

1 **Title: Quantifying species contributions to ecosystem processes: a**
2 **global assessment of functional trait and phylogenetic metrics across**
3 **avian seed-dispersal networks**

4

5 **Authors:** Alexander L. Pigot^{1,2}, Tom Bregman^{3,4}, Catherine Sheard^{3,5}, Benjamin
6 Daly³, Rampal S. Etienne¹, Joseph A. Tobias^{3,6}

7

8 **Affiliations:** ¹Groningen Institute for Evolutionary Life Sciences, University of
9 Groningen, Groningen, The Netherlands, PO Box 11103, Groningen 9700 CC, The
10 Netherlands. ²Centre for Biodiversity and Environment Research, Department of
11 Genetics, Evolution and Environment, University College London, Gower Street,
12 London, WC1E 6BT. ³Edward Grey Institute, Department of Zoology, University of
13 Oxford, Oxford, OX1 3PS, UK. ⁴Global Canopy Programme, 23 Park End Street,
14 Oxford, OX1 1HU, UK. ⁵Department of Archaeology & Anthropology, University of
15 Bristol, 43 Woodland Drive, Bristol BS8 1UU. ⁶Imperial College London, Silwood
16 Park, Ascot SL5 7PY, UK.

17

18 *Correspondence to: alex.pigot1@gmail.com

19

20 **Keywords:** ecological network, ecosystem function, functional diversity, interaction
21 network, mutualism, phylogenetic diversity, seed dispersal.

22

23 Number of words (6100)

24 Number of tables (0)

25 Number of references (59)

26 Number of figures (2)

27

28

29 Quantifying the role of biodiversity in ecosystems not only requires understanding the
30 links between species and the ecological functions and services they provide, but also
31 how these factors relate to measurable indices such as functional traits and
32 phylogenetic diversity. However, these relationships remain poorly understood,
33 especially for heterotrophic organisms within complex ecological networks. Here we
34 assemble data on avian traits across a global sample of mutualistic plant-frugivore
35 networks to critically assess how the functional roles of frugivores are associated with
36 their intrinsic traits, as well as their evolutionary and functional distinctiveness. We
37 find strong evidence for niche complementarity, with phenotypically and
38 phylogenetically distinct birds interacting with more unique sets of plants. However,
39 interaction strengths — the number of plant species dependent on a frugivore — were
40 unrelated to evolutionary or functional distinctiveness, largely because distinct
41 frugivores tend to be locally rare, and thus have fewer connections across the
42 network. Instead, interaction strengths were better predicted by intrinsic traits,
43 including body size, gape width and dietary specialisation. Our analysis provides
44 general support for the utility of traits in quantifying species ecological functions, but
45 also highlights the need to go beyond simple metrics of functional or phylogenetic
46 diversity to consider the multiple pathways through which traits may determine
47 ecological processes.

48

49

50

51 **Introduction**

52 Anthropogenic activity is driving a worldwide decline in the abundance and diversity
53 of species [1], threatening the functional integrity of Earth's ecosystems [2, 3].
54 Reliably predicting and thus mitigating against the effects of biodiversity loss, is
55 contingent upon a robust understanding of the contributions of species to the
56 functioning, stability and resilience of ecosystems [4, 5]. However, direct
57 measurements of such contributions are rarely available, leading to the widespread
58 use of functional traits and phylogenetic history as surrogates for species ecological
59 roles [6-11].

60 The use of trait-based and phylogenetic tree-based proxies is largely based on
61 the idea of niche complementarity, whereby species with similar functional traits and
62 thus partially overlapping niches are expected to perform similar, and to a certain
63 degree redundant, ecological roles [12, 13]. This theory predicts that the functional
64 contributions of species increase with their functional trait distinctiveness (hereafter
65 FD) relative to other members of the community [14]. Because closely related species
66 are expected to share similar traits, ecological redundancy is also expected to decrease
67 with species evolutionary distinctiveness (ED), typically quantified using
68 phylogenetic branch lengths [15]. As a result, for a given richness, assemblages
69 containing a greater functional or phylogenetic diversity of species are expected to
70 provide a greater variety and efficiency of ecological functions [12, 15-17].

71 Spurred by a growing availability of phenotypic and phylogenetic data, the
72 idea that species functional roles can be quantified on the basis of FD or ED has
73 rapidly been incorporated into conservation biology [6-11]. However, the extent to
74 which simple metrics of functional and phylogenetic diversity provide reliable
75 surrogates for the functional integrity of ecosystems remains unclear for at least two

76 key reasons [4, 18, 19]. First, most theory and evidence for the effects of functional
77 diversity is based on experimentally assembled plant communities structured
78 primarily by competition [20]. The extent to which this framework generalizes across
79 naturally assembled ecosystems, comprising complex ecological networks of species
80 linked by different kinds of interactions (e.g. predation, mutualism) has yet to be
81 established [19, 21]. Second, in addition to FD, species functional contributions are
82 also expected to vary due to differences in abundance [22, 23] and the possession of
83 particular intrinsic traits, such as large body size, that may confer a disproportionate
84 impact on ecological processes [24, 25]. These effects of abundance and intrinsic
85 traits have the potential to amplify, counteract or even reverse the positive effects of
86 FD, but we know little about how these different factors co-vary across species and
87 thus combine to determine species functional roles [26-28]. This is especially the case
88 across large, heterotrophic organisms that are generally not amenable to experimental
89 manipulation and where species ecological roles are difficult to quantify.

90 Here we address this issue, using frugivorous birds as a model system for
91 examining the links between FD and species functional roles. Seed dispersal by
92 frugivorous birds is an essential process in plant recruitment, especially in tropical
93 forests where co-evolution between fruiting plants and their seed dispersal agents is
94 most pronounced [29, 30]. Furthermore, many studies have demonstrated that the
95 mutualistic interactions between plants and frugivorous birds are strongly structured
96 according to several clearly defined and easily measured functional traits [31-34]. For
97 instance, while foraging height determines which plants a bird is likely to encounter
98 [33], morphological traits such as beak shape and body size influence the rewards and
99 handling efficiency of feeding on different fruits [31, 34]. This tight association
100 between traits and resource use, leads to the prediction that frugivores with more

101 distinct traits will perform more unique functional roles [21, 35] and, all else being
102 equal, will thus support a greater number of plant species within the network than
103 those frugivores with less distinct traits [36-38].

104 To test the extent to which FD can provide a surrogate for frugivore functional
105 roles we assembled a comprