z = 3.513, p < 0.001$) indicating that larger species tend to be more specialized and
 281 interact with a particular smaller numbersubset of species (Table 1 and Fig. 2). On the contrary,
 282 body mass was negatively associated with closeness centrality indicating that larger species are
 283 more peripheral in the network ($\beta_{estimate} = -0.012 \pm 0.003; z = -4.091, p < 0.001$) (Fig. 2).
 284 Additionally, a positive relationship between body mass and species interaction strength was
 285 observed, meaning that larger species have stronger interactionsdepend more on few species
 286 ($\beta_{estimate} = 0.073 \pm 0.027; z = 2.673, p = 0.008$). This relationship remained significant when
 287 weighted networks were used (Table S2, Fig. S1). No significant relationship was found
 288 between body mass and interaction degree ($\beta_{estimate} = -0.002 \pm 0.022; z = -0.072, p = 0.943$).

289 Beak width was positively associated with specialization ($\beta_{estimate} = 0.087 \pm 0.026; z$
 290 $= 3.361, p < 0.001$) and negatively with degree ($\beta_{estimate} = -0.112 \pm 0.024, z = -4.597, p$

291 <0.001), indicating that species with wider beaks are more specialized and has fewer
 292 interactions (Fig. 2). In addition, a wider beak was associated with a decrease in closeness,
 293 meaning that species with wider beaks occupy a less central position in the network (β_{estimate}
 294 $= -0.011 \pm 0.003, z = -3.762, p < 0.001$). No significant relationship was found between beak
 295 width and species interaction strength (estimate $= -0.006 \pm 0.018; z = -0.350, p = 0.726$) (Fig.
 296 2). The relationship between species traits and their specialization was still significant after
 297 accounting for phylogenetic relatedness and degree of frugivory (Table S4).

298 Results at the bioregional scale showed that these relationships were not universal and
 299 were mainly driven by patterns in the tropical bioregion (Fig. 3), with similar trends in the
 300 Austral and Oceanic Islands bioregions. In temperate bioregions, however, larger and wide-
 301 beaked species were not significantly more specialized (d') (see Appendix S1 and Fig. 3).

303 Results of Trait-based scenarios on network-level metrics

304 Trait-based removal scenarios targeted species occupying the lower and upper extremes of the
 305 body mass and beak width distributions Body mass and beak width followed a normal
 306 distribution, with long tails, and the species removed were in these extremes (Fig. 43). The
 307 removal of the top 10% largest species (Table S54) had a positive impact on both the average
 308 number of links that each species has within the network and Shannon diversity (“Largest
 309 species removed” High Mass-free” scenarios in Table 2). Specifically, the estimates for links
 310 per species and Shannon diversity were 0.044 ± 0.006 ($\text{df} = 187, t_{187} = 7.722, p < 0.001$) and
 311 0.047 ± 0.008 ($\text{df} = 187, t_{187} = 5.623, p < 0.001$), respectively. This effect remained when a
 312 higher percentage of the largest species was removed (Table 2). Conversely, removing the top
 313 10% and 20% of the largest species negatively affected nestedness, with estimates of $-0.586 \pm$
 314 0.181 ($\text{df} = 187, t_{187} = -3.235, p < 0.001$) and -0.802 ± 0.274 ($\text{df} = 190, t_{190} = -2.924, p = 0.004$)
 315 for the 10% and 20%, respectively. No significant effects were observed for the removal of the
 316 top 30% of species (Table 2).

317 When excluding the smallest 10% (Table S65) and 20% of species (“Smallest species
 318 removed” Low Mass-free” scenarios), we observed it positively impacted the average number
 319 of links per species and Shannon diversity, with estimates of 0.068 ± 0.005 ($\text{df} = 196, t_{196} =$

320 15.120, $p < 0.001$) and 0.078 ± 0.004 ($df = 196$, $t_{196} = 19.640$, $p < 0.001$), respectively, for the
 321 10% level (Table 2). Additionally, no significant effects on nestedness were found when
 322 removing the smallest species (Table 2).

323 Regarding beak width, the removal of species with the widest beaks consistently
 324 increased the average number of links that each species has within the network ($\beta = 0.042 \pm$
 325 0.008 ; $t_{192} = 5.404$, $p < 0.001$) and Shannon diversity ($\beta = 0.049 \pm 0.010$; $t_{192} = 4.492$, $p < 0.001$)
 326 at the 10% level of the “*Wide_{st} beaks removed Beak-free*” scenario compared to the null
 327 scenario. ~~At the 10% level, the extirpation of those species with the widest beaks had a positive~~
 328 ~~impact on link per species (estimate $\beta = 0.042 \pm 0.008$; $df = 192$, $t = 5.404$, $p < 0.001$) and~~
 329 ~~Shannon diversity ($\beta = 0.049 \pm 0.010$; $df = 192$, $t = 4.492$, $p < 0.001$)~~. Excluding these
 330 species also affected links per species and Shannon diversity at the higher levels (Table 2). In
 331 contrast, the removal of the top 10% of species with the widest beaks negatively affected
 332 nestedness, with an estimate of -0.389 ± 0.145 (t_{192} , $df = 192$, $t = -2.683$, $p < 0.008$) (Table S76).
 333 No significant effects were found for the 20% and 30% levels (Table 2).

334 When removing the species with the narrowest beaks (Table S87) (“*Narrow_{est} Beak-*
 335 *free*” *beaks removed*”- scenario), we found it negatively impacted the average number of links
 336 ($\beta = 0.066 \pm 0.016$; t_{196} , $df = 196$, $t = -4.242$, $p < 0.001$) and Shannon diversity (β
 337 $= 0.106 \pm 0.021$; t_{196} , $df = 196$, $t = -4.956$, $p < 0.001$) at the 10% level. These effects
 338 persisted at the 20% and 30% levels for Shannon diversity (Table 2). Removing species with the
 339 narrowest beaks did not have a significant effect on nestedness (Table 2).

340 Network connectance was also tested for all scenarios and levels, but this metric was
 341 not significantly affected in any case.

342 Finally, the observed network metrics for larger-bodied and wider-beaked species
 343 differed significantly from those expected under a random interaction structure, given the same
 344 number of interactions (Fig. 54).

345
 346 *Relationship between morphological traits and frugivory*
 347 We found a significant relationship between both morphological traits and the species’ degree
 348 of frugivory (Fig. S3); the level of dependence on this food resource increases with body mass

349 [\(PGLS; lambda: 0.924 \[CI: 0.903-0.942\], \$\beta = 11.93 \pm 2.75\$, \$t = 4.33\$, \$p < 0.001\$ \) and beak width](#)
 350 [\(lambda: 0.928 \[CI: 0.907-0.945\], \$\beta = 14.86 \pm 5.65\$, \$t = 2.63\$, \$p < 0.01\$ \).](#)

351

352 DISCUSSION

353 Understanding how functional traits shape the strategies and roles of avian species in seed
 354 dispersal networks offers valuable ecological insights with important implications for
 355 conservation. Our study demonstrates that body size and beak width are key predictors of the
 356 roles [that](#) birds play in frugivory networks [across the globe](#). At the species level, we found that
 357 large-bodied birds and those with wider beaks tend to occupy more specialized positions,
 358 engaging in fewer but stronger interactions and exhibiting lower network centrality. At the
 359 community level, our simulations revealed that removing these species significantly alters
 360 network structure: nestedness increases, as do both the number of interactions and mean
 361 interaction diversity. These findings highlight the unique and specialized roles of large-bodied,
 362 wide-beaked frugivores and their importance in maintaining network integrity. More broadly,
 363 our results reinforce the idea that downsizing in ecological networks can have far-reaching
 364 consequences for ecosystem functioning, particularly in mutualistic systems structured by trait-
 365 matching, as predicted by previous theoretical work ([Donoso et al., 2017](#)).

366

367 [*Relationship between species traits and network roles*](#)

368 Contrary to our initial hypothesis, we found that larger species tend to occupy more peripheral
 369 positions in frugivory networks, as evidenced by the negative relationship between body mass
 370 and closeness centrality. This pattern suggests that, although these species form strong
 371 interactions, they do so selectively. Our findings align with several local-scale studies. For
 372 example, [Naniwadekar et al. \(2019\)](#) reported that large frugivores, such as hornbills and
 373 imperial pigeons, were less connected than intermediate-sized species like barbets and bulbuls
 374 in Indian forests [\(see also . Similarly, Montoya-Arango et al., \(2019\) found that large-bodied](#)
 375 [birds occupied peripheral positions in a disturbed forest network in Colombia.](#) In contrast,
 376 [Palacio et al. \(2016\)](#) observed that large frugivores such as cotingas and toucans held more

377 central roles in networks from a nearby, more pristine region in the Colombian Andes. These
 378 contrasting results may reflect variation in network properties across ecosystems, elevations,
 379 and bioregions (e.g., differences in trait distributions; [Acevedo-Quintero et al., 2020b](#)), as well
 380 as the effects of anthropogenic disturbance ([Martins et al., 2022](#); [Emer et al., 2018](#)). Despite this
 381 environmental variability, our findings indicate that the peripheral role of the largest species in
 382 frugivory networks is consistent and generalizable at a global scale ([see also Moulatlet et al.,](#)
 383 [2023](#)).

384 In line with these findings, we observed that large-bodied species tend to adopt a
 385 foraging strategy characterized by fewer but stronger and more specialized interactions. The
 386 positive association between body mass, species strength, and specialization suggests that these
 387 birds typically occupy more specialized roles within frugivory networks. This pattern may be
 388 shaped in part by energetic constraints: large-bodied frugivores require higher caloric intake and
 389 are likely to selectively target energy-rich fruits while avoiding those with lower nutritional
 390 value ([Sebastián-González, 2017](#); [Quintero et al., 2020](#)). Such behavior aligns with predictions
 391 from optimal foraging theory, which proposes that animals maximize energy gain per unit effort
 392 ([Pyke, 1978](#)). In addition to energetic demands, trait-matching mechanisms may further
 393 reinforce specialization ([Martins et al., 2024](#)). Species with extreme morphological traits, such
 394 as large body size or wide beaks, tend to fill distinct functional niches, interacting preferentially
 395 with plants whose fruit traits align closely with their morphology ([Dehling et al., 2016](#); [Pigot et](#)
 396 [al., 2016](#); [Bender et al., 2018](#)). For example, large-bodied birds often favor heavier fruits
 397 ([Buitrón-Jurado & Sanz, 2021](#)), and their limited number of interactions may result from
 398 morphological mismatches ~~or “forbidden links”~~ that restrict their ability to interact with smaller-
 399 fruited species ([Dehling et al., 2014](#)). [The relationship between specialization and](#)
 400 [morphological traits does not constitute an artifact of phylogenetic inertia; there was significant](#)
 401 [relationship between the species’ average specialization \(\$d'\$ \) and their body mass \(and beak](#)
 402 [width\) after accounting for phylogenetic relatedness \(Table S4\)](#). [The existence of a moderate](#)
 403 [phylogenetic signal for this metric \(\$\lambda = 0.67\$ \) suggests that high specialization values are not](#)
 404 [heavily concentrated on a few clades](#). Taken together, these results suggest that evolutionary
 405 pressures have contributed to the specialization of large-bodied frugivores, increasing their

406 vulnerability by tying them to a narrower range of functionally distinctive fruiting plants. This
 407 pattern highlights the importance of trait-matching and optimal foraging in frugivores' ecology,
 408 and might partly explain why bird assemblages in more productive regions tend to be more
 409 specialized globally ([Malmagro et al., 2025](#)).

410 Dietary preferences for large, energy-rich fruits (consistent with optimal foraging
 411 theory) may also explain why wide-beaked birds occupy less central positions in frugivory
 412 networks and display a high degree of specialization. Despite their potential to handle a broad
 413 range of fruit sizes due to reduced gape limitations ([Dehling et al., 2014](#)), these species interact
 414 with only a narrow subset of plants, showcasing the key difference between potential or
 415 fundamental dietary niche and the actual realized niche. Fruit profitability often increases with
 416 size, likely shaping birds' foraging decisions. Trait-matching mechanisms, especially under
 417 stressful conditions, may further reinforce this specialization, as birds tend to select fruits that
 418 align with their beak size ([Wheelwright, 1985](#); [Martins et al., 2024](#)). In this context, our findings
 419 suggest that both large-bodied and wide-beaked frugivores specialize in interacting with a
 420 limited group of plants producing large, high-reward fruits, [which may be](#) driven by energetic
 421 demands and cost-benefit trade-offs.

422

423 *Effects of trait-based species loss on network-level metrics*

424 Notably, the effects of body mass and beak width scale up to the network level even when only
 425 10% of species at trait extremes are removed. This highlights the disproportionate structural role
 426 of a few species with extreme morphologies. Contrary to our second hypothesis, removing the
 427 largest species led to increases in Shannon diversity and links per species, but decreased
 428 nestedness—indicating that these species (e.g., toucans, hornbills, wood pigeons, curassows,
 429 and crows) engage in fewer interactions than expected by chance. These results support the idea
 430 that peripheral generalists can enhance nestedness and contribute to network stability (see also
 431 [Moulatlet et al., 2023](#)). Our findings are consistent with previous studies at smaller scales
 432 showing that large-bodied birds tend to engage in stronger, but fewer, interactions ([Saavedra et](#)
 433 [al., 2014](#)). Similarly, the removal of the smallest species (e.g., flowerpeckers, sunbirds, finches,
 434 New World flycatchers) increased interaction diversity without significantly affecting

435 nestedness, suggesting that they also interact with a limited number of plants—likely due to
 436 morphological constraints and mixed diets (Pigot et al., 2016; Galetti et al., 2013; Wheelwright,
 437 1985). As facultative frugivorous, smaller species seem to rely less on fruits and more on
 438 alternative resources such as nectar, insects, or non-fruiting plants, which could explain their
 439 lower number of links in frugivory networks (Fig. S3).

440 Although many species with the widest beaks were not among the top-10 largest species
 441 (e.g., barbets, trogons, tityras, and parakeets), the removal of these species still increased the
 442 average number of links that each species has within the network and reduced network
 443 nestedness. This means that wide-beaked species also exhibit a high level of specialization,
 444 interacting with a small subset of flesh-fruit plants. On the other hand, opposite to this in
 445 contrast, the removal of narrow-beaked species (mostly canopy-gleaners, including doves, tree
 446 warblers, Sylviid warblers, and white-eyes, among others) showed that they interact with a
 447 wider range of species than the average. This suggests that while a wide beak imposes major
 448 constraints and leads to specialization, narrow-beaked species do not seem morphologically
 449 constrained in their ability to interact with a broad range of plant species within their habitats.
 450 These results were unexpected, as previous studies have shown that species with wider beaks
 451 can consume a broader range of fruits while narrow-beaked species are usually restricted to
 452 smaller fruits (Wheelwright, 1985; Burns, 2013; Galetti et al., 2013; Pigot et al., 2016). This
 453 could be related to the existence of intraspecific variability in fruit sizes, resulting from
 454 phenotypic plasticity and local adaptations of ecotypes (Sultan, 1995). Such variability
 455 may result in small-beaked frugivores interacting with an ecotype of a plant species that
 456 typically produces large fruits, but in this case, bears smaller fruits. In addition, unlike species at
 457 the other end of the spectrum, most narrow-beaked species are small passerines whose energy
 458 needs are generally lower. Our findings thus suggest that plant-disperser interactions are only
 459 minimally constrained by beak-size limitations. Instead, the energy requirements of each species
 460 might play a more significant role in determining foraging behavior and food selection.
 461 It is likely that as a result of the higher energy demands of large-bodied species may be
 462 forced to become semi-obligate specialists despite their potential to exploit a broad
 463 spectrum of food items. These findings align with previous research that points to a more

464 important role of the energy content of fruits, rather than morphological constraints, in shaping
465 frugivory interactions (Sebastián-González, 2017). This study challenges the assumption that
466 beak width directly correlates with broader realized feeding interactions, highlighting a more
467 complex relationship between beak morphology and ecological roles in frugivory networks, and
468 reinforcing the view that beak shape is far from being an ideal feeding adaptation (e.g., Navalón
469 et al., 2019).

470 When analyzing our results across bioregions, we found that the positive relationship
471 between both traits (body mass and beak size) and specialization largely reflects the pattern
472 observed in the bioregion that constitutes the bulk of the dataset, namely the tropical region. A
473 similar trend was detected in the Austral and Oceanic island regions, whereas the temperate
474 region exhibited an opposite relationship. This discrepancy between the temperate region and
475 the other bioregions may be explained by several factors. First, unlike in the tropics, frugivory
476 networks in temperate regions are dominated by songbirds, most of which are considered
477 facultative frugivores, as they rely on fruits mainly during the autumn period, and large non-
478 passeriform birds are comparatively scarce (Kissling et al., 2009; Fleming & Kress, 2011).
479 Second, temperate forests are smaller, more fragmented, and less productive, and, unlike
480 rainforests in South America or Australasia, fleshy fruits are typically produced by woody
481 plants only seasonally (Kissling et al., 2009). Consequently, the overall pattern emerging from
482 this study is largely driven by frugivory networks dominated by large, forest-specialist species.
483 Finally, it should be noted that most available data come from South America and southern
484 Europe (Mediterranean region), whereas regions such as northern Asia, North America, and
485 Africa are strongly underrepresented, potentially limiting the generalizability of our findings.
486 Expanding the dataset to include networks from these understudied regions would allow a more
487 comprehensive assessment of the observed patterns. This study covers a wide geographic scope
488 and includes a large number of different ecosystems. However, there are still important gaps in
489 the distribution of the analyzed networks. Most information comes from South America and
490 southern Europe (Mediterranean region), while regions such as northern Asia, North America,
491 and Africa are strongly underrepresented, potentially limiting the generalizability of our

492 findings to all these areas. Expanding the dataset to include networks from these understudied
493 regions would provide a more comprehensive assessment of the observed patterns.

494

495 *Conclusions*

496 ~~T~~In conclusion, this study provides critical insights into the role of bird species with extreme
497 traits, offering a deeper understanding of the importance of functional traits in shaping
498 mutualistic interactions on a global scale. This is especially challenging given the variability of
499 foraging strategies and niche breadths in avian frugivores (Hargreaves & Alexander, 2024).

500 ~~S~~pecifically, our findings emphasize the importance of considering the energy requirements that
501 affect foraging decisions when understanding frugivory dynamics. Results shown here contest
502 previous studies and reveal an even higher-than-expected vulnerability of large avian species
503 due to their reliance on a narrower range of fruiting plants, which could threaten important
504 ecosystem services such as seed dispersal (Wotton & Kelly, 2012). Additionally, our study
505 uncovers a complex relationship between beak morphology and species' ecological roles in
506 frugivory networks, so that wide-beaked species, despite their potential to exploit a greater
507 diversity of fruits, interact with fewer plants than species with narrower beaks, possibly due to
508 their physiological requirements. The topological importance of large-bodied ~~and wide-beaked~~
509 species ~~and those with more distinctive beaks~~, coupled with the pressure they face from habitat
510 loss, selective hunting, and/or illegal trade, highlights the need for targeted conservation
511 strategies in order to preserve key ecological functions crucial for maintaining ecosystems'
512 health.

513

514 **Data and Code Availability Statement**

515 **Data availability statement**

516 All the data and the R code used in this study are publicly available in Figshare, following the
517 link: <https://figshare.com/s/79662e7682d7b186f0e2>.

518

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739 **Table 1.** Description of the species-level and network-level metrics used in the present study.

Metric	Description	Reference
(a) Species-level		
<i>Species degree</i>	Sum of links per species and constitutes the most intuitive measure of centrality.	Bascompte et al. (2006)
<i>Species strength</i>	Sum of dependencies of each species, quantifying its relevance of a species across all its partners.	Bascompte et al. (2006)
<i>Closeness centrality</i>	Proximity of a species (node) to all other species (nodes) in the network, indicating how rapidly one node can affect other nodes in a network.	Moulatlet et al., (2023)
<i>Specialization (d')</i>	Degree of interaction specialization at the species level, based on its discrimination from random selection of partners.	Blüthgen et al., (2006)
(b) Network-level		
<i>Network connectance</i>	Proportion of all possible links that are realized in a network. It can be interpreted biologically as the average of species-specific links and thus provides a measure of how “dense” or “connected” the ecological network is.	Dunne et al. (2002)
<i>Nestedness</i>	Hierarchical organization of interactions within ecological networks. It constitutes an important metric for understanding the stability, resilience, and functionality of ecological networks.	Bascompte et al. (2003)
<i>Links per species</i>	Mean number of links per species in a network. A higher value of this metric indicates that species are highly involved in ecological interactions, often implying a more complex and interdependent ecological network.	(Blüthgen et al., 2006).
<i>Shannon diversity</i>	Diversity of interactions in a network. A higher score of this metric indicates a more diverse network, where interactions are more evenly distributed among species, contributing to the overall complexity and stability of the ecological system	Bersier et al. (2002)

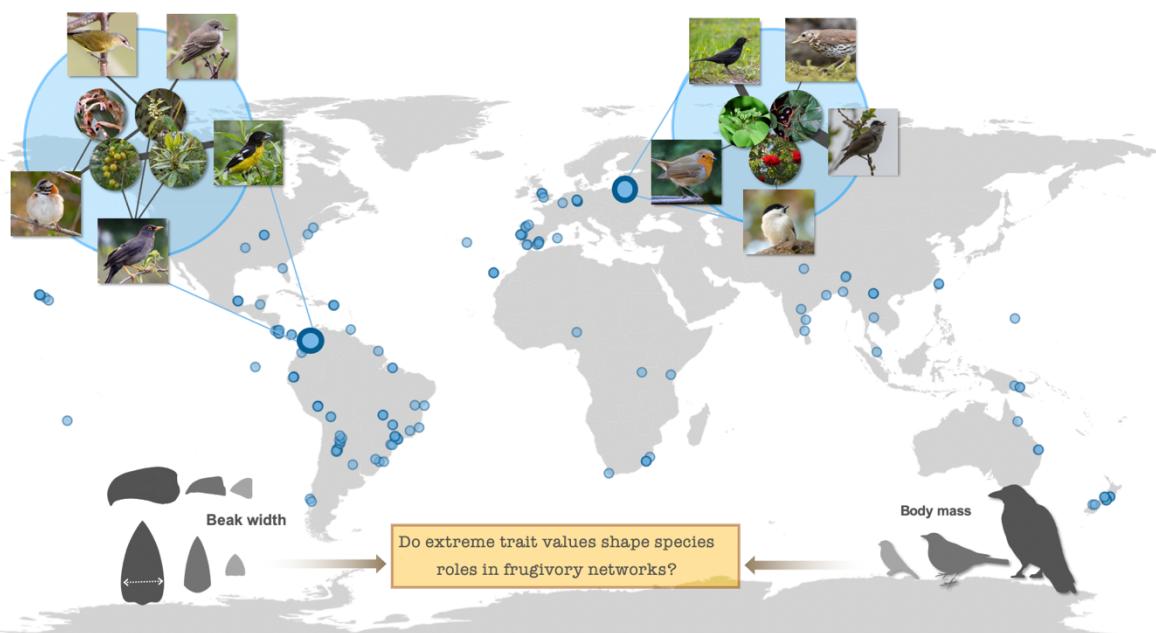
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741 **Table 2. Impact of trait-based species removal on network-level metrics across scenarios**
 742 **and levels.** Results from linear mixed-effects models assessing how species removal based on
 743 body mass (high, low) and beak width (wide, narrow) at three removal levels (10%, 20%, 30%)
 744 affects four network metrics: connectance, nestedness, links per species, and Shannon diversity.
 745 The table reports fixed-effect estimates (\pm SE), degrees of freedom, *t*-statistics, and *p*-values for
 746 each scenario and removal intensity.

Scenarios effects on network-level metrics

		Connectance				Links per species			
		Estimate \pm SE	df	<i>t</i>	<i>p</i> -value	Estimate \pm SE	df	<i>t</i>	<i>p</i> -value
MASS SCENARIOS	HIGH MASS-FREE SCENARIOS	10%	0.004 \pm 0.004	187	1.067	0.287	0.044 \pm 0.006	187	7.722 <0.001
		20%	-0.003 \pm 0.003	190	-1.203	0.230	0.093 \pm 0.012	190	7.629 <0.001
		30%	0.000 \pm 0.004	196	-0.052	0.959	0.063 \pm 0.016	196	3.899 <0.001
	LOW MASS-FREE SCENARIOS	10%	-0.002 \pm 0.002	196	-1.555	0.122	0.068 \pm 0.005	196	15.120 <0.001
		20%	0.001 \pm 0.003	207	0.177	0.859	0.079 \pm 0.010	207	8.187 <0.001
		30%	-0.002 \pm 0.004	197	-0.372	0.710	0.014 \pm 0.018	197	0.764 0.446
	WIDE BEAK-FREE SCENARIOS	10%	-0.005 \pm 0.002	192	-2.532	0.012	0.042 \pm 0.008	192	5.404 <0.001
		20%	0.000 \pm 0.003	198	-0.100	0.921	0.086 \pm 0.012	198	8.019 <0.001
		30%	-0.004 \pm 0.004	199	-1.002	0.317	0.116 \pm 0.017	199	6.860 <0.001
BEAK WIDTH SCENARIOS	NARROW BEAK-FREE SCENARIOS	10%	0.006 \pm 0.004	196	1.714	0.088	-0.066 \pm 0.016	196	-4.242 <0.001
		20%	0.006 \pm 0.004	198	1.722	0.087	-0.034 \pm 0.018	198	-1.836 0.068
		30%	0.002 \pm 0.004	192	0.461	0.645	-0.036 \pm 0.018	192	-1.955 0.052
	HIGH MASS-FREE SCENARIOS	10%	-0.586 \pm 0.181	187	-3.235	<0.001	0.047 \pm 0.008	187	5.623 <0.001
		20%	-0.802 \pm 0.274	190	-2.924	0.004	0.108 \pm 0.015	190	7.432 <0.001
		30%	-0.248 \pm 0.441	196	-0.563	0.574	0.071 \pm 0.022	196	3.200 0.002
	LOW MASS-FREE SCENARIOS	10%	-0.324 \pm 0.135	196	-2.407	0.017	0.078 \pm 0.004	196	19.640 <0.001
		20%	0.002 \pm 0.368	207	0.004	0.997	0.081 \pm 0.011	207	7.177 <0.001
		30%	-0.182 \pm 0.447	197	-0.408	0.683	0.007 \pm 0.024	197	0.273 0.785
BEAK WIDTH SCENARIOS	WIDE BEAK-FREE SCENARIOS	10%	-0.389 \pm 0.145	192	-2.683	0.008	0.049 \pm 0.010	192	4.492 <0.001
		20%	0.001 \pm 0.268	198	0.003	0.998	0.084 \pm 0.014	198	6.157 <0.001
		30%	-0.201 \pm 0.330	199	-0.609	0.543	0.112 \pm 0.024	199	4.772 <0.001
	NARROW BEAK-FREE SCENARIOS	10%	0.324 \pm 0.391	196	0.826	0.410	-0.106 \pm 0.021	196	-4.956 <0.001
		20%	0.126 \pm 0.444	198	0.284	0.777	-0.076 \pm 0.025	198	-3.006 0.003
		30%	-0.456 \pm 0.422	192	-1.077	0.283	-0.060 \pm 0.024	192	-2.507 0.013

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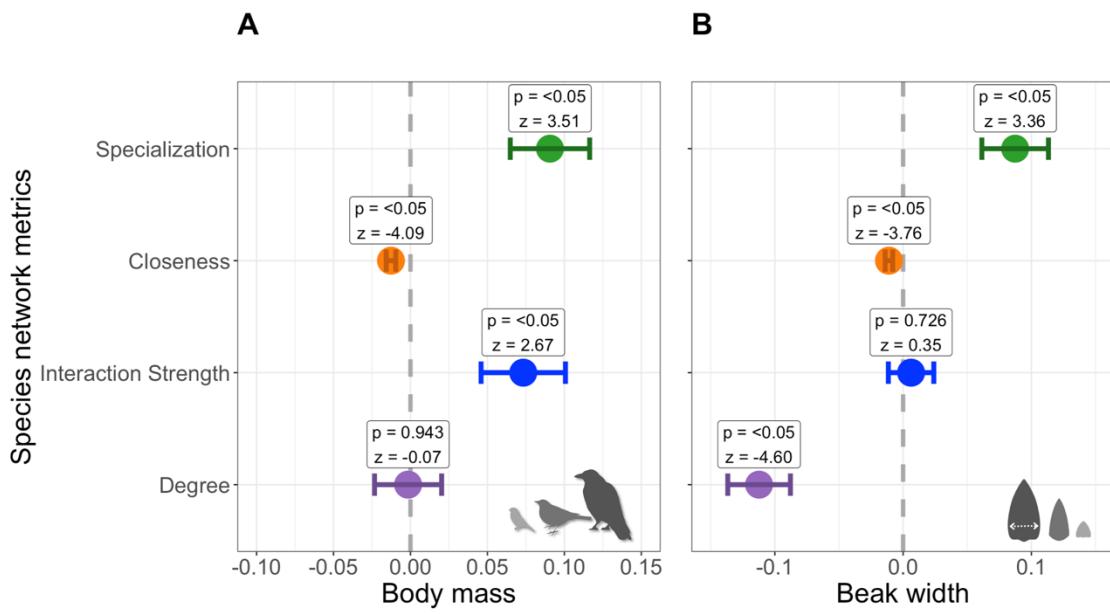


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749 **Fig. 1. Geographic distribution of frugivory networks in the dataset and trait-based
750 framework.** Networks' locations and the theoretical framework of the study. The 215 networks
751 of study are represented on the map, distributed in 6 continents, 7 biogeographical regions and
752 several subregions (see Table S1). In this study, we explore the role of avian frugivores' body
753 mass and beak width in shaping their roles in frugivory networks.

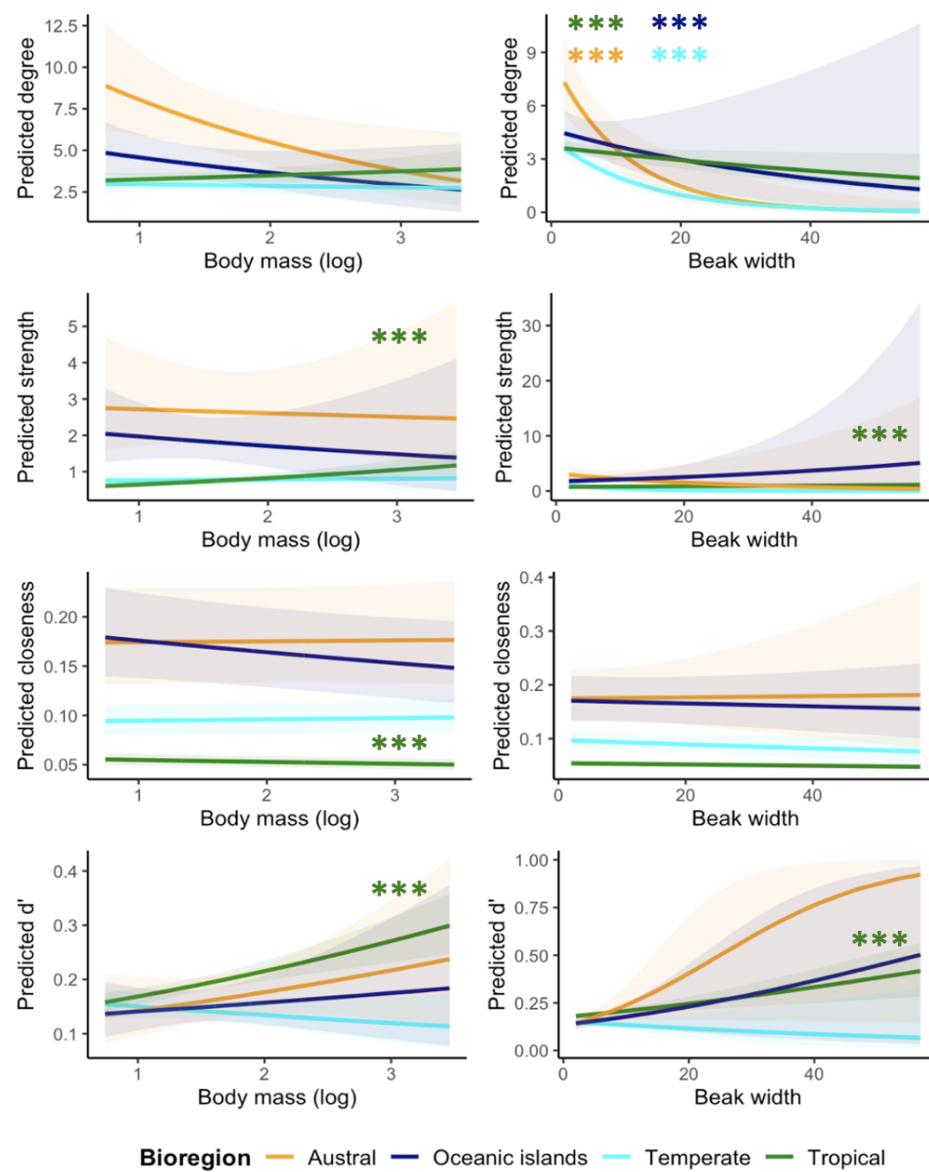
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757 **Fig. 2. Effects of body mass and beak width on species-level network roles.** Effects of (A)
 758 body mass (log-transformed) and (B) beak width on ~~three~~^{four} species-level metrics
 759 (specialization, closeness, interaction strength, and degree). The colored dots represent the
 760 estimates of the models (β , slope), p -values and z -statistics are represented inside squares.
 761



762

763 **Fig. 3. Relationship between bird traits and network roles in different bioregional**
 764 **categories.** Predicted species degree, interaction strength, closeness, and specialization d' as a
 765 function of their body mass (log) and beak width in Austral, Oceanic Islands, Temperate, and
 766 Tropical bioregional categories. Solid lines show marginal effects with 95% CI. Asterisks (***)
 767 show significantly positive or negative slopes.

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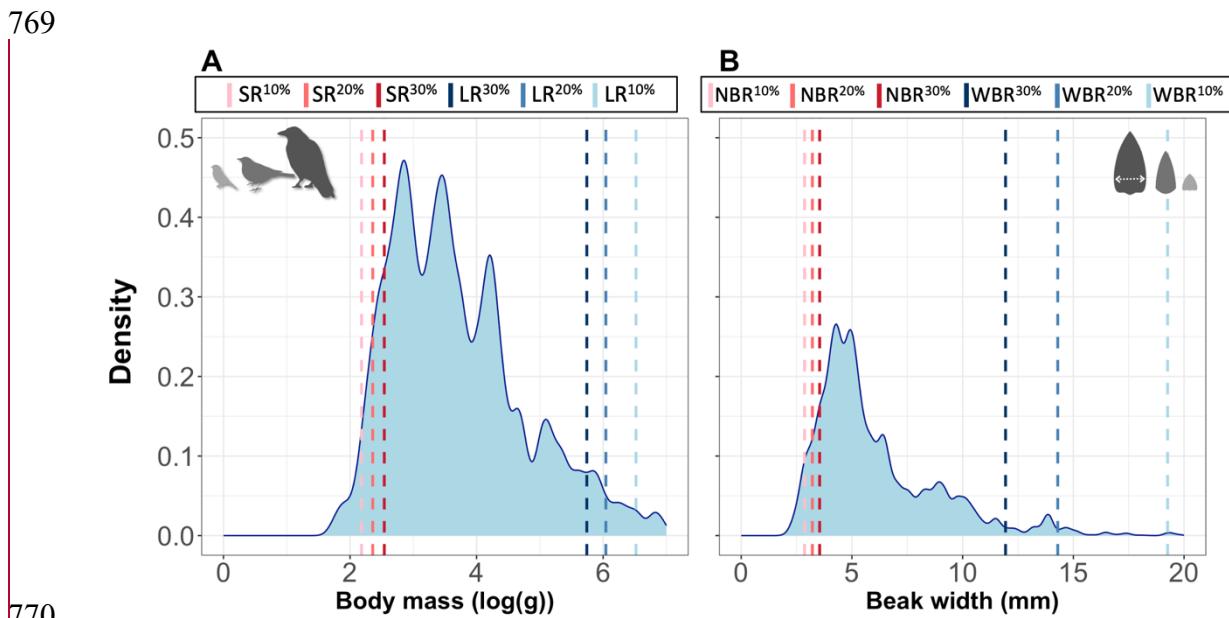
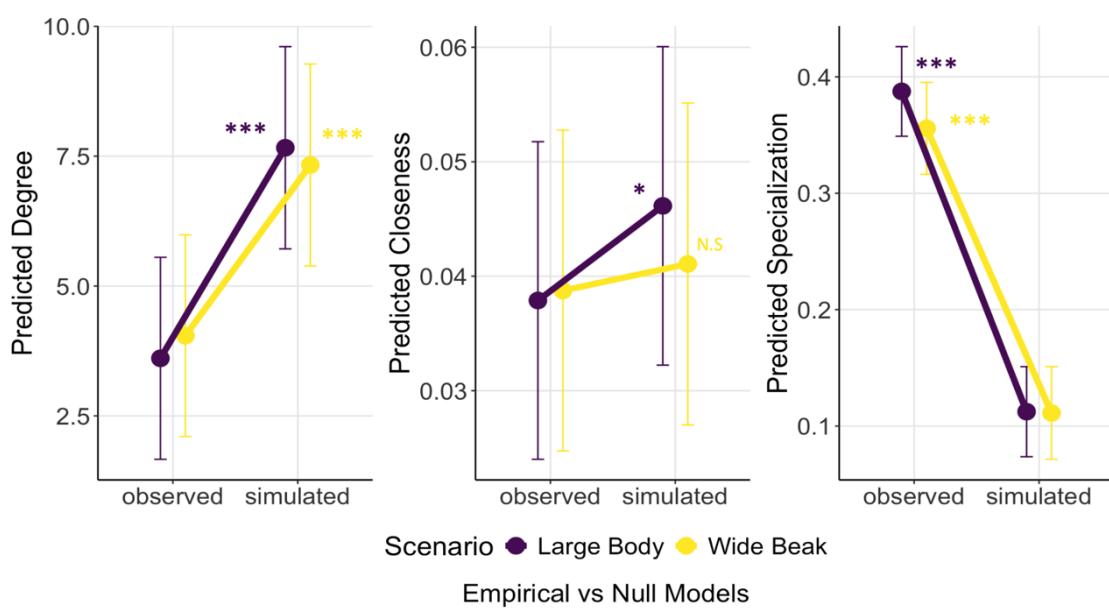


Fig. 43. Trait distributions and selection thresholds for body mass and beak width.

Distribution of (A) body mass (log-transformed) and (B) beak width. Mean values of the species eliminated on different levels of each scenario are represented with dotted lines (SLRM: low Small species removed, mass; LRHM: Larger species removed, high mass; NBR: narrowes beaks removed, and WBR: widest beaks removed).



777 **Fig. 5. Differences between observed and null metrics for large-bodied and wide-beaked**
 778 **species.** Predicted values of degree, closeness, and specialization for empirical and null-model
 779 ([Patefield algorithm](#)) networks, considering only quantitative networks and focusing on the 10%
 780 largest-bodied species (“Large Body”) and the 10% widest-beaked species (“Wide Beak”).
 781 Simulated values are based on null models that randomize interactions while preserving [each](#)
 782 [species’](#) [the](#) interaction frequency [of each species](#). Dots represent model-predicted means with
 783 95% confidence intervals. Asterisks indicate statistically significant differences between observed
 784 and simulated values within each scenario (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; N.S., not
 785 significant).

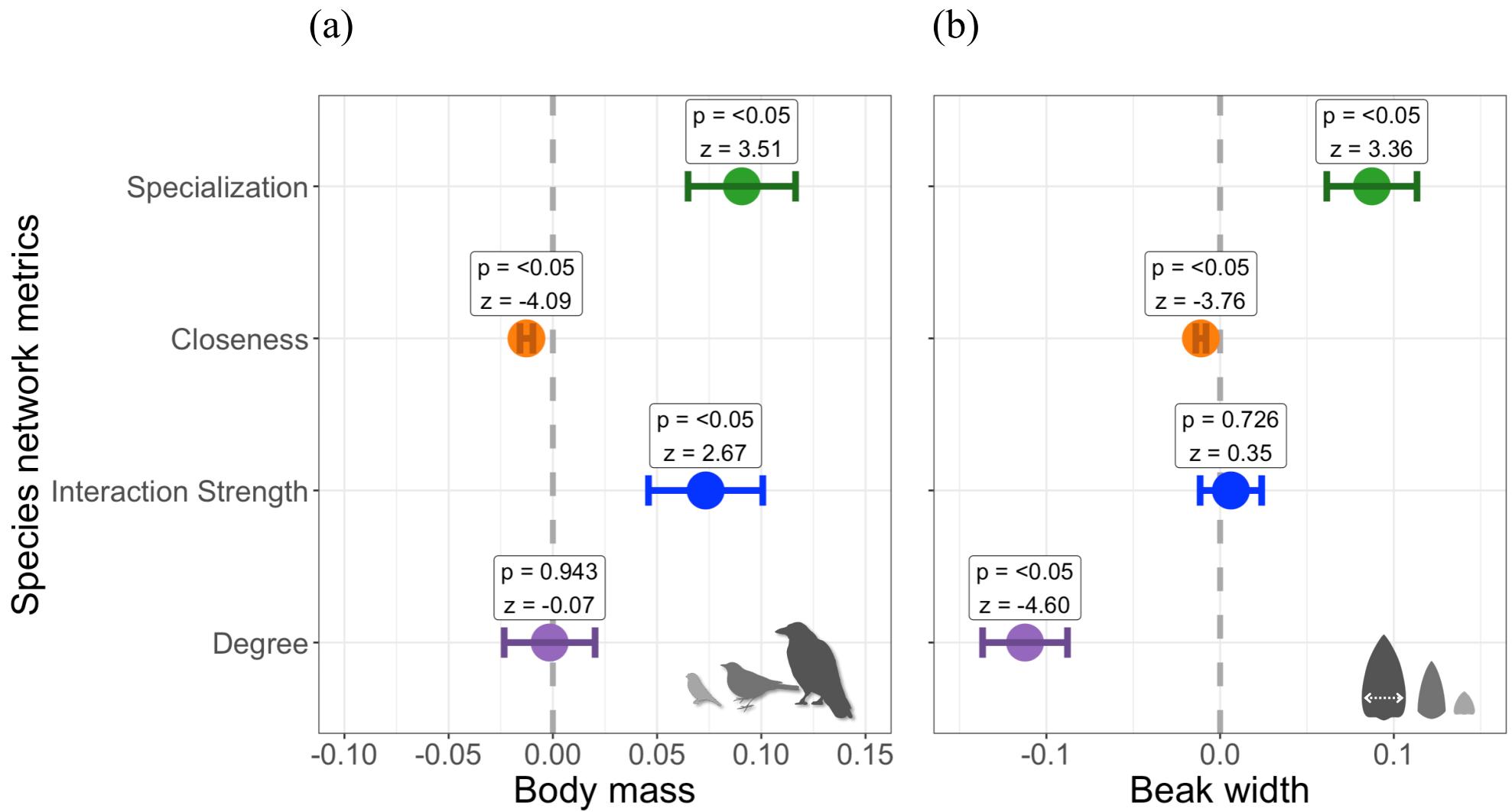
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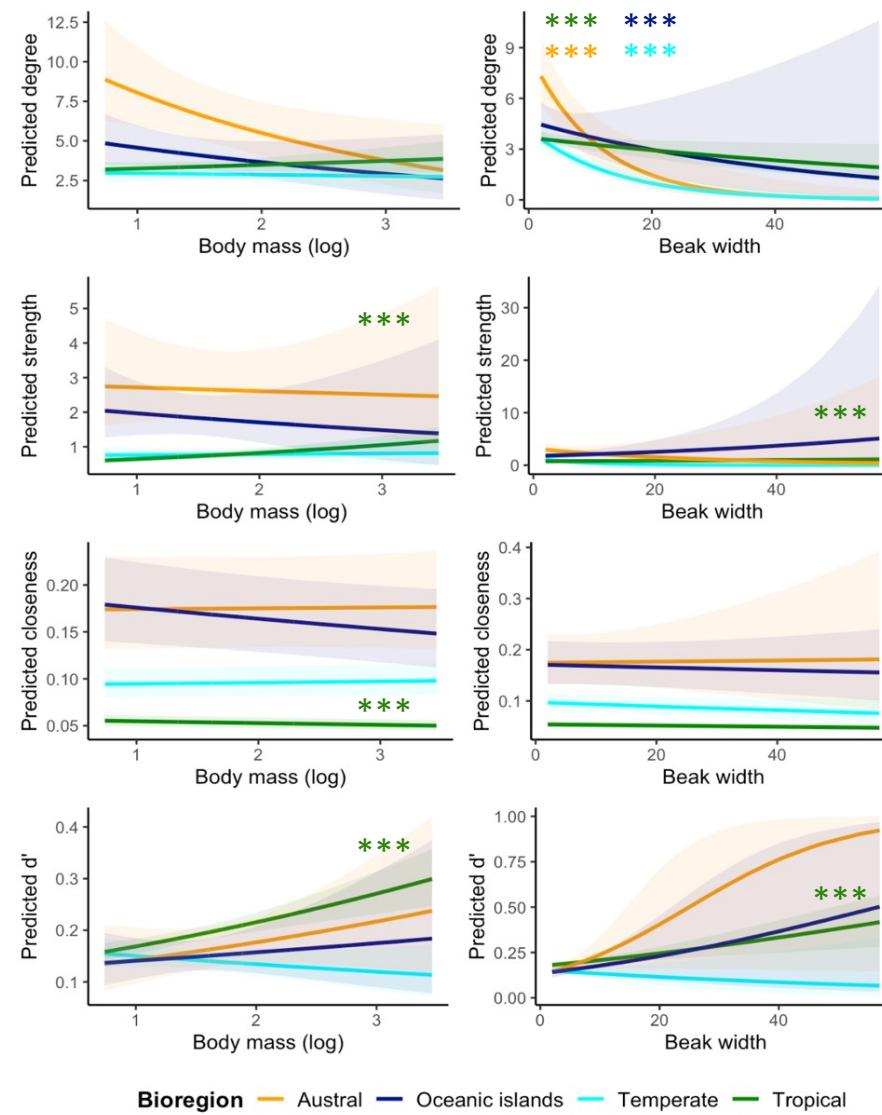
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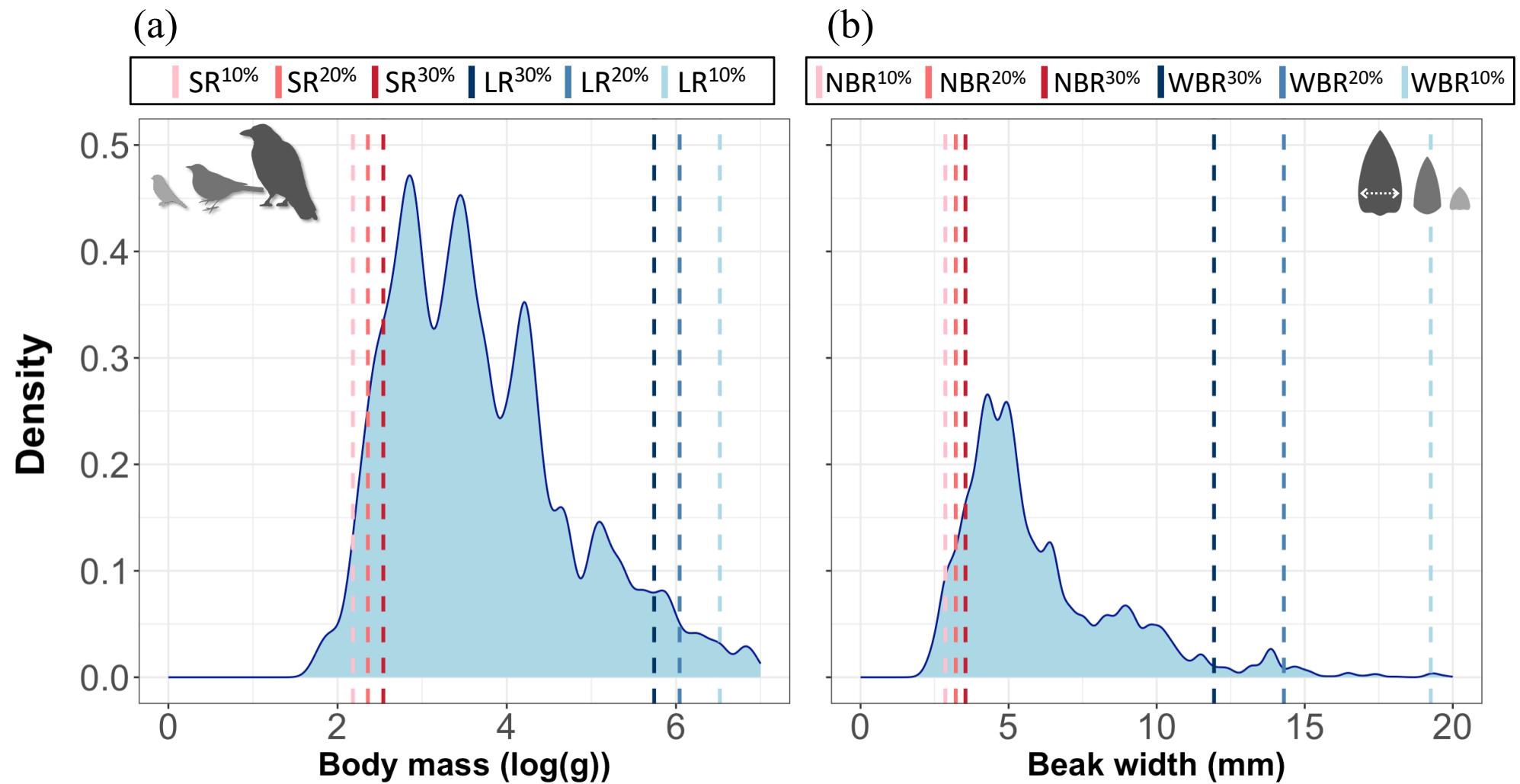
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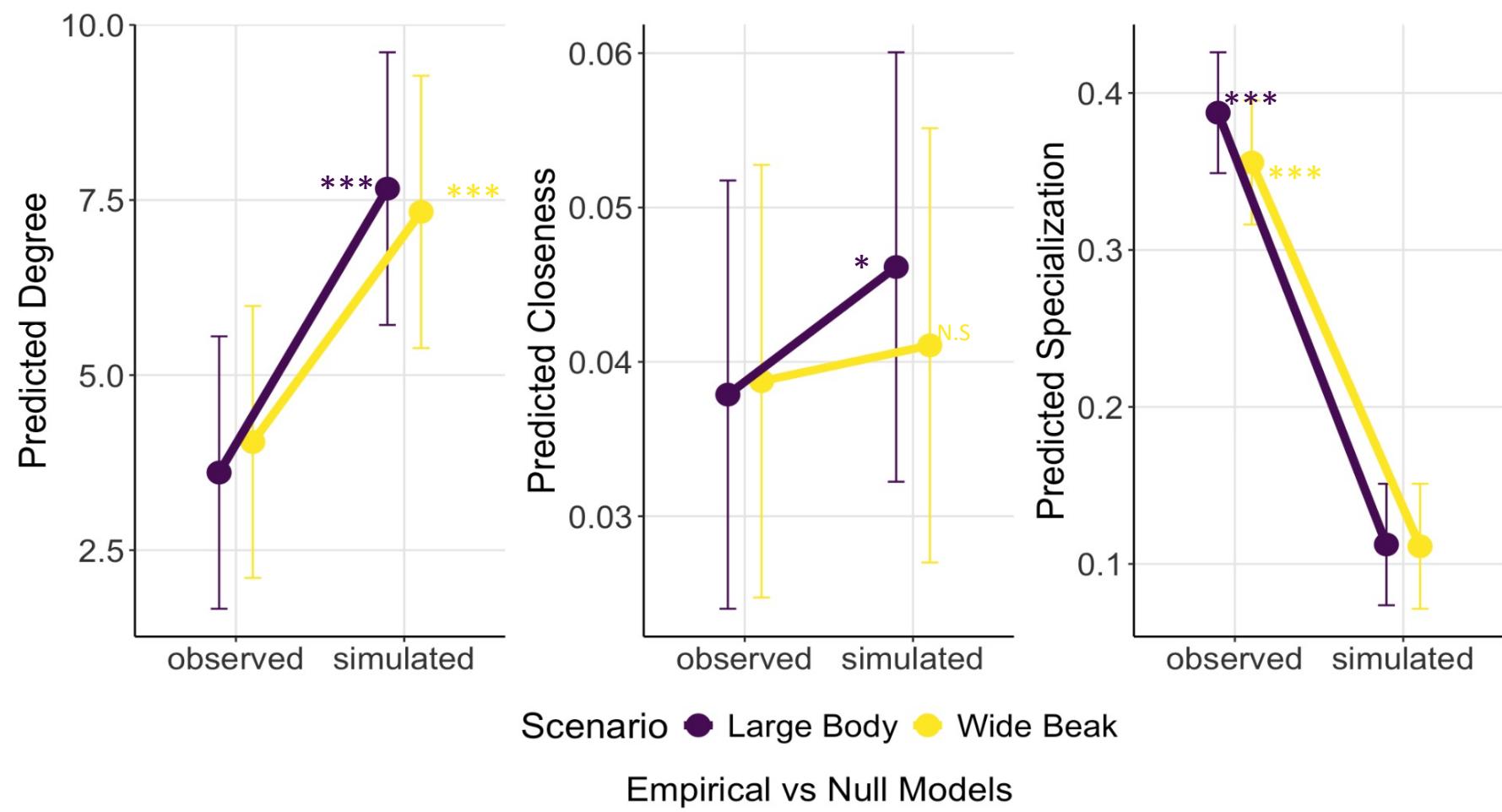
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1 **SUPPLEMENTARY MATERIAL**
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4**Large-bodied and wide-beaked avian frugivores show greater specialisation
in tropical seed dispersal networks**5 **Table S1.** Metadata of frugivory networks.
6
78 **Table S2.** Effects of body mass and beak width on species-level network metrics using
9 weighted data.
1011 **Table S3.** Percentage of networks affected by species removal scenarios.
1213 **Table S4.** Results of PGLS examining the relationship between specialization and
14 morphological traits.
1516 **Table S5.** Top 10% highest mass species across networks.
1718 **Table S6.** Top 10% smaller species across networks.
1920 **Table S7.** Top 10% widest-beaked species across networks.
2122 **Table S8.** Top 10% narrowest-beaked species across networks.
2324 **Fig. S1.** Effects of body mass and beak width on species-level network roles using both
25 weighted and unweighted networks.
2627 **Fig. S2.** Interaction network completeness.
2829 **Fig. S3.** Relationship between species traits and their degree of frugivory.
3031 **Appendix S1.** Sensitive analysis and analysis across bioregions.
32
33

Table S1. Metadata of frugivory networks. This table lists network IDs, sampling localities, and bioregions. It also includes the study IDs and references for the original sources of each network.

Network ID	Locality	Bioregion	Study ID	Reference
M_SD_001	USA	Nearctic	M_SD_001	Baird, J. W. (1980). The selection and use of fruit by birds in an eastern forest. <i>The Wilson Bulletin</i> , 63-73.
M_SD_002	Papua New Guinea	Oceanian	M_SD_002	Beehler, B. (1983). Frugivory and polygamy in birds of paradise. <i>The Auk</i> , 100(1), 1-12.
M_SD_003	Puerto Rico	Panamanian	M_SD_003	Carlo, T. A., Collazo, J. A., & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. <i>Oecologia</i> , 134(1), 119-131.
M_SD_004	Puerto Rico	Panamanian	M_SD_004	Carlo, T. A., Collazo, J. A., & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. <i>Oecologia</i> , 134(1), 119-131.
M_SD_005	Puerto Rico	Panamanian	M_SD_005	Carlo, T. A., Collazo, J. A., & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. <i>Oecologia</i> , 134(1), 119-131.
M_SD_006	Puerto Rico	Panamanian	M_SD_006	Carlo, T. A., Collazo, J. A., & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. <i>Oecologia</i> , 134(1), 119-131.
M_SD_007	Australia	Australian	M_SD_007	Crome, F. H. J. (1975). The ecology of fruit pigeons in tropical Northern Queensland. <i>Wildlife Research</i> , 2(2), 155-185.
M_SD_008	South Africa	Afrotropical	M_SD_008	Frost, P. G. H. (1980). Fruit-frugivore interactions in a South African coastal dune forest. <i>Acta XVII Congressus Internationalis Ornithologici</i> , 2, 71-1184.
M_SD_009	Brazil	Neotropical	M_SD_009	Galetti, M., & Pizo, M. A. (1996). Fruit eating by birds in a forest fragment in southeastern Brazil. <i>Ararajuba</i> , 4(2), 71-79.
M_SD_010 single partners added	Trinidad and Tobago	Neotropical	M_SD_010	Snow, B. K., & Snow, D. W. (1971). The feeding ecology of tanagers and honeycreepers in Trinidad. <i>The Auk</i> , 88(2), 291-322.
M_SD_012	Brazil	Neotropical	M_SD_012	Galetti, M., & Pizo, M. A. (1996). Fruit eating by birds in a forest fragment in southeastern Brazil. <i>Ararajuba</i> , 4(2), 71-79.
M_SD_014	Spain	Palearctic	M_SD_014	Jordano, P. (1985) El ciclo anual de los paseriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. <i>Ardeola</i> , 32, 69-94.

M_SD_015	Mexico	Panamanian	M_SD_015	Kantak, G. E. (1979). Observations on some fruit-eating birds in Mexico. <i>The Auk</i> , 96(1), 183-186.
M_SD_016	Malaysia	Oriental	M_SD_016	Lambert, F. (1989). Fig-eating by birds in a Malaysian lowland rain forest. <i>Journal of Tropical Ecology</i> , 5(4), 401-412.
M_SD_018	Papua New Guinea	Oceanian	M_SD_018	Mack, A. L., & Wright, D. D. (1996). Notes on occurrence and feeding of birds at Crater Mountain biological research station, Papua New Guinea. <i>Emu</i> , 96(2), 89-101.
M_SD_019	Costa Rica	Panamanian	M_SD_019	Wheelwright, N. T., Haber, W. A., Murray, K. G., & Guindon, C. (1984). Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. <i>Biotropica</i> , 173-192.
M_SD_020	Spain	Palearctic	M_SD_020	Jordano, P., unpubl.
M_SD_021	Spain	Palearctic	M_SD_021	
M_SD_024	Spain	Palearctic	M_SD_024	Guitián, J. (1983). Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera cantábrica occidental. Thesis. Universidad de Santiago de Compostela, Spain.
M_SD_026	Spain	Palearctic	M_SD_026	Data unpublished, however see Jordano, P. (1993). Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. <i>Vegetatio</i> , 107(1), 85-104.
M_SD_027	Spain	Palearctic	M_SD_027	
M_SD_028	Spain	Palearctic	M_SD_028	
M_SD_029	Spain	Palearctic	M_SD_029	
M_SD_030	Spain	Palearctic	M_SD_030	
M_SD_031	Azores	Azores	M_SD_031	Heleno, R. H., Ramos, J. A., & Memmott, J. (2013). Integration of exotic seeds into an Azorean seed dispersal network. <i>Biological Invasions</i> , 15(5), 1143-1154.
M_SD_032	Panama	Panamanian	M_SD_032	Poulin, B., Wright, S. J., Lefebvre, G., & Calderon, O. (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. <i>Journal of Tropical Ecology</i> , 15(2), 213-227.
M_SD_033	Panama	Panamanian	M_SD_033	Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. <i>Oecologia</i> , 176(3), 837-848.
SAAV1	Bolivia	Neotropical	SAAV	
SAAV2	Bolivia	Neotropical		

VELHO	India	Oriental	VELHO	Velho, N., Ratnam, J., Srinivasan, U., & Sankaran, M. (2012). Shifts in community structure of tropical trees and avian frugivores in forests recovering from past logging. <i>Biological conservation</i> , 153, 32-40.
VELHO2	India	Oriental		
Albrecht 13_2012	Poland	Palearctic	Albrecht 2013	Albrecht, J., Bohle, V., Berens, D. G., Jaroszewicz, B., Selva, N., & Farwig, N. (2015). Variation in neighbourhood context shapes frugivore-mediated facilitation and competition among co-dispersed plant species. <i>Journal of Ecology</i> , 103(2), 526-536.
Albrecht 15_2012	Poland	Palearctic		
Albrecht 35_2012	Poland	Palearctic		
Albrecht 36_2012	Poland	Palearctic		
Albrecht 102_2011	Poland	Palearctic		
Albrecht 111_2011	Poland	Palearctic		
Albrecht 111_2012	Poland	Palearctic		
Albrecht 112_2011	Poland	Palearctic		
Albrecht 112_2012	Poland	Palearctic		
Albrecht 203_2011	Poland	Palearctic		
Albrecht 301_2011	Poland	Palearctic		
Albrecht 315_2011	Poland	Palearctic		
Andrade 2011	Brazil	Neotropical	Andrade 2011	Andrade, P. C., J. V. L. Mota, and A. A. F. Carvalho. 2011. Interações mutualísticas entre aves frugívoras e plantas em um fragmento urbano de Mata Atlântica, Salvador, BA. . <i>Revista Brasileira De Ornitologia</i> 19:63-73.
Armesto 1987	Chile	Neotropical	Armesto 1987	Armesto, J. J., Rozzi, R. I. C. A. R. D. O., Miranda, P. A. M. E. L. A., & Sabag, C. A. R. L. O. S. (1987). Plant/frugivore interactions in South American temperate forests. <i>Revista Chilena de Historia Natural</i> , 60(2), 321-336.
Athie 2009	Brazil	Neotropical	Athie 2009	Athié, S. (2009). Composição da avifauna e frugivoria por aves em um mosaico de vegetação secundária em Rio Claro, região centro-leste do estado de São Paulo. Thesis. Universidade Federal de São Carlos, Brazil.
Balasubramanian 1996	India	Oriental	Balasubramanian 1996	Balasubramanian, P. (1996). Interactions between fruit-eating birds and bird-dispersed plants in the tropical dry evergreen forest of Point Calimere, South India. <i>Journal of Bombay Natural History Society</i> , 93, 428-441.

Bastazini 2018	Brazil	Neotropical	Bastazini 2018	Bastazini, V. A., Debastiani, V. J., Azambuja, B. O., Guimaraes, P. R., & Pillar, V. D. (2019). Loss of generalist plant species and functional diversity decreases the robustness of a seed dispersal network. <i>Environmental Conservation</i> , 46(1), 52-58.
Blake 1992	Costa Rica	Panamanian	Blake 1992	Blake, J. G., & Loiselle, B. A. (1992). Fruits in the diets of Neotropical migrant birds in Costa Rica. <i>Biotropica</i> , 24(2), 200-210.
Blendinger 2015	Argentina	Neotropical	Blendinger 2015	Blendinger, P. G., Jiménez, J., Macchi, L., Martín, E., Sánchez, M. S., & Ayup, M. M. (2015). Scale_dependent spatial match between fruits and fruit_eating birds during the breeding season in Yungas Andean forests. <i>Biotropica</i> , 47(6), 702-711.
Blendinger 2016	Argentina	Neotropical	Blendinger 2016	Blendinger, P. G., Martín, E., Osinaga Acosta, O., Ruggera, R. A., & Aráoz, E. (2016). Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. <i>Biotropica</i> , 48(5), 677-686.
Burns 2013	New Zealand	Novozelandic	Burns 2013	Burns, K. C. (2013). What causes size coupling in fruit-frugivore interaction webs?. <i>Ecology</i> , 94(2), 295-300.
Castro 2015	Brazil	Neotropical	Castro 2015	Castro, E. R. D. (2007). Fenologia reprodutiva da palmito Euterpe edulis (Arecaceae) e sua influência na abundância de aves frugívoras na floresta Atlântica. Thesis. Universidade Estadual Paulista "Júlio de Mesquita Filho", Brazil.
Chama 2013 net1	South Africa	Afrotropical	Chama 2013	Chama, L., Berens, D. G., Downs, C. T., & Farwig, N. (2013). Habitat characteristics of forest fragments determine specialisation of plant-frugivore networks in a mosaic forest landscape. <i>PloS one</i> , 8(1), e54956.
Chama 2013 net2	South Africa	Afrotropical		
Chama 2013 net3	South Africa	Afrotropical		
Chama 2013 net4	South Africa	Afrotropical		
Chama 2013 net5	South Africa	Afrotropical		
Chama 2013 net6	South Africa	Afrotropical		
Chama 2013 net7	South Africa	Afrotropical		
Chama 2013 net8	South Africa	Afrotropical		
Chama 2013 net9	South Africa	Afrotropical		

Chatterjee 2014	India	Oriental	Chatterjee 2014	Chatterjee, S., & Basu, P. (2015, December). Differential effect of fruit availability on avian frugivore guilds in a moist deciduous forest of India. In Proceedings of the Zoological Society (Vol. 68, No. 2, pp. 147-154). Springer India.
Chen 1999	Taiwan	Oriental	Chen 1999	Chen, C., & Chou, L. (1999). The diet of forest birds at Fushan Experimental Forest. Taiwan Journal of Forest Science, 14(3), 275-287.
Chimera 2010	Hawaii	Hawaiian Islands	Chimera 2010	Chimera, C. G., & Drake, D. R. (2010). Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. <i>Biotropica</i> , 42(4), 493-502.
Costa 2013 endozoochory	Portugal	Palearctic	Costa 2013 endozoochory	Costa, J. M., Ramos, J. A., da Silva, L. P., Timoteo, S., Araújo, P. M., Felgueiras, M. S., ... & Heleno, R. H. (2014). Endozoochory largely outweighs epizoochory in migrating passerines. <i>Journal of Avian Biology</i> , 45(1), 59-64.
Costa 2016	Portugal	Palearctic	Costa 2016	Costa, J. M., da Silva, L. P., Ramos, J. A., & Heleno, R. H. (2016). Sampling completeness in seed dispersal networks: when enough is enough. <i>Basic and Applied Ecology</i> , 17(2), 155-164.
Costa 2018 before only	Portugal	Palearctic	Costa 2018 before only	Costa, J. M., Ramos, J. A., da Silva, L. P., Timóteo, S., Andrade, P., Araújo, P. M., ... & Godinho, C. (2018). Rewiring of experimentally disturbed seed dispersal networks might lead to unexpected network configurations. <i>Basic and Applied Ecology</i> , 30, 11-22.
Cruz 2013 Summer	Portugal	Palearctic	Cruz 2013	Cruz, J. C., Ramos, J. A., Da Silva, L. P., Tenreiro, P. Q., & Heleno, R. H. (2013). Seed dispersal networks in an urban novel ecosystem. <i>European journal of forest research</i> , 132(5-6), 887-897.
Cruz 2013 Autumn	Portugal	Palearctic		
Cruz 2013 Winter	Portugal	Palearctic		
da Silva 2015 site A	Brazil	Neotropical	da Silva 2015	Ribeiro da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M. A., & Rodrigues, R. R. (2015). The restoration of tropical seed dispersal networks. <i>Restoration Ecology</i> , 23(6), 852-860.
da Silva 2015 site B	Brazil	Neotropical		
da Silva 2015 site C	Brazil	Neotropical		
Daru 2015	Nigeria	Afrotropical	Daru 2015	Daru, B. H., Yessoufou, K., Nuttman, C., & Abalaka, J. (2015). A preliminary study of bird use of fig Ficus species in Amurum Forest Reserve, Nigeria. <i>Malimbus</i> , 37, 1-15.

David 2011 tree focal watches	India	Oriental	David 2011	David, J. P., Murugan, B. S., & Mankadan, R. (2011). Frugivory by birds and mammals in Sriharikota Island, southern India. <i>Journal of Bombay Natural History Society</i> , 108(1), 24-40.
de la Pena 2003	Argentina	Neotropical	de la Pena 2003	de la Peña, M. R., & Pensiero, J. F. (2003). Contribución de la flora en los hábitos alimentarios de las aves en un bosque del centro de la provincia de Santa Fe, Argentina. <i>Ornitología Neotropical</i> , 14, 499-513.
de Oliveira 1999	Brazil	Neotropical	de Oliveira 1999	de-Oliveira, A. M. M. (1999). Frugivoria por aves em um fragmento de floresta de restinga no Estado do Espírito Santo, Brasil. Thesis. Universidade Estadual de Campinas, Brazil.
Dehling 2017 San Pedro 1	Peru	Neotropical	Dehling 2017	Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning_Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. <i>Ecography</i> , 37(11), 1047-1055.
Dehling 2017 San Pedro 2	Peru	Neotropical		
Dehling 2017 San Pedro 3	Peru	Neotropical		
Dehling 2017 San Pedro 4	Peru	Neotropical		
Dehling 2017 Wayqecha 1	Peru	Neotropical		
Dehling 2017 Wayqecha 2	Peru	Neotropical		
Dehling 2017 Wayqecha 3	Peru	Neotropical		
Dehling 2017 Wayqecha 4	Peru	Neotropical		
Dupont 1997	Belgium	Palearctic	Dupont 1997	Dupont, É., Dulière, J. F., & Malaisse, F. (1997). Aspects de l'ornithochorie et de la germination des semences des arbustes en fruticée calcicole de Calestienne. <i>Biotechnologie, Agronomie, Société et Environnement</i> , 1(4), 264-271.
Erard 2007	French Guiana	Neotropical	Erard 2007	Erard, C., Théry, M., & Sabatier, D. (2007). Fruit characters in the diet of syntopic large frugivorous forest bird species in French Guiana. <i>Revue d'écologie</i> .
Fadini 2004	Brazil	Neotropical	Fadini 2004	Fadini, R. F. (2004). Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. <i>Ararajuba</i> , 97-103.
Faustino 2006	Brazil	Neotropical	Faustino 2006	Faustino, T. C., & Machado, C. G. (2006). Frugivoria por aves em uma área de campo rupestre na Chapada Diamantina, BA. <i>Revista Brasileira de Ornitologia</i> , 14(2), 137-143.

Fonseca 2007	Brazil	Neotropical	Fonseca 2007	Fonseca, F. Y., & Antunes, A. Z. (2007). Frugivoria e predação de sementes por aves no Parque Estadual Alberto Löfgren, São Paulo, SP. Frugivory and seed predation by birds in Alberto Löfgren State Park, São Paulo, Southeast Brazil. <i>Revista do Instituto Florestal</i> .
Fontanari 2018	Brazil	Neotropical	Fontanari 2018	Fontanari, V. A. (2018). Rede de interações entre aves frugívoras e plantas em áreas de floresta estacional decidual, RS. Thesis. Universidade Federal de Santa Maria Brazil.
Fricke 2018 Rota	Mariana Islands	Mariana Islands	Fricke 2018	Fricke, E. C., Tewksbury, J. J., & Rogers, H. S. (2018). Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network. <i>Global change biology</i> , 24(1), e190-e200.
Fuentes 1994	Spain	Palearctic	Fuentes 1994	Fuentes, M. (1994). Diets of fruit-eating birds: what are the causes of interspecific differences?. <i>Oecologia</i> , 97(1), 134-142.
Garcia 2014 Wrights Hill	New Zealand	Novozelandic	Garcia 2014	García, D., Martínez, D., Stouffer, D. B., & Tylianakis, J. M. (2014). Exotic birds increase generalization and compensate for native bird decline in plant-frugivore assemblages. <i>Journal of Animal Ecology</i> , 83(6), 1441-1450.
Garcia 2014 Zealandia	New Zealand	Novozelandic		
Garcia 2014 George Denton	New Zealand	Novozelandic		
Garcia 2014 Charles Plimmer	New Zealand	Novozelandic		
Garcia 2014 Northern Town Belt	New Zealand	Novozelandic		
Garcia 2014 Hinau	New Zealand	Novozelandic		
Garcia 2014 Mount Fyfee Reserve	New Zealand	Novozelandic		
Garcia 2014 Puhi-Puhi River	New Zealand	Novozelandic		
Garcia 2014 Blue Duck	New Zealand	Novozelandic		
Garcia 2016	Spain	Palearctic	Garcia 2016	García, D. (2016). Birds in ecological networks: insights from bird-plant mutualistic interactions. <i>Ardeola</i> , 63(1), 151-181.
Githiru 2002	Kenya	Afrotropical	Githiru 2002	Githiru, M., Lens, L., Bennur, L. A., & Ogol, C. P. K. O. (2002). Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. <i>Oikos</i> , 96(2), 320-330.
Gonzalez-Castro 2012 Summer 08	Canary Islands	Canary Islands	Gonzalez-Castro 2012	González-Castro, A., Yang, S., Nogales, M., & Carlo, T. A. (2012). What determines the temporal changes of species degree and strength in an oceanic island plant-disperser network?. <i>PLoS One</i> , 7(7), e41385.
Gonzalez-Castro 2012 Autumn 08	Canary Islands	Canary Islands		
Gonzalez-Castro 2012 Winter 09	Canary Islands	Canary Islands		
Gonzalez-Castro 2012 Spring 09	Canary Islands	Canary Islands		

Gonzalez-Castro 2012 Winter 10	Canary Islands	Canary Islands		
Gonzalez-Castro 2012 Spring 10	Canary Islands	Canary Islands		
Gonzalez-Castro 2012 Summer 10	Canary Islands	Canary Islands		
Gonzalez-Castro 2012 Autumn 10	Canary Islands	Canary Islands		
Hasui 1998	Brazil	Neotropical	Hasui 1998	Hasui, E., & Hofling, E. (1998). Food Preference Of The Frugivorous Birds In A Fragment Of Semideciduous Forest, Sao Paulo. <i>Iheringia, Sér. Zool.</i> , 84, 43-64.
Howe 1984	Costa Rica	Panamanian	Howe 1984	Howe, H. F. (1984). Implications of seed dispersal by animals for tropical reserve management. <i>Biological Conservation</i> , 30(3), 261-281.
Ikuta 2013	Brazil	Neotropical	Ikuta 2013	Ikuta, K. G., & de Campos Martins, F. (2013). Interação entre aves frugívoras e plantas no Parque Estadual da Cantareira, estado de São Paulo.
Innis 1989 ANVF	Australia	Australian	Innis 1989	Innis, G. J. (1989). Feeding ecology of fruit pigeons in subtropical rainforests of south-eastern Queensland. <i>Wildlife Research</i> , 16(4), 365-394.
Innis 1989 NVF CNVF	Australia	Australian		
Kamruzzaman 2008	Bangladesh	Oriental	Kamruzzaman 2008	Kamruzzaman, M. (2008) Seasonal variations of fruit preference among frugivorous birds in Chittagong, Bangladesh. <i>Bangladesh Journal of Zoology</i> . 36(2), 187-206.
Kessler-Rios 2012	Colombia	Neotropical	Kessler-Rios 2012	Kessler-Rios, M. M., & Kattan, G. H. (2012). Fruits of Melastomataceae: phenology in Andean forest and role as a food resource for birds. <i>Journal of Tropical Ecology</i> , 28(1), 11-21.
Labbe 2011	USA	Nearctic	Labbe 2011	Labbe, M. A. (2011). Habitat use, productivity, and fruit selection of birds in early-successional habitats in western Massachusetts. Thesis. University of Massachusetts Amherst, USA.
MacFarlane 2016	New Zealand	Novozelandic	MacFarlane 2016	MacFarlane, A. E., Kelly, D., & Briskie, J. V. (2016). Introduced blackbirds and song thrushes: useful substitutes for lost mid-sized native frugivores, or weed vectors?. <i>New Zealand Journal of Ecology</i> , 40(1), 80-87.
Machado-de-Souza 2019	Brazil	Neotropical	Machado-de-Souza 2019	Machado-de-Souza, T., Campos, R. P., Devoto, M., & Varassin, I. G. (2019). Local drivers of the structure of a tropical bird-seed dispersal network. <i>Oecologia</i> , 189(2), 421-433.

Malacco da Silva 2014	Brazil	Neotropical	Malacco da Silva 2014	Silva, G. D., & Pedroni, F. (2014). Frugivoria por aves em área de cerrado no município de Uberlândia, Minas Gerais..[Frugivory by birds in cerrado in the city of Uberlândia, Minas Gerais.]. Revista árvore-Sociedade de Investigações Florestais (Viçosa-Brasil)., 38(3), 433-442.
Malmborg 1988 1980	USA	Nearctic	Malmborg 1988	Malmborg, P. K., & Willson, M. F. (1988). Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. <i>The Condor</i> , 90(1), 173-186.
Malmborg 1988 1981	USA	Nearctic		
Malmborg 1988 1982	USA	Nearctic		
Marcos da Silva 2013	Brazil	Neotropical	Marcos da Silva 2013	Silva, A. M. D. (2013). Sobreposição em assembleias de aves frugívoras e dispersão de sementes no cerrado Sensu stricto. Thesis. Universidade Federal de Uberlandia, Brazil.
Mokotjomela 2013	South Africa	Afrotropical	Mokotjomela 2013	Mokotjomela, T. M., Musil, C. F., & Esler, K. J. (2013). Frugivorous birds visit fruits of emerging alien shrub species more frequently than those of native shrub species in the South African Mediterranean climate region. <i>South African Journal of Botany</i> , 86, 73-78.
Odonnell 1994	New Zealand	Novozelandic	Odonnell 1994	O'Donnell, C. F., & Dilks, P. J. (1994). Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. <i>New Zealand Journal of Ecology</i> , 18(2), 87-107.
Olesen 2018	Galapagos	Galapagos	Olesen 2018	Olesen, J. M., Damgaard, C. F., Fuster, F., Heleno, R. H., Nogales, M., Rumeu, B., ... & Traveset, A. (2018). Disclosing the double mutualist role of birds on Galápagos. <i>Scientific reports</i> , 8(1), 57.
Ortiz-Pulido 2000	Mexico	Panamanian	Ortiz-Pulido 2000	Ortiz_Pulido, R., Laborde, J., & Guevara, S. (2000). Frugivoría por Aves en un Paisaje Fragmentado: Consecuencias en la Dispersión de Semillas 1. <i>Biotropica</i> , 32(3), 473-488.
Palacios 2016	Colombia	Neotropical	Palacios 2016	Palacio, R. D., Valderrama_Ardila, C., & Kattan, G. H. (2016). Generalist species have a central role in a highly diverse plant-frugivore network. <i>Biotropica</i> , 48(3), 349-355.
Palita 2011	India	Oriental	Palita 2011	Palita, S. K., Ponkshe, A. V., & Dhar, U. (2011). Habitat enrichment and its impact on avian diversity: a study at GBPIHED, Kosi-Katarmal, Uttarakhand, India. <i>Current Science</i> , 100(11), 1681.

Pejchar 2015	Hawaii	Hawaiian Islands	Pejchar 2015	Pejchar, L. (2015). Introduced birds incompletely replace seed dispersal by a native frugivore. <i>AoB Plants</i> , 7.
Plein 2013 Farmland summer	Germany	Palearctic	Plein 2013	Plein, M., Längsfeld, L., Neuschulz, E. L., Schultheiß, C., Ingmann, L., Töpfer, T., ... & Schleuning, M. (2013). Constant properties of plant-frugivore networks despite fluctuations in fruit and bird communities in space and time. <i>Ecology</i> , 94(6), 1296-1306.
Plein 2013 Farmland autumn	Germany	Palearctic		
Plein 2013 Orchard summer	Germany	Palearctic		
Plein 2013 Orchard autumn	Germany	Palearctic		
Plein 2013 Forest summer	Germany	Palearctic		
Plein 2013 Forest autumn	Germany	Palearctic		
Prather 2000	USA	Nearctic	Prather 2000	Prather, J. W., Smith, K. G., Mlodinow, M. A., & Riley, C. M. (2000). Characteristics of some fruiting plant species in northwest Arkansas, and the avian assemblages that feed on them. <i>Journal of the Arkansas Academy of Science</i> , 54(1), 103-108.
Pratt 1985	Papua New Guinea	Oceanian	Pratt 1985	Pratt, T. K., & Stiles, E. W. (1985). The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. <i>Biotropica</i> , 314-321.
Purificacao 2014 forest rainy	Brazil	Neotropical	Purificacao 2014	Purificação, K. N., Pascotto, M. C., Pedroni, F., Pereira, J. M. N., & Lima, N. A. (2014). Interactions between frugivorous birds and plants in savanna and forest formations of the Cerrado. <i>Biota Neotropica</i> , 14(4).
Purificacao 2014 forest dry	Brazil	Neotropical		
Purificacao 2014 savannah rainy	Brazil	Neotropical		
Purificacao 2014 savannah dry	Brazil	Neotropical		
Quitian 2018 1000Fragmented	Ecuador	Neotropical	Quitian 2018	Quitíán, M., Santillán, V., Bender, I. M., Espinosa, C. I., Homeier, J., Böhning_Gaese, K., ... & Lena Neuschulz, E. (2019). Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests. <i>Functional Ecology</i> , 33(3), 399-410.
Quitian 2018 1000Natural	Ecuador	Neotropical		
Quitian 2018 2000Fragmented	Ecuador	Neotropical		
Quitian 2018 2000Natural	Ecuador	Neotropical		
Quitian 2018 3000Fragmented	Ecuador	Neotropical		
Quitian 2018 3000Natural	Ecuador	Neotropical		
Ramaswami 2017	India	Oriental	Ramaswami 2017	Ramaswami, G., Somnath, P., & Quader, S. (2017). Plant-disperser mutualisms in a semi-arid habitat invaded by <i>Lantana camara</i> L. <i>Plant Ecology</i> , 218(8), 935-946.
Ramos-Robles 2016 net1	Mexico	Panamanian	Ramos-Robles 2016	Ramos-Robles, M., Andresen, E., & Díaz-Castelazo, C. (2016). Temporal changes in the structure of a plant-frugivore network
Ramos-Robles 2016 net2	Mexico	Panamanian		

Ramos-Robles 2016 net3	Mexico	Panamanian		
Ramos-Robles 2016 net4	Mexico	Panamanian		
Ramos-Robles 2016 net5	Mexico	Panamanian		
Ramos-Robles 2016 net6	Mexico	Panamanian		
Ramos-Robles 2016 net7	Mexico	Panamanian		
Ramos-Robles 2016 net8	Mexico	Panamanian		
Ramos-Robles 2016 net9	Mexico	Panamanian		
Ramos-Robles 2016 net10	Mexico	Panamanian		
Robinson 2015	Brazil	Neotropical	Robinson 2015	Robinson, V. (2015). Índice de importância de diferentes espécies de plantas na atração de aves para uma área reflorestada em Piracicaba. Thesis. Universidade Estadual Paulista "Júlio de Mesquita Filho", Brazil.
Rozzi 1996	Chile	Neotropical	Rozzi 1996	Rozzi, R., Armesto, J. J., Correa, A., Torres-Mura, J. C., & Sallaberry, M. (1996). Avifauna de bosques primarios templados en islas deshabitadas del archipiélago de Chiloé, Chile. Revista Chilena de Historia Natural, 69, 125-139.
Ruggera 2016 La Florida	Argentina	Neotropical	Ruggera 2016	Ruggera, R. A., Blendinger, P. G., Gomez, M. D., & Marshak, C. (2016). Linking structure and functionality in mutualistic networks: do core frugivores disperse more seeds than peripheral species?. Oikos, 125(4), 541-555.
Ruggera 2016 San Javier	Argentina	Neotropical		
Ruggera 2016 Los Chorizos	Argentina	Neotropical		
Ruggera 2016 Quebrada del Port	Argentina	Neotropical		
Ruggera 2016 Chorro de Loros	Argentina	Neotropical		
Ruggera 2016 Pozo Verde	Argentina	Neotropical		
Ruggera 2016 EcoPortal	Argentina	Neotropical		
Ruggera 2016 A. Tres Cruces	Argentina	Neotropical		
Ruggera 2016 Sevenguillar	Argentina	Neotropical		
Ruggera 2016 El Noglar	Argentina	Neotropical		
Sanitjan 2009 XTBG arboretum	China	Oriental	Sanitjan 2009	Sanitjan, S., & Chen, J. (2009). Habitat and fig characteristics influence the bird assemblage and network properties of fig trees from Xishuangbanna, South-West China. Journal of Tropical Ecology, 25(2), 161-170.
Sanitjan 2009 XTBG forest	China	Oriental		
Sanitjan 2009 Limestone forest	China	Oriental		
Sanitjan 2009 ML primary forest	China	Oriental		
are influenced by bird migration and fruit availability. PeerJ, 4, e2048.				

Sankamethawee 2011	Thailand	Oriental	Sankamethawee 2011	Sankamethawee, W., Pierce, A. J., Gale, G. A., & Hardesty, B. D. (2011). Plant_frugivore interactions in an intact tropical forest in north_east Thailand. <i>Integrative Zoology</i> , 6(3), 195-212.
Scherer 2007	Brazil	Neotropical	Scherer 2007	Scherer, A., Maraschin-Silva, F., & Baptista, L. D. M. (2007). Padrões de interações mutualísticas entre espécies arbóreas e aves frugívoras em uma comunidade de Restinga no Parque Estadual de Itapuã, RS, Brasil. <i>Acta Botanica Brasiliensis</i> , 21(1), 203-212.
Skeate 1985	USA	Nearctic	Skeate 1985	Skeate, S. T. (1985). Mutualistic interactions between birds and fruits in a northern Florida hammock community. Thesis. University of Florida, USA.
Skutch 1980	Costa Rica	Panamanian	Skutch 1980	Skutch, A. F. (1980). Arils as food of tropical American birds. <i>The Condor</i> , 82(1), 31-42.
Snow 1988 DJF	United Kingdom of Great Britain and Northern Ireland	Palearctic	Snow 1988	Snow, B., & Snow, D. (1988). Birds and berries. A&C Black.
Snow 1988 MAM	United Kingdom of Great Britain and Northern Ireland	Palearctic		
Snow 1988 JJA	United Kingdom of Great Britain and Northern Ireland	Palearctic		
Snow 1988 SON	United Kingdom of Great Britain and Northern Ireland	Palearctic		
Sorensen 1981	United Kingdom of Great Britain and Northern Ireland	Palearctic	Sorensen 1981	Sorensen, A. E. (1981). Interactions between birds and fruit in a temperate woodland. <i>Oecologia</i> , 50(2), 242-249.
Souza Gomes 2008 primary forest Souza Gomes 2008 secondary fore	Brazil Brazil	Neotropical Neotropical	Souza Gomes 2008	Gomes, A. D. L. S. (2008). Interação mutualística entre aves frugívoras de sub-bosque e plantas no Parque Ecológico de Gunma, Santa Bárbara do Pará. Thesis. Universidade Federal do Pará, Brazil.

Spotswood 2012 Moorea	French Polynesia	Society Islands	Spotswood 2012	Spotswood, E. N., Meyer, J. Y., & Bartolome, J. W. (2012). An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. <i>Journal of Biogeography</i> , 39(11), 2007-2020.
Stiebel 2008 Spring	Germany	Palearctic	Stiebel 2008	Stiebel, H., & Bairlein, F. (2008). Frugivorie mitteleuropäischer Vögel I: Nahrung und Nahrungserwerb. <i>Vogelwarte</i> , 46, 1-23.
Stiebel 2008 Winter	Germany	Palearctic		
Stiebel 2008 Summer	Germany	Palearctic		
Stiebel 2008 Autumn	Germany	Palearctic		
Sun 1997	Rwanda	Afrotropical	Sun 1997	Sun, C., & Moermond, T. C. (1997). Foraging ecology of three sympatric turacos in a montane forest in Rwanda. <i>The Auk</i> , 396-404.
Toledo 2018	Brazil	Neotropical	Toledo 2018	Toledo, C. D. (2018). Frugivoria e dispersão de sementes por aves em uma área urbanizada. Thesis. Universidade Estadual Paulista "Júlio de Mesquita Filho", Brazil.
Traveset 1992	Baleares	Palearctic	Traveset 1992	Traveset, A. (1992). Resultats preliminars sobre el consum de fruits per ocells a l'illa de Cabrera (Illes Balears). <i>Anuari Ornitològic de les Balears: revista d'observació estudi i conservació dels aucells</i> , (7), 3-10.
Velazquez 2010	Colombia	Neotropical	Velazquez 2010	Moreno Velázquez, J. S. (2010). Aves dispersoras de semillas en un remanente de bosque seco tropical en la finca Betanci-Gucamayas (Córdoba). Thesis. Pontificia Universidad Javeriana, Colombia.
Villate Suarez 2017	Colombia	Neotropical	Villate Suarez 2017	Villate Suárez, C. A. (2017). Las perchas para aves como estrategia de restauración ecológica, su influencia sobre la dispersión de semillas y reclutamiento de plántulas en la microcuenca del río La Vega, Tunja-Boyacá.
Vizentin-Bugoni 2019 EKA	Hawaii	Hawaiian Islands	Vizentin-Bugoni 2019	Vizentin-Bugoni, J., Tarwater, C. E., Foster, J. T., Drake, D. R., Gleditsch, J. M., Hruska, A. M., ... & Sperry, J. H. (2019). Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai_i. <i>Science</i> , 364(6435), 78-82.
Vizentin-Bugoni 2019 KAH	Hawaii	Hawaiian Islands		
Vizentin-Bugoni 2019 MOA	Hawaii	Hawaiian Islands		

Vizentin-Bugoni 2019 MTK	Hawaii	Hawaiian Islands		
Vizentin-Bugoni 2019 PAH	Hawaii	Hawaiian Islands		
Vizentin-Bugoni 2019 TAN	Hawaii	Hawaiian Islands		
Vizentin-Bugoni 2019 WAI	Hawaii	Hawaiian Islands		
Walther 2018	Taiwan	Oriental	Walther 2018	Walther, B. A., Geier, J., Chou, L. S., & Bain, A. (2018). The figs of winter: Seasonal importance of fruiting fig trees (<i>Ficus: Moraceae</i>) for urban birds. <i>Acta Oecologica</i> , 90, 28-34.
Williams 1996 Eves	New Zealand	Novozelandic	Williams 1996	Williams, P. A., & Karl, B. J. (1996). Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. <i>New Zealand Journal of Ecology</i> , 127-145.
Williams 1996 Marsden	New Zealand	Novozelandic		
Williams 1996 Faulkners	New Zealand	Novozelandic		
Wilms 2006	Costa Rica	Panamanian	Wilms 2006	Wilms, J. J. A. M., & Kappelle, M. (2006). Frugivorous birds, habitat preference and seed dispersal in a fragmented Costa Rican montane oak forest landscape. In <i>Ecology and conservation of neotropical montane oak forests</i> (pp. 309-324). Springer, Berlin, Heidelberg.
Wolfe 2014	Costa Rica	Panamanian	Wolfe 2014	Wolfe, J. D., Johnson, M. D., & Ralph, C. J. (2014). Do birds select habitat or food resources? Nearctic-Neotropic migrants in northeastern Costa Rica. <i>PloS one</i> , 9(1), e86221.
Young 2012	New Zealand	Novozelandic	Young 2012	Young, L. M. (2012). Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. Thesis. University of Canterbury, New Zealand.

Table S2. Effects of body mass and beak width on species-level network metrics using weighted data. Results from generalized linear mixed models showing the effects of log-transformed body mass and beak width on degree, interaction strength, closeness centrality, and specialization (d'). Models were run on weighted networks without converting them to unweighted. Estimates (\pm SE), z -values, and p -values are shown for each model.

Body mass and beak width effects on species level metrics

	Body mass			Beak Width		
	Estimate \pm SE	z value	p value	Estimate \pm SE	z value	p value
Degree	-0.000 \pm 0.024	-0.011	0.991	-0.112 \pm 0.024	-4.693	<0.001
Interaction strength	0.257 \pm 0.071	3.95	<0.001	-0.025 \pm 0.019	-0.221	0.328
Closeness	-0.001 \pm 0.000	-2.606	0.009	-0.001 \pm 0.000	-2.913	0.004
Specialization	0.025 \pm 0.005	4.850	<0.001	0.026 \pm 0.006	4.432	<0.001

Table S3. Percentage of networks affected by species removal scenarios. Proportion of networks impacted under each removal scenario based on species traits (high mass, low mass, wide beak, narrow beak, and random) and at three removal levels (10%, 20%, and 30%).

Scenario	Percentage of affected networks in each scenario		
	10% species removal	20% species removal	30% species removal
High mass	90%	92%	98%
Low mass	93%	97%	98%
Wide beak	89%	93%	94%
Narrow beak	96%	98%	97%
Random	100%	100%	100%

Table S4. Results of PGLS models examining the relationship between d' (specialization) and two morphological traits: body mass and beak width. For each trait, we fitted two models; a simple model and a second model including the degree of frugivory as a covariate. PGLS Models were implemented using the “ML” method.

	estimate	Std.	<i>t</i>	<i>p</i>	<i>Lambda</i>
<i>Body mass</i>	0.105	0.037	2.812	0.005	0.673 [CI:0.55-0.76]
<i>Body mass</i>	0.096	0.038	2.518	0.011	0.680 [CI:0.56-0.77]
<i>Frugivory</i>	0.001	0.000	1.347	0.178	
<i>Beak width</i>	0.253	0.079	3.189	0.001	0.676 [CI: 0.56-0.77]
<i>Beak width</i>	0.240	0.080	2.998	0.003	0.684 [CI:0.57-0.77]
<i>Frugivory</i>	0.001	0.000	1.484	0.138	

Table S5. Top 10% highest mass species across networks. List of species comprising the top 10% highest body mass within the networks, including their scientific names, genus, and family.

Family	Genus	Species	Family	Genus	Species
Anatidae	<i>Branta</i>	<i>Branta canadensis</i>	Corvidae	<i>Urocissa</i>	<i>Urocissa caerulea</i>
Ardeidae	<i>Bubulcus</i>	<i>Bubulcus ibis</i>	Cotingidae	<i>Cephalopterus</i>	<i>Cephalopterus ornatus</i>
Bucerotidae	<i>Aceros</i>	<i>Aceros corrugatus</i>	Cotingidae	<i>Pyroderus</i>	<i>Pyroderus scutatus</i>
Bucerotidae	<i>Anorrhinus</i>	<i>Anorrhinus austeni</i>	Cotingidae	<i>Rupicola</i>	<i>Rupicola peruvianus</i>
Bucerotidae	<i>Anorrhinus</i>	<i>Anorrhinus galeritus</i>	Cracidae	<i>Aburria</i>	<i>Aburria jacutinga</i>
Bucerotidae	<i>Anthracoceros</i>	<i>Anthracoceros albirostris</i>	Cracidae	<i>Chamaepetes</i>	<i>Chamaepetes goudotii</i>
Bucerotidae	<i>Anthracoceros</i>	<i>Anthracoceros coronatus</i>	Cracidae	<i>Chamaepetes</i>	<i>Chamaepetes unicolor</i>
Bucerotidae	<i>Anthracoceros</i>	<i>Anthracoceros malayanus</i>	Cracidae	<i>Crax</i>	<i>Crax alector</i>
Bucerotidae	<i>Buceros</i>	<i>Buceros bicornis</i>	Cracidae	<i>Ortalis</i>	<i>Ortalis cinereiceps</i>
Bucerotidae	<i>Buceros</i>	<i>Buceros rhinoceros</i>	Cracidae	<i>Ortalis</i>	<i>Ortalis guttata</i>
Bucerotidae	<i>Bycanistes</i>	<i>Bycanistes bucinator</i>	Cracidae	<i>Ortalis</i>	<i>Ortalis vetula</i>
Bucerotidae	<i>Rhinoplax</i>	<i>Rhinoplax vigil</i>	Cracidae	<i>Penelope</i>	<i>Penelope barbata</i>
Bucerotidae	<i>Rhyticeros</i>	<i>Rhyticeros plicatus</i>	Cracidae	<i>Penelope</i>	<i>Penelope marail</i>
Bucerotidae	<i>Rhyticeros</i>	<i>Rhyticeros undulatus</i>	Cracidae	<i>Penelope</i>	<i>Penelope montagnii</i>
Cacatuidae	<i>Cacatua</i>	<i>Cacatua galerita</i>	Cracidae	<i>Penelope</i>	<i>Penelope obscura</i>
Columbidae	<i>Columba</i>	<i>Columba arquatrix</i>	Cracidae	<i>Penelope</i>	<i>Penelope purpurascens</i>
Columbidae	<i>Columba</i>	<i>Columba guinea</i>	Cracidae	<i>Penelope</i>	<i>Penelope superciliaris</i>
Columbidae	<i>Columba</i>	<i>Columba leucomela</i>	Falconidae	<i>Falco</i>	<i>Falco novaeseelandiae</i>
Columbidae	<i>Columba</i>	<i>Columba oenas</i>	Icteridae	<i>Psarocolius</i>	<i>Psarocolius angustifrons</i>
Columbidae	<i>Columba</i>	<i>Columba palumbus</i>	Icteridae	<i>Psarocolius</i>	<i>Psarocolius montezuma</i>
Columbidae	<i>Columba</i>	<i>Columba pulchricollis</i>	Musophagidae	<i>Corythaeola</i>	<i>Corythaeola cristata</i>
Columbidae	<i>Ducula</i>	<i>Ducula aenea</i>	Musophagidae	<i>Crinifer</i>	<i>Crinifer piscator</i>
Columbidae	<i>Ducula</i>	<i>Ducula badia</i>	Musophagidae	<i>Musophaga</i>	<i>Musophaga violacea</i>
Columbidae	<i>Ducula</i>	<i>Ducula bicolor</i>	Musophagidae	<i>Ruwenzorornis</i>	<i>Ruwenzorornis johnstoni</i>
Columbidae	<i>Ducula</i>	<i>Ducula rufigaster</i>	Musophagidae	<i>Tauraco</i>	<i>Tauraco corythaix</i>
Columbidae	<i>Ducula</i>	<i>Ducula zoeae</i>	Musophagidae	<i>Tauraco</i>	<i>Tauraco porphyreolophus</i>

Columbidae	<i>Geotrygon</i>	<i>Geotrygon frenata</i>	Musophagidae	<i>Tauraco</i>	<i>Tauraco schuetii</i>
Columbidae	<i>Gymnophaps</i>	<i>Gymnophaps albertisii</i>	Phasianidae	<i>Bambusicola</i>	<i>Bambusicola thoracicus</i>
Columbidae	<i>Hemiphaga</i>	<i>Hemiphaga novaeseelandiae</i>	Phasianidae	<i>Lophura</i>	<i>Lophura ignita</i>
Columbidae	<i>Lopholaimus</i>	<i>Lopholaimus antarcticus</i>	Phasianidae	<i>Lophura</i>	<i>Lophura swinhonis</i>
Columbidae	<i>Macropygia</i>	<i>Macropygia amboinensis</i>	Picidae	<i>Dryocopus</i>	<i>Dryocopus pileatus</i>
Columbidae	<i>Macropygia</i>	<i>Macropygia phasianella</i>	Psittacidae	<i>Amazona</i>	<i>Amazona aestiva</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas araucana</i>	Psittacidae	<i>Amazona</i>	<i>Amazona autumnalis</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas fasciata</i>	Psittacidae	<i>Amazona</i>	<i>Amazona guatemalae</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas flavirostris</i>	Psittacidae	<i>Amazona</i>	<i>Amazona mercenaria</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas picazuro</i>	Psittacidae	<i>Ara</i>	<i>Ara chloropterus</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas speciosa</i>	Psittacidae	<i>Nestor</i>	<i>Nestor meridionalis</i>
Columbidae	<i>Patagioenas</i>	<i>Patagioenas squamosa</i>	Psittacidae	<i>Nestor</i>	<i>Nestor notabilis</i>
Columbidae	<i>Reinwardtoena</i>	<i>Reinwardtoena reinwardtii</i>	Psittacidae	<i>Orthopsittaca</i>	<i>Orthopsittaca manilata</i>
Columbidae	<i>Treron</i>	<i>Treron capellei</i>	Psittacidae	<i>Pionus</i>	<i>Pionus maximiliani</i>
Columbidae	<i>Treron</i>	<i>Treron phoenicopterus</i>	Psittacidae	<i>Pionus</i>	<i>Pionus tumultuosus</i>
Columbidae	<i>Treron</i>	<i>Treron pompadoura</i>	Psophiidae	<i>Psophia</i>	<i>Psophia crepitans</i>
Columbidae	<i>Treron</i>	<i>Treron sieboldii</i>	Rallidae	<i>Gallinula</i>	<i>Gallinula chloropus</i>
Columbidae	<i>Treron</i>	<i>Treron waalia</i>	Ramphastidae	<i>Andigena</i>	<i>Andigena hypoglauca</i>
Corvidae	<i>Corvus</i>	<i>Corvus corax</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus aracari</i>
Corvidae	<i>Corvus</i>	<i>Corvus corone</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus frantzii</i>
Corvidae	<i>Corvus</i>	<i>Corvus culminatus</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos dicolorus</i>
Corvidae	<i>Corvus</i>	<i>Corvus enca</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos sulfuratus</i>
Corvidae	<i>Corvus</i>	<i>Corvus kubaryi</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos swainsonii</i>
Corvidae	<i>Corvus</i>	<i>Corvus levaillantii</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos toco</i>
Corvidae	<i>Corvus</i>	<i>Corvus macrorhynchos</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos vitellinus</i>
Corvidae	<i>Corvus</i>	<i>Corvus splendens</i>	Tinamidae	<i>Tinamus</i>	<i>Tinamus major</i>
Corvidae	<i>Cyanocorax</i>	<i>Cyanocorax caeruleus</i>			

Table S6. Top 10% smaller species across networks. List of species comprising the top 10% lowest body mass within the networks, including their scientific names, genus, and family.

Family	Genus	Species	Family	Genus	Species
Acanthisittidae	<i>Acanthisitta</i>	<i>Acanthisitta chloris</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus trochilus</i>
Acanthizidae	<i>Gerygone</i>	<i>Gerygone igata</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus xanthoschistos</i>
Aegithalidae	<i>Aegithalos</i>	<i>Aegithalos caudatus</i>	Pipridae	<i>Lepidothrix</i>	<i>Lepidothrix coeruleocapilla</i>
Aegithalidae	<i>Aegithalos</i>	<i>Aegithalos concinnus</i>	Pipridae	<i>Lepidothrix</i>	<i>Lepidothrix coronata</i>
Certhiidae	<i>Polioptila</i>	<i>Polioptila caerulea</i>	Pipridae	<i>Lepidothrix</i>	<i>Lepidothrix iris</i>
Certhiidae	<i>Troglodytes</i>	<i>Troglodytes aedon</i>	Pipridae	<i>Lepidothrix</i>	<i>Lepidothrix isidorei</i>
Certhiidae	<i>Troglodytes</i>	<i>Troglodytes troglodytes</i>	Pipridae	<i>Machaeropterus</i>	<i>Machaeropterus regulus</i>
Cisticolidae	<i>Camaroptera</i>	<i>Camaroptera brachyura</i>	Platysteiridae	<i>Batis</i>	<i>Batis senegalensis</i>
Cisticolidae	<i>Prinia</i>	<i>Prinia subflava</i>	Rhipiduridae	<i>Rhipidura</i>	<i>Rhipidura fuliginosa</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum agile</i>	Sylviidae	<i>Eremomela</i>	<i>Eremomela pusilla</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum chrysorrheum</i>	Sylviidae	<i>Hippolais</i>	<i>Hippolais polyglotta</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum concolor</i>	Sylviidae	<i>Regulus</i>	<i>Regulus calendula</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum cruentatum</i>	Sylviidae	<i>Regulus</i>	<i>Regulus ignicapilla</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum erythrorhynchos</i>	Sylviidae	<i>Regulus</i>	<i>Regulus regulus</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum ignipectus</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia cantillans</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum trigonostigma</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia conspicillata</i>
Dicaeidae	<i>Prionochilus</i>	<i>Prionochilus maculatus</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia undata</i>
Dicaeidae	<i>Prionochilus</i>	<i>Prionochilus percussus</i>	Sylviidae	<i>Sylvietta</i>	<i>Sylvietta brachyura</i>
Estrildidae	<i>Estrilda</i>	<i>Estrilda astrild</i>	Thamnophilidae	<i>Formicivora</i>	<i>Formicivora rufa</i>
Fringillidae	<i>Euphonia</i>	<i>Euphonia affinis</i>	Thraupidae	<i>Certhidea</i>	<i>Certhidea fusca</i>
Fringillidae	<i>Euphonia</i>	<i>Euphonia chlorotica</i>	Thraupidae	<i>Certhidea</i>	<i>Certhidea olivacea</i>
Fringillidae	<i>Euphonia</i>	<i>Euphonia fulvicrissa</i>	Thraupidae	<i>Coereba</i>	<i>Coereba flaveola</i>
Fringillidae	<i>Spinus</i>	<i>Spinus psaltria</i>	Thraupidae	<i>Conirostrum</i>	<i>Conirostrum speciosum</i>
Lybiidae	<i>Pogoniulus</i>	<i>Pogoniulus chrysoconus</i>	Thraupidae	<i>Dacnis</i>	<i>Dacnis lineata</i>

Lybiidae	<i>Pogoniulus</i>	<i>Pogoniulus pusillus</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa albilateralis</i>
Muscicapidae	<i>Ficedula</i>	<i>Ficedula parva</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa sitoides</i>
Nectariniidae	<i>Aethopyga</i>	<i>Aethopyga siparaja</i>	Thraupidae	<i>Hemithraupis</i>	<i>Hemithraupis ruficapilla</i>
Nectariniidae	<i>Cinnyris</i>	<i>Cinnyris asiaticus</i>	Thraupidae	<i>Sporophila</i>	<i>Sporophila caerulescens</i>
Nectariniidae	<i>Cinnyris</i>	<i>Cinnyris chalybeus</i>	Thraupidae	<i>Sporophila</i>	<i>Sporophila corvina</i>
Nectariniidae	<i>Cinnyris</i>	<i>Cinnyris venustus</i>	Thraupidae	<i>Sporophila</i>	<i>Sporophila nigricollis</i>
Nectariniidae	<i>Cyanomitra</i>	<i>Cyanomitra olivacea</i>	Thraupidae	<i>Thlypopsis</i>	<i>Thlypopsis ruficeps</i>
Nectariniidae	<i>Hedydipna</i>	<i>Hedydipna collaris</i>	Thraupidae	<i>Tiaris</i>	<i>Tiaris bicolor</i>
Nectariniidae	<i>Leptocoma</i>	<i>Leptocoma zeylonica</i>	Thraupidae	<i>Tiaris</i>	<i>Tiaris olivaceus</i>

Table S7. Top 10% widest-beaked species across networks. List of species comprising the top 10% with the widest beak widths within the networks, including their scientific names, genus, and family.

Family	Genus	Species	Family	Genus	Species
Anatidae	Branta	<i>Branta canadensis</i>	Phasianidae	Lophura	<i>Lophura ignita</i>
Artamidae	Cracticus	<i>Cracticus cassicus</i>	Picidae	Dryocopus	<i>Dryocopus pileatus</i>
Bucerotidae	Aceros	<i>Aceros corrugatus</i>	Picidae	Picus	<i>Picus viridis</i>
Bucerotidae	Anorrhinus	<i>Anorrhinus austeni</i>	Psittacidae	Amazona	<i>Amazona aestiva</i>
Bucerotidae	Anorrhinus	<i>Anorrhinus galeritus</i>	Psittacidae	Amazona	<i>Amazona albifrons</i>
Bucerotidae	Anthracoceros	<i>Anthracoceros albirostris</i>	Psittacidae	Amazona	<i>Amazona autumnalis</i>
Bucerotidae	Anthracoceros	<i>Anthracoceros coronatus</i>	Psittacidae	Amazona	<i>Amazona guatemalae</i>
Bucerotidae	Anthracoceros	<i>Anthracoceros malayanus</i>	Psittacidae	Amazona	<i>Amazona mercenaria</i>
Bucerotidae	Buceros	<i>Buceros bicornis</i>	Psittacidae	Ara	<i>Ara chloropterus</i>
Bucerotidae	Buceros	<i>Buceros rhinoceros</i>	Psittacidae	Aratinga	<i>Aratinga aurea</i>
Bucerotidae	Bycanistes	<i>Bycanistes bucinator</i>	Psittacidae	Aratinga	<i>Aratinga leucophthalma</i>
Bucerotidae	Rhinoplax	<i>Rhinoplax vigil</i>	Psittacidae	Aratinga	<i>Aratinga nana</i>
Bucerotidae	Rhyticeros	<i>Rhyticeros plicatus</i>	Psittacidae	Aratinga	<i>Aratinga wagleri</i>
Bucerotidae	Rhyticeros	<i>Rhyticeros undulatus</i>	Psittacidae	Diopsittaca	<i>Diopsittaca nobilis</i>
Bucerotidae	Tockus	<i>Tockus alboterminatus</i>	Psittacidae	Eupsittula	<i>Eupsittula nana</i>
Bucerotidae	Tockus	<i>Tockus erythrorhynchus</i>	Psittacidae	Myiopsitta	<i>Myiopsitta monachus</i>
Bucerotidae	Tockus	<i>Tockus nasutus</i>	Psittacidae	Nestor	<i>Nestor meridionalis</i>
Cacatuidae	Cacatua	<i>Cacatua galerita</i>	Psittacidae	Nestor	<i>Nestor notabilis</i>
Campephagidae	Coracina	<i>Coracina striata</i>	Psittacidae	Orthopsittaca	<i>Orthopsittaca manilata</i>
Corvidae	Corvus	<i>Corvus corax</i>	Psittacidae	Pionus	<i>Pionus maximiliani</i>
Corvidae	Corvus	<i>Corvus corone</i>	Psittacidae	Pionus	<i>Pionus senilis</i>
Corvidae	Corvus	<i>Corvus culminatus</i>	Psittacidae	Pionus	<i>Pionus tumultuosus</i>
Corvidae	Corvus	<i>Corvus enca</i>	Psittacidae	Psittacula	<i>Psittacula cyanocephala</i>
Corvidae	Corvus	<i>Corvus kubaryi</i>	Psittacidae	Psittacula	<i>Psittacula himalayana</i>
Corvidae	Corvus	<i>Corvus levaillantii</i>	Psittacidae	Psittacula	<i>Psittacula krameri</i>

Corvidae	Corvus	<i>Corvus macrorhynchos</i>	Psittacidae	<i>Pyrrhura</i>	<i>Pyrrhura albipectus</i>
Corvidae	Corvus	<i>Corvus splendens</i>	Psittacidae	<i>Pyrrhura</i>	<i>Pyrrhura frontalis</i>
Corvidae	Cyanocorax	<i>Cyanocorax caeruleus</i>	Psittacidae	<i>Pyrrhura</i>	<i>Pyrrhura hoffmanni</i>
Corvidae	Cyanocorax	<i>Cyanocorax cristatellus</i>	Ramphastidae	<i>Andigena</i>	<i>Andigena hypoglauca</i>
Corvidae	Cyanocorax	<i>Cyanocorax cyanomelas</i>	Ramphastidae	<i>Aulacorhynchus</i>	<i>Aulacorhynchus coeruleicinctis</i>
Corvidae	Cyanocorax	<i>Cyanocorax yucatanicus</i>	Ramphastidae	<i>Aulacorhynchus</i>	<i>Aulacorhynchus derbianus</i>
Corvidae	Dendrocitta	<i>Dendrocitta formosae</i>	Ramphastidae	<i>Aulacorhynchus</i>	<i>Aulacorhynchus haematopygus</i>
Corvidae	Pica	<i>Pica pica</i>	Ramphastidae	<i>Aulacorhynchus</i>	<i>Aulacorhynchus prasinus</i>
Corvidae	Platysmurus	<i>Platysmurus leucopterus</i>	Ramphastidae	<i>Baillonius</i>	<i>Baillonius bailloni</i>
Corvidae	Psilorhinus	<i>Psilorhinus morio</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus aracari</i>
Corvidae	Urocissa	<i>Urocissa caerulea</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus bailloni</i>
Corvidae	Urocissa	<i>Urocissa erythrorhyncha</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus frantzii</i>
Cotingidae	Cephalopterus	<i>Cephalopterus ornatus</i>	Ramphastidae	<i>Pteroglossus</i>	<i>Pteroglossus torquatus</i>
Cotingidae	Pyroderus	<i>Pyroderus scutatus</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos dicolorus</i>
Cotingidae	Querula	<i>Querula purpurata</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos sulfuratus</i>
Cracidae	Crax	<i>Crax alector</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos swainsonii</i>
Crotophagidae	Crotophaga	<i>Crotophaga major</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos toco</i>
Fringillidae	Coccothraustes	<i>Coccothraustes coccothraustes</i>	Ramphastidae	<i>Ramphastos</i>	<i>Ramphastos vitellinus</i>
Icteridae	Psarocolius	<i>Psarocolius montezuma</i>	Ramphastidae	<i>Selenidera</i>	<i>Selenidera maculirostris</i>
Icteridae	Psarocolius	<i>Psarocolius wagleri</i>	Thraupidae	<i>Geospiza</i>	<i>Geospiza magnirostris</i>
Lybiidae	Lybius	<i>Lybius dubius</i>	Trogonidae	<i>Harpactes</i>	<i>Harpactes diardi</i>
Megalaimidae	Megalaima	<i>Megalaima chrysopogon</i>	Trogonidae	<i>Pharomachrus</i>	<i>Pharomachrus auriceps</i>
Megalaimidae	Megalaima	<i>Megalaima lineata</i>	Trogonidae	<i>Trogon</i>	<i>Trogon massena</i>
Megalaimidae	Megalaima	<i>Megalaima mystacophanous</i>	Tyrannidae	<i>Megarynchus</i>	<i>Megarynchus pitangua</i>
Megalaimidae	Megalaima	<i>Megalaima virens</i>	Tyrannidae	<i>Tityra</i>	<i>Tityra cayana</i>
Megalaimidae	Megalaima	<i>Megalaima zeylanica</i>	Tyrannidae	<i>Tityra</i>	<i>Tityra inquisitor</i>
Momotidae	Baryphthengus	<i>Baryphthengus martii</i>	Tyrannidae	<i>Tyrannus</i>	<i>Tyrannus dominicensis</i>
Musophagidae	Crinifer	<i>Crinifer piscator</i>			

Table S8. Top 10% narrowest-beaked species across networks. List of species comprising the top 10% with the narrowest beak widths within the networks, including their scientific names, genus, and family.

Family	Genus	Species	Family	Genus	Species
Acanthisittidae	<i>Acanthisitta</i>	<i>Acanthisitta chloris</i>	Parulidae	<i>Setophaga</i>	<i>Setophaga tigrina</i>
Acanthizidae	<i>Gerygone</i>	<i>Gerygone igata</i>	Petroicidae	<i>Petroica</i>	<i>Petroica macrocephala</i>
Acanthizidae	<i>Mohoua</i>	<i>Mohoua albicilla</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus bonelli</i>
Aegithalidae	<i>Aegithalos</i>	<i>Aegithalos caudatus</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus collybita</i>
Aegithalidae	<i>Aegithalos</i>	<i>Aegithalos concinnus</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus coronatus</i>
Certhiidae	<i>Polioptila</i>	<i>Polioptila caerulea</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus trochilus</i>
Certhiidae	<i>Troglodytes</i>	<i>Troglodytes aedon</i>	Phylloscopidae	<i>Phylloscopus</i>	<i>Phylloscopus xanthoschistos</i>
Certhiidae	<i>Troglodytes</i>	<i>Troglodytes solstitialis</i>	Pipridae	<i>Ilicura</i>	<i>Ilicura militaris</i>
Certhiidae	<i>Troglodytes</i>	<i>Troglodytes troglodytes</i>	Pipridae	<i>Lepidothrix</i>	<i>Lepidothrix isidorei</i>
Cisticolidae	<i>Camaroptera</i>	<i>Camaroptera brachyura</i>	Pipridae	<i>Machaeropterus</i>	<i>Machaeropterus regulus</i>
Cisticolidae	<i>Prinia</i>	<i>Prinia crinigera</i>	Rhipiduridae	<i>Rhipidura</i>	<i>Rhipidura fuliginosa</i>
Cisticolidae	<i>Prinia</i>	<i>Prinia subflava</i>	Sylviidae	<i>Cettia</i>	<i>Cettia cetti</i>
Columbidae	<i>Chalcophaps</i>	<i>Chalcophaps indica</i>	Sylviidae	<i>Eremomela</i>	<i>Eremomela pusilla</i>
Columbidae	<i>Columba</i>	<i>Columba larvata</i>	Sylviidae	<i>Regulus</i>	<i>Regulus calendula</i>
Columbidae	<i>Columbina</i>	<i>Columbina talpacoti</i>	Sylviidae	<i>Regulus</i>	<i>Regulus ignicapilla</i>
Columbidae	<i>Geopelia</i>	<i>Geopelia striata</i>	Sylviidae	<i>Regulus</i>	<i>Regulus regulus</i>
Columbidae	<i>Leptotila</i>	<i>Leptotila megalura</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia atricapilla</i>
Columbidae	<i>Macropygia</i>	<i>Macropygia unchall</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia cantillans</i>
Columbidae	<i>Streptopelia</i>	<i>Streptopelia capicola</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia communis</i>
Columbidae	<i>Streptopelia</i>	<i>Streptopelia orientalis</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia conspicillata</i>
Columbidae	<i>Streptopelia</i>	<i>Streptopelia senegalensis</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia curruca</i>
Columbidae	<i>Streptopelia</i>	<i>Streptopelia vinacea</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia melanocephala</i>
Columbidae	<i>Turtur</i>	<i>Turtur abyssinicus</i>	Sylviidae	<i>Sylvia</i>	<i>Sylvia undata</i>
Columbidae	<i>Turtur</i>	<i>Turtur tympanistria</i>	Sylviidae	<i>Sylvietta</i>	<i>Sylvietta brachyura</i>
Columbidae	<i>Zenaida</i>	<i>Zenaida aurita</i>	Thamnophilidae	<i>Formicivora</i>	<i>Formicivora rufa</i>

Columbidae	<i>Zenaida</i>	<i>Zenaida macroura</i>	Thraupidae	<i>Certhidea</i>	<i>Certhidea fusca</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum concolor</i>	Thraupidae	<i>Conirostrum</i>	<i>Conirostrum speciosum</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum cruentatum</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa albilateralis</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum erythrorhynchos</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa brunneiventris</i>
Dicaeidae	<i>Dicaeum</i>	<i>Dicaeum ignipectus</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa caerulescens</i>
Furnariidae	<i>Cinclodes</i>	<i>Cinclodes fuscus</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa cyanea</i>
Furnariidae	<i>Cranioleuca</i>	<i>Cranioleuca pallida</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa glauca</i>
Locustellidae	<i>Bradypterus</i>	<i>Bradypterus barratti</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa mystacalis</i>
Meliphagidae	<i>Anthornis</i>	<i>Anthornis melanura</i>	Thraupidae	<i>Diglossa</i>	<i>Diglossa sitoides</i>
Meliphagidae	<i>Timeliopsis</i>	<i>Timeliopsis fallax</i>	Thraupidae	<i>Thlypopsis</i>	<i>Thlypopsis ruficeps</i>
Mohouidae	<i>Finschia</i>	<i>Finschia novaeseelandiae</i>	Timaliidae	<i>Alcippe</i>	<i>Alcippe brunnea</i>
Muscicapidae	<i>Phoenicurus</i>	<i>Phoenicurus ochruros</i>	Timaliidae	<i>Alcippe</i>	<i>Alcippe morrisonia</i>
Muscicapidae	<i>Phoenicurus</i>	<i>Phoenicurus phoenicurus</i>	Timaliidae	<i>Macronus</i>	<i>Macronus gularis</i>
Nectariniidae	<i>Chalcomitra</i>	<i>Chalcomitra senegalensis</i>	Timaliidae	<i>Stachyridopsis</i>	<i>Stachyridopsis ruficeps</i>
Nectariniidae	<i>Cinnyris</i>	<i>Cinnyris chalybeus</i>	Timaliidae	<i>Yuhina</i>	<i>Yuhina brunneiceps</i>
Nectariniidae	<i>Cinnyris</i>	<i>Cinnyris venustus</i>	Turdidae	<i>Catharus</i>	<i>Catharus gracilirostris</i>
Nectariniidae	<i>Hedydipna</i>	<i>Hedydipna collaris</i>	Turdidae	<i>Erithacus</i>	<i>Erithacus rubecula</i>
Nectariniidae	<i>Leptocoma</i>	<i>Leptocoma zeylonica</i>	Tyrannidae	<i>Anairetes</i>	<i>Anairetes parulus</i>
Paramythiidae	<i>Oreocharis</i>	<i>Oreocharis arfaki</i>	Tyrannidae	<i>Camptostoma</i>	<i>Camptostoma obsoletum</i>
Paridae	<i>Anthoscopus</i>	<i>Anthoscopus parvulus</i>	Tyrannidae	<i>Phyllosmyias</i>	<i>Phyllosmyias sclateri</i>
Paridae	<i>Cyanistes</i>	<i>Cyanistes caeruleus</i>	Tyrannidae	<i>Phyllosmyias</i>	<i>Phyllosmyias uropygialis</i>
Paridae	<i>Lophophanes</i>	<i>Lophophanes cristatus</i>	Tyrannidae	<i>Serpophaga</i>	<i>Serpophaga subcristata</i>
Paridae	<i>Parus</i>	<i>Parus ater</i>	Tyrannidae	<i>Zimmerius</i>	<i>Zimmerius bolivianus</i>
Paridae	<i>Periparus</i>	<i>Periparus ater</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops erythropleurus</i>
Paridae	<i>Poecile</i>	<i>Poecile palustris</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops everetti</i>
Parulidae	<i>Geothlypis</i>	<i>Geothlypis philadelphia</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops japonicus</i>
Parulidae	<i>Leiothlypis</i>	<i>Leiothlypis peregrina</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops lateralis</i>
Parulidae	<i>Mniotilla</i>	<i>Mniotilla varia</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops novaeguineae</i>
Parulidae	<i>Setophaga</i>	<i>Setophaga dominica</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops pallidus</i>
Parulidae	<i>Setophaga</i>	<i>Setophaga occidentalis</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops palpebrosus</i>

Parulidae	<i>Setophaga</i>	<i>Setophaga pinus</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops senegalensis</i>
Parulidae	<i>Setophaga</i>	<i>Setophaga pitiayumi</i>	Zosteropidae	<i>Zosterops</i>	<i>Zosterops silvanus</i>

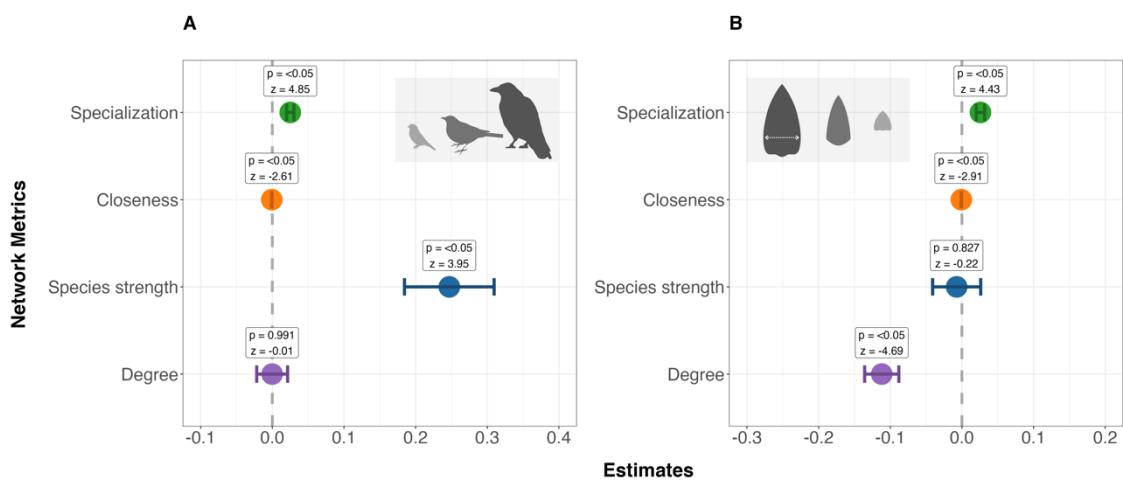


Fig. S1. Effects of body mass and beak width on species-level network roles using both weighted and unweighted networks. Effects of (A) body mass (log) and (B) beak width on species-level metrics. The colored dots represent the estimates of the models (slope), p values, and z values are represented inside squares. The metrics used for the models were calculated using a dataset containing both weighted and unweighted networks in their original form.

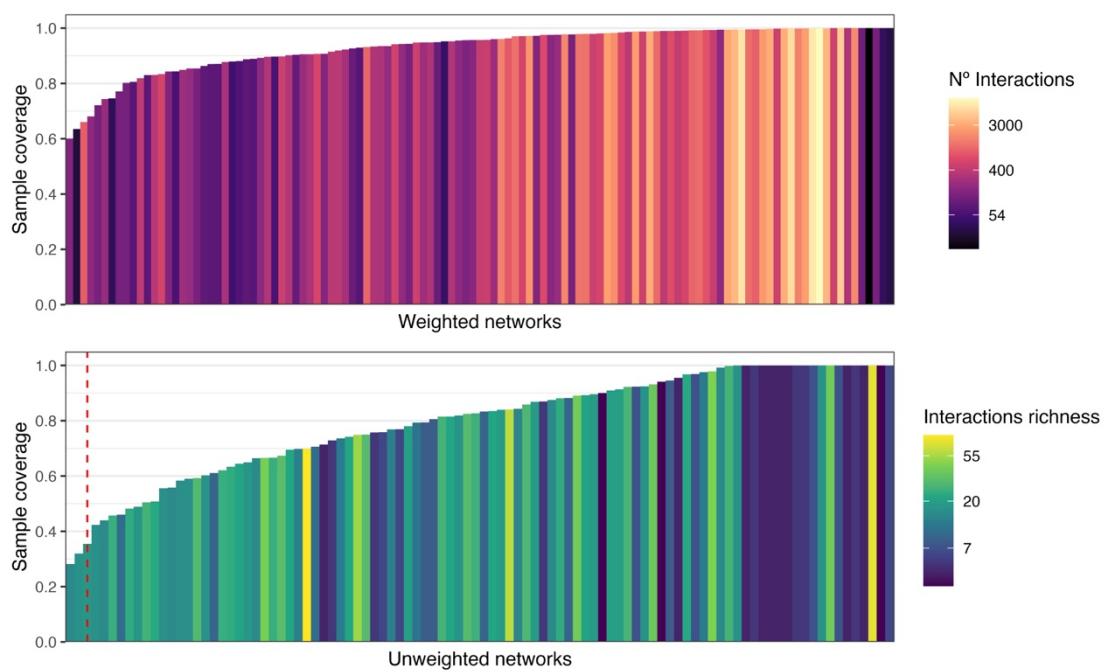


Fig. S2. Interaction network completeness. The completeness of quantitative (top) and qualitative (bottom) interaction networks. Interaction richness is displayed as colours, and the vertical dashed red line shows the threshold for the networks with a relatively low completeness ($< 40\%$, $n = 3$).

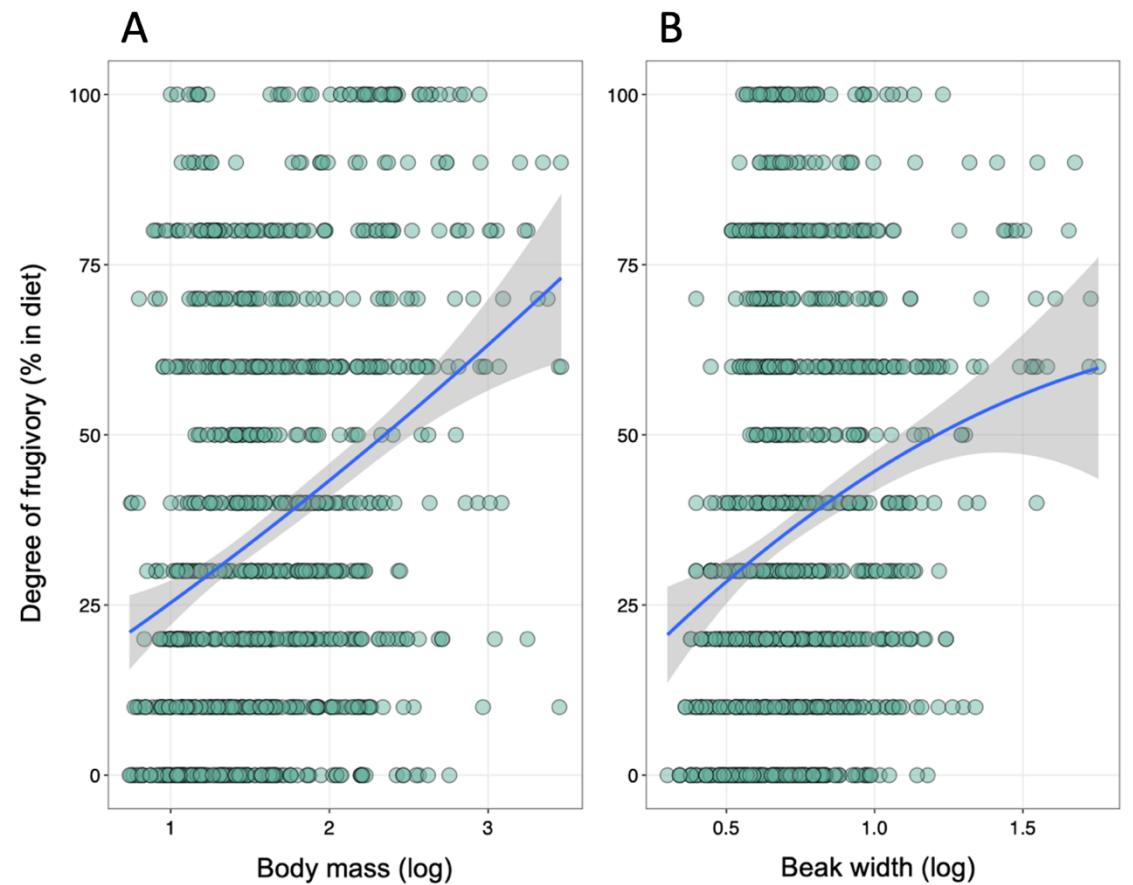


Fig. S3. Relationship between (A) (log-transformed) body mass and (B) beak width, and degree of frugivory for 1,031 bird species. Species' degree of frugivory was obtained from AVONICHE (Sayol et al., 2026). Both relationships were statistically significant ($p < 0.001$) after accounting for phylogenetic effects using PGLS (see main text). The shaded area indicates the 95% CI.

APPENDIX S1

Large-bodied and wide-beaked avian frugivores show greater specialisation in tropical seed dispersal networks

Extended Methods and Results

Sensitivity analysis

Although the interaction networks employed in this study exhibit high completeness, we conducted a sensitivity analysis to assess whether the observed roles and positions in the network of large-bodied, wide-beaked species might be influenced by sampling bias. Specifically, we sought to rule out the possibility that their inferred level of specialization is an artifact of species low abundance and, consequently, fewer recorded interactions. Such species may appear more specialized due to limited sampling rather than reflecting true ecological patterns. For this analysis, we used a subset of 113 quantitative (weighted) networks that included interaction frequencies (see Supplementary Material for further details). Within each network, frugivorous bird species were ranked by body mass and beak width, and two groups were identified: (i) the top 10% in body mass and (ii) the top 10% in beak width. For each species in these groups, we calculated three species-level network metrics (degree, closeness, and specialization, d') using the *specieslevel* function from the ‘bipartite’ R package (Dormann, 2009). To test whether these observed values could result from sampling limitations alone, we implemented a null model that randomized the identity of each species’ interaction partners within each network, while preserving the observed number of interactions per species. This procedure was repeated 1,000 times per species and network, recalculating the same three metrics after each iteration. Finally, we fitted a linear mixed model to compare the observed metric values for the top 10% largest-bodied and widest-beaked species with their distributions under the null model. The models included Network ID and species as random intercepts. This allowed us to assess whether their observed roles and position in the network differed significantly from expectations under random interaction structure, given their observed interaction frequencies.

Differences across bioregions

To assess whether the trait–network role relationships identified in the main analysis are consistent across broad biogeographic contexts, we conducted an additional set of analyses explicitly accounting for bioregional variation.

Our global dataset comprises interaction networks distributed across multiple biogeographic regions, including Afrotropical, Neotropical, Palearctic, Nearctic, Oriental,

Australasian, and several oceanic island systems (Table A2.1). While this fine-grained classification reflects the geographic origin of each network, sample sizes varied substantially among regions, with some island systems being sparsely represented.

To ensure robust inference while retaining meaningful ecological contrasts, we grouped regions into four broad bioregional categories: Tropical, Temperate, Austral, and Oceanic islands. This classification captures major climatic and biogeographic differences while avoiding overparameterization driven by uneven regional sampling. In total, there were 19 networks in the Austral bioregion, 24 in Oceanic Islands, 53 in Temperate bioregions, and 119 in Tropical bioregions. Using this reduced classification, we refitted the same generalized linear mixed models described in the main text, but including an interaction between each focal trait and bioregion. Specifically, we fitted models including either body mass or beak width, their interaction with bioregion, and random effects of network identity. We then generated predicted trait–response relationships for each bioregion, which are presented in Figure A2.1.

Table A2.1. Number of interaction networks per biogeographic region.

Original Bioregion	Number of networks	Final Bioregion
Afrotropical	14	Tropical
Australian	3	Austral
Azores	1	Oceanic Islands
Canary Islands	8	Oceanic Islands
Galapagos	1	Oceanic Islands
Hawaiian Islands	9	Oceanic Islands
Mariana Islands	1	Oceanic Islands
Nearctic	7	Temperate
Neotropical	65	Tropical
Novozelandic	16	Austral
Oceanian	3	Oceanic Islands
Oriental	16	Tropical
Paleartic	46	Temperate
Panamanian	24	Tropical
Society Islands	1	Oceanic Islands

The obtained results (Fig. 3 in the main text) show that the specialisation of larger and wide-beaked species is led by a stronger pattern in tropical frugivory networks.

Degree

For degree, the non-significant relationship with body mass observed in the global model was largely consistent across bioregions. Estimated slopes of body mass did not differ strongly among regions, and none of the regional trends departed markedly from the global pattern.

Although the direction of the effect varied slightly among regions, there was no evidence of a strong signal of the body mass–degree relationship. In contrast, beak width showed a consistently negative association with degree across all four bioregions. All regional slopes significantly negative. This indicates that the global negative relationship between beak width and degree reflects a broadly shared pattern across biogeographic contexts.

Strength

The relationship between body mass and interaction strength showed clear regional heterogeneity. A significant positive effect of body mass was detected only in tropical regions, whereas trends in temperate, austral, and oceanic island regions were weak and not significantly different from zero. This suggests that the positive global relationship between body mass and strength is primarily driven by tropical networks, which also constitute the largest proportion of the dataset.

For beak width, no consistent global pattern was detected. Only temperate regions exhibited a significant (negative) relationship between beak width and strength, while trends in other regions were weak or highly uncertain. This regional specificity is consistent with the absence of a strong overall global effect in the main analysis.

Closeness

For closeness, both body mass and beak width showed significant negative relationships exclusively in tropical regions. In all other bioregions, slopes were not significantly different from zero.

Specialization (d')

Patterns for specialization mirrored those observed for closeness. Both body mass and beak width were positively associated with specialization in tropical regions, whereas no significant trends were detected in temperate, austral, or oceanic island regions. Although austral and oceanic island regions showed trends in similar directions, uncertainty around these estimates was high, reflecting substantially lower sample sizes in these regions.

Our bioregional analyses reveal that while some trait–network role relationships are broadly consistent across regions, others are strongly context dependent. In particular, relationships involving degree appear robust across biogeographic contexts, supporting the interpretation that certain aspects of species generalism are constrained by functional traits worldwide.

In contrast, relationships involving interaction strength, closeness, and specialization are largely driven by tropical networks. This likely reflects both ecological differences among bioregions and the fact that tropical regions are disproportionately represented in the global dataset. Consequently, the global patterns reported in the main text for these metrics should be

interpreted as reflecting dominant trends in tropical systems rather than universally applicable relationships.

Notably, austral and oceanic island regions often showed trends in similar directions to tropical regions but with much greater uncertainty, highlighting the need for caution when generalizing patterns from underrepresented regions.

Overall, these results reinforce our central conclusion that functional traits are important predictors of species roles in interaction networks, while also demonstrating that the generality of trait–role relationships varies among network metrics and biogeographic contexts. Explicitly accounting for regional heterogeneity clarifies which patterns are globally consistent and which emerge primarily from specific ecological settings.

Comments from the handling editor, Dr. Huijie Qiao

Both reviewers commend the manuscript for its well-written content, appropriate analytical approach, and impressive global dataset used to tackle the timely topic of large-bodied frugivores' specialization in seed dispersal networks. However, their main concerns revolve around the interpretation of the global findings.

RESPONSE: Thank you for handling our manuscript and for the positive feedback. We have carefully addressed all comments raised by the reviewers, with particular attention to clarifying the interpretation of the global patterns and the scope of the analyses. In doing so, we implemented several additional analyses and revised the Methods, Results, and Discussion accordingly. To accommodate these changes while maintaining a reasonable manuscript length, we streamlined some sections and moved detailed sensitivity analyses and additional figures to the supplementary material. All modifications are provided with tracked changes to facilitate evaluation. Line numbers correspond to the version with track-changes.

Reviewer 1 highlights that the conclusion regarding large-body specialization might overlook crucial environmental and temporal heterogeneity, questioning whether the findings apply uniformly across vastly different biomes (e.g., tropical vs. temperate) or if seasonal variation in foraging strategies is being masked by aggregating data from different times of the year.

RESPONSE: Thank you for rising this important point. We agree that evaluating whether trait–role relationships are consistent across major biomes can strengthen the interpretation of our results. In the revised manuscript, we have therefore added an additional analysis explicitly assigning networks to four bioregional groupings: Tropical (119 networks), Temperate (53 networks), Austral (19 networks) and Oceanic islands (24 networks). While some patterns are consistent across these bioregions (e.g., wide-beaked species having fewer partners everywhere), others, such as higher specialization index in larger, wide-beaked species, are primarily driven by tropical networks, which comprise over half of the dataset. We have updated the whole manuscript accordingly, including the title, to reflect this focus, added a new figure presenting bioregion-specific results, and expanded the discussion to address differences between tropical and temperate networks. This new analysis provides a more comprehensive, enriched, and nuanced perspective to the topic. We thank you and the reviewer for suggesting this new analysis.

Reviewer 2 raises a major methodological and interpretative concern, suggesting the study overlooks the "degree of frugivory" (a species' dependence on fruits), leading to a discussion that is overly focused on foraging and energetic aspects. The reviewer suggests that the observed high specialization might actually be explained by large, generalist birds having a lower overall dependence on fruits, rather than being a sole consequence of body size or beak width. Therefore, the authors are advised to either incorporate the degree of frugivory into the analysis or provide a dedicated and detailed discussion to address this alternative explanation for the observed global patterns.

RESPONSE: We thank the reviewer for this important suggestion. To address the proposed alternative explanation, we conducted additional complementary analyses integrating information about species frugivory from the recently published AVONICHE dataset (Sayol et al., 2026; <https://doi.org/10.1111/geb.70197>) to quantify the relationship between species traits and the degree of frugivory across the 1,031 species in our study. Contrary to the reviewer's concern, we found a positive relationship between body size (and beak width) and degree of frugivory, indicating that larger species are not less dependent on fruits, rather the contrary (Fig. S3). In addition, we conducted another additional analysis to assess if the relationship between specialization (d') and species traits hold after accounting for the degree of frugivory and phylogenetic relatedness. Finally, we have toned down the discussion of energetic mechanisms, as appropriately suggested by the reviewer, given the absence of fruit nutritional data (please, see the answer to the related comment by the reviewer).

REVIEWER COMMENTS TO AUTHOR

Referee: #1

I commend the authors for their impressive effort in compiling and analyzing this global dataset of 215 frugivory networks. The methodological approach, particularly the use of GLMMs and sensitivity analyses, is appropriate for the questions at hand. Overall, I am satisfied with the manuscript. However, I have some concerns regarding the interpretation of the global data.

RESPONSE: Thank you very much for the time dedicated to review our manuscript, and the constructive comments provided.

1. The study's key strength is its global scale, but it currently overlooks the potential mediation by environmental context. Bird behavior, particularly foraging, is known to be highly plastic. Is it appropriate to assume this finding (large-body specialization) applies uniformly across vastly different biomes, such as tropical vs. temperate zones, or lowland vs. montane ecosystems? The authors should discuss how their global finding compares to previous literature in different contexts. A critical discussion is needed to justify why environmental variables might be considered to have a minor effect, if that is the (implied) case.

RESPONSE: Thank you for this comment. We agree that environmental context may mediate trait–role relationships in frugivory networks. In the revised manuscript, we therefore added a new analysis explicitly accounting for bioregion, which shows that the observed patterns are indeed not universal. While some relationships are consistent across these bioregional categories, others (particularly the association between large body size or wider beaks and higher specialization) are primarily driven by patterns in tropical networks. We now updated the manuscript to show this context-dependency, and compare our findings with previous

studies, avoiding implying global uniformity (see Appendix, Fig 3, Results and dedicated section at the end of the Discussion L469-492).

2. The dataset aggregates studies from diverse sources, which were likely conducted during different seasons. Avian foraging strategies and fruit availability can shift dramatically based on seasonal resource availability (e.g., breeding vs. non-breeding season). The authors need to address whether this potential source of variance might impact their findings. Is the observed pattern consistent across seasons, or could this aggregation be masking important temporal dynamics?

RESPONSE: We agree that seasonal variation in fruit availability and avian foraging behavior can influence the realized interactions within a network. However, our aim was not to characterize seasonal dynamics, but to test whether species functional traits impose consistent constraints on interaction breadth across networks. Each network in our dataset represents a snapshot of interactions under a specific ecological and temporal context. By including network identity as a random effect, our models explicitly account for among-network variation arising from differences in season, sampling period, resource availability, and local conditions. While seasonality may affect the absolute number of interactions observed, it is unlikely to generate consistent trait–role relationships across more than 200 independent networks. If anything, aggregating networks across seasons increases unexplained variance and makes our tests more conservative. The persistence of trait effects despite this heterogeneity suggests that the observed patterns reflect general trait-based constraints rather than season-specific dynamics. In addition, it would be very difficult to track and homogenize seasonality across studies (some bioregions have only two seasons while others have four), and some studies merged data temporally in different ways.

I also have several detailed comments that I hope will help improve the clarity and robustness of the paper:

Introduction:

L103-107: It is noted that the initial hypothesis (that larger birds are more generalist) contrasts with the final results. The Discussion aptly introduces foraging theory to explain this. I suggest the authors briefly introduce this theory in the Introduction as well, perhaps as an alternative hypothesis. This would create better synergy between the sections and immediately engage the reader's curiosity about the competing mechanisms.

RESPONSE: Thank you, we agree, and introduce this as an alternative hypothesis in the revised version of Introduction (L 56-61): “Large-bodied species have higher absolute energy requirements than smaller species, which strongly influences their foraging decisions. Given similar diets and food densities, larger birds must consume greater amounts of food, yet they are often more energetically efficient per unit body mass. As a result, they tend to target larger and/or more energy-rich food items and to exploit environments that maximize the balance

between energetic costs and benefits, as predicted by “optimal foraging theory” (Pyke 1978).”).

L53, L98: The emphasis on the "global scale" is the study's unique selling point. However, I feel this contribution is currently underdeveloped. The main conclusion that large birds are specialists could arguably be (and has been) drawn from local network studies. The true incremental value of a global dataset would be to discover novel patterns that emerge from this scale. It feels like a missed opportunity not to explore this variation. For instance, do the roles of large birds differ significantly across bioregions or habitat types (e.g., shrubs, subtropical forests, arid zones, highlands, wetlands)? This would provide genuinely new insights that local studies cannot.

RESPONSE: Thank you for this suggestion. We did additional analyses including bioregional category as an interacting factor and show now differences across major bioregions, providing a more comprehensive and enriched set of results and discussion (see Appendix, Fig. 3, Results and dedicated paragraph in the Discussion).

L57-62: The text discusses the functional importance of "gape width" but the methods and analysis use "beak width". While these are related, they are not identical. For the sake of non-expert readers, the authors should explicitly state the relationship between these two metrics (e.g., that beak width is used as a reliable proxy for gape width) in the Introduction.

RESPONSE: Thank you, we do this in the new version (L64: “is limited by gape width (for which beak width is often used as a proxy)”).

Methods:

L124-129: The decision to binarize all networks for consistency, thereby losing quantitative information from 113 weighted networks, is a significant trade-off. While the authors state the results are similar (which is reassuring), this point is undermined by a small but crucial inconsistency: The Y-axis order of metrics in Figure 2 and Figure S1 is reversed. These should be made consistent to facilitate comparison.

RESPONSE: Thank you, we have harmonised both figures to facilitate the comparison.

L181-183: I was surprised that the authors did not incorporate phylogenetic controls (e.g., PGLS) in their trait-based analysis, especially since avian phylogenies are widely available. Without controlling for phylogeny, it is impossible to determine whether the observed specialization is truly a function of the trait (body mass) itself, or simply an artifact of phylogenetic inertia (e.g., the fact that hornbills and toucans, which are large, belong to specific clades that are already specialized). This omission is a significant methodological gap and should be addressed or, at minimum, robustly justified.

RESPONSE: We agree that phylogenetic relatedness can structure trait variation among species. Because our study is not aimed at disentangling evolutionary components of trait

variation, but at identifying functional drivers of network roles we did not include an explicit phylogenetic covariance structure in the previous version (i.e., we aimed to show that larger species have specific network roles and their extinction can have major impacts on network structure, regardless whether this trait-role relationship has a stronger ecological or evolutionary origin). However, for completeness we ran extra analyses controlling for phylogenetic relatedness following the Reviewer's recommendation. In this new version of the manuscript, we include PGLS analyses in which we show that: i) the relationship between interaction specialization and morphological traits remains highly significant even after controlling for phylogenetic effects; and ii) large-bodied species show a higher dependence on fruits than the smallest ones. A new table and a new figure showing these results have been added to the Supplementary Material (Table S4 and Figure S3) and discussed in the main text.

Results:

L257: For statistical notation, the "estimate = 0.090" is a regression slope (a coefficient) and would be more conventionally represented by its statistical symbol, beta.

RESPONSE: We agree, and name it with the symbol beta in the new version.

L257-266: The narrative order in which Specialization, Closeness, Interaction Strength, and Degree are presented in the text does not match the visual order in Figure 2 (though it does match Fig S1). All figures and text should be harmonized for consistency.

RESPONSE: We have harmonized the order in Figure 2 for consistency.

L276: The text claims a "normal distribution" for body mass and beak width, but no formal test (e.g., Shapiro test).

RESPONSE: Initially, we visually inspected the distributions of body mass and beak width and described them as roughly normal. However, following this feedback, we formally tested normality using Shapiro-Wilk tests, which confirmed that these trait distributions are not strictly normal. Importantly, this does not affect our methodological approach, as we focus on removing species from the extremes of the distributions (e.g., the smallest or largest 10–30%), regardless of the precise distributional shape. To clarify, we have revised the text (L303–L304) to avoid stating that the traits are normally distributed and instead now read: "Trait-based removal scenarios targeted species occupying the lower and upper extremes of the body mass and beak width distributions (Fig. 4)."

L292-296: This section is redundant. The sentences in L292-294 and L295-296 ("...increased the average number of links..." and "...had a positive impact on link per species...") are nearly identical. This should be condensed into a clear statement.

RESPONSE: Thank you, we refined the section to avoid redundancy.

Discussion:

The Discussion section is well-argued but dense. I strongly recommend breaking it into distinct sections with subheadings to improve readability and structure.

RESPONSE: Thank you, we agree. We have split the Discussion into sections with subheadings. We have also simplified and reduced some parts to make it more concise and compensate for the new additions.

Figures:

Figure 2: This figure needs improvement.

- (a) It lacks clear X ('Estimate'?) and Y ('Network Metric'?) axis titles.
- (b) Panel titles ('Body Mass', 'Beak Width') should be added directly above panels A and B; the icons below are not sufficiently clear.
- (c) The X-axis range is stretched, which makes the error bars appear small and difficult to read, especially for effects near zero (like 'Closeness'). The axis should be compressed (as in Fig S1, or even more so) to make the error bars and their overlap with zero more legible.
- (d) The 'A' and 'B' labels are too small.

RESPONSE: Thank you, we implemented all these improvements in the Figure 2.

Figure 3: The font size for labels and legends is too small to be easily read.

RESPONSE: We increased the font size for labels and legends.

Figure 4:

- (a) The panels should be labeled 'A', 'B', 'C' for easy reference.
- (b) The X-axis title is repeated three times; one larger, centered title is sufficient.
- (c) The legend on the right side cramps the horizontal space of the plots. I suggest moving the legend to the top or bottom of the figure array.

RESPONSE: Thank you, we implemented these three suggested modifications to the Figure 4 (Figure 5 in the new version).

Reviewer 2 Comments to the Author

I have reviewed with interest the Ms “Large-bodied and wide-beaked avian frugivores show greater specialization in global seed dispersal networks” submitted to Global Ecology and Biogeography. The Ms tackles a timely topic: the role of large-bodied frugivores in seed dispersal networks globally. It is well written, and the analytical approach seems appropriate.

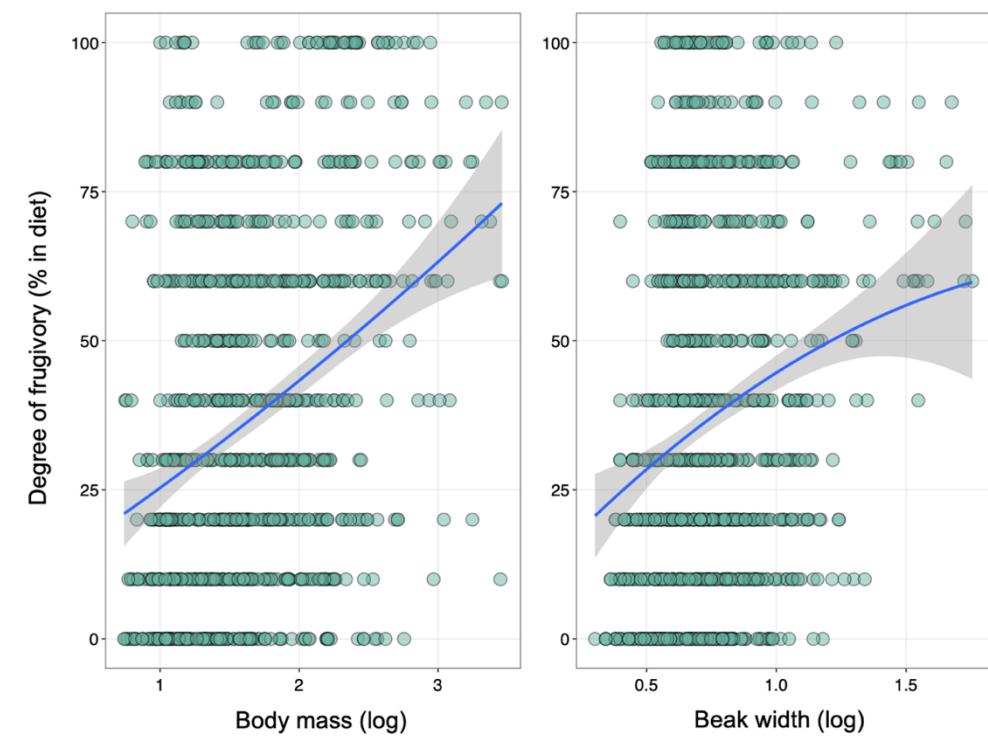
RESPONSE: Thank you very much for your revision and the positive feedback provided. We addressed all the points raised.

I have only a few points to raise.

My main general comment is that degree of frugivory is overlooked in this study and, accordingly, all the interpretations in the Discussion are too biased towards foraging and energetic aspects. The authors use species as example in a sentence (“...e.g., toucans, hornbills, wood pigeons, curassows, and crows) engage in fewer interactions than expected by chance...”) and the reader can realize how much these large-sized species differ in their dependence on fleshy fruits. I thus suggest taking degree of frugivory into account in the study, either explicitly in the analysis or in the Discussion, as an explanation for the observed patterns.

For instance, a recent study (<https://doi.org/10.1073/pnas.2302440120>) found that seed dispersal networks across Europe are more specialized in open matrix habitats, where seed dispersers (mostly birds) are larger-bodied species than in the forest, but such specialization seems to arise from a lower dependence on fruits by generalist birds such as wood pigeons and starlings, leading to strong interactions but with fewer species. I wonder to what extent this may be happening in this study.

RESPONSE: Thank you for raising this interesting point. We agree that the degree of frugivory was overlooked, and we pay more attention to this aspect in the new version, as suggested. In this new version, we examined the relationship between degree of frugivory (according to AVONICHE; Sayol et al., 2026) and body size (data from AVONET; Tobias et al., 2022). Unlike in the temperate zone, in the Neotropics and Australasia, large species (chachalacas, hornbills, fruit-eating pigeons and doves, guans, etc.) are highly dependent on fruits and can be considered frugivorous species. In the Palearctic region, the level of frugivory is low (Kissling et al., 2009), and most species that exploit fruits do it occasionally or seasonally (thus, they are considered facultative frugivorous or generalists/omnivorous). Consequently, results found in temperate areas are not extrapolated to other regions, as revealed when discerning among bioregions (please see the new Results section and Fig. 5). This point is also discussed in the revised version of the manuscript (see L205-214 in Methods, L345-349 in Results and Fig. S3 in supplementary material). Furthermore, we have incorporated a new analysis in which we examined the relationship between specialization and morphological traits, including the level of frugivory as a covariate in our PGLS models. (L295-296 in Results).



I'd also suggest testing effects on the complementary specialization index ($H2'$), which is the network-level metric that would be closest linked to the species level specialization (d').

RESPONSE: Thank you for this suggestion. We agree that, conceptually, it may seem natural to ask whether species-level specialization (d') scales up to affect network-level specialization ($H2'$). However, in our study, species traits are already shown to predict species-level specialization (d'), and trait-biased extinctions therefore implicitly target more or less specialized species. Under this design, any change in $H2'$ would be a direct and expected consequence of the extinction rule itself, rather than an additional network-level pattern requiring separate evaluation. Our extinction analyses are instead aimed at testing whether this trait-biased species removal leaves a consistent signature on other network properties that are not mathematically defined as direct aggregates of the species-level metrics underlying extinction risk. For these reasons, we decided not to extend the analyses to $H2'$ in the revised version.

SPECIFIC COMMENTS

L50: Check also <https://doi.org/10.1002/ece3.10638>.

RESPONSE: Done and added this relevant reference.

L58-60: Place to cite Wheelwright 1985

RESPONSE: Done, thank you!

L107-109: But which mechanism explains the alternative hypothesis?

RESPONSE: We mention now the optimal foraging theory to support this alternative hypothesis L59-64. “Large-bodied species have higher absolute energy requirements than smaller species, which strongly influences their foraging decisions. Given similar diets and food densities, larger birds must consume greater amounts of food, yet they are often more energetically efficient per unit body mass. As a result, they tend to target larger and/or more energy-rich food items and to exploit environments that maximize the balance between energetic costs and benefits, as predicted by “optimal foraging theory” (Pyke 1978).”

L190: I wonder whether fitting some models with both variables could be insightful as an exercise about their importance

RESPONSE: Interesting point. We initially fitted these models, but they suffered from instability because the two traits are partly correlated. Moreover, our models include a random intercept and slope of the trait within each network. Including two random slopes per network, plus the covariates give convergence and stability problems.

L191-193: Some species must be participating in multiple networks (e.g. *Sylvia atricapilla* across the Palearctic). How should species ID be treated in these models?

RESPONSE: This is a good point that we discussed internally when building the models. Although some species occur in multiple networks, we decided not to include species identity as a random effect. In this context, each species–network combination represents a distinct ecological realisation of that species under a specific interaction context (i.e., we included within-network random slopes in the models). Including species identity would substantially increase model complexity by requiring random intercepts for many species that are represented by only one or a few observations. Moreover, because we use body mass and beak width as species-level traits that do not vary within species, species-level random effects would largely absorb variance already captured by these predictors, leading to overparameterization and shifting inference away from our objective of estimating trait-based roles across networks.

L197: Why these names?

RESPONSE: We thought these names were nice and self-explanatory, but we have renamed the scenarios to make them more descriptive. They are now named: “Largest species removed scenario”, “Smallest species removed scenario”, “Widest beaks removed scenario”, “Narrowest beaks removed scenario”, and “Random species removed scenario”.

L203: The 10% comes from the overall list of bird species, is that right? – not 10% from each network.

RESPONSE: Yes, the 10% is based on the overall list of bird species, not within each network. This ensures we identify truly large species in a broad ecological context (the ones that are really endangered), avoiding misclassification of species that are only relatively larger within a single network.

L259: “... with a smaller number of species ” – this is not true, as you haven’t found effects of body size on degree.

RESPONSE: We agree and rephrased the sentence to “indicating that larger species tend to be more specialized and interact with a particular subset of species”

L263: The meaning of the “strength” metric is not about “stronger interactions”.

RESPONSE: We agree, and changed the wording to avoid confusion: “a positive relationship between body mass and species interaction strength was observed, meaning that larger species depend on few species” (L283-285).

L276: I do not see anything resembling a normal distribution in Fig. 3.

RESPONSE: You are right, the distributions are not normal according to the Shapiro-Wilk tests. This does not affect our methodological approach, as we focus on removing species from the extremes of the distributions (e.g., the smallest or largest 10–30%), regardless of the precise distributional shape. To clarify, we have revised the text (L303–L305) to: “Trait-based removal scenarios targeted species occupying the lower and upper extremes of the body mass and beak width distributions (Fig. 4).”

L358: I don’t think the concept “forbidden link” fits in this case

RESPONSE: We removed this term to avoid confusion.

L400-405: As pointed above, what about the degree of frugivory?

RESPONSE: Thank you for this comment. In the new version, we analysed the relationship between the degree of frugivory of each species (retrieved from a recently published database: AVONICHE; Sayol et al., 2026 Global Ecol Biogeogr) and their traits (body size and beak width), finding an overall positive relationship (both across regions and within regions) between body mass and dependence on fruits. This relationship supports our findings and emphasises that on top of being more specialized, bigger and wider-beaked species rely more on fruits than smaller ones. We added a new figure showing this relationship in the Supplementary Material (Fig. S3 in the new version, and added the corresponding text in the methods, results and discussion).

L413-onwards: Too speculative without information on the other dietary components of each species.

RESPONSE: We toned down this part of the Discussion and included a new analysis in which we show that large-bodied species show a higher degree of frugivory than the small ones.

L421: This is because many bird species are omnivores.

RESPONSE: We agree. The proportion of true specialists is low compared to the percentage of birds that can be considered as generalist species.

L429-onwards: Again, too speculative, and too much Discussion on issues not explicitly addressed here (energetics/foraging)

RESPONSE: We agree and have adopted a more cautionary language in this new version of the manuscript as the Reviewer suggested.

Table 1 and Figure 2 are fully redundant – only one of both items should be presented

RESPONSE: We agree, and changed the Table 1 for a new one in which we show details about the network metrics used, to alleviate space pressure on the main text.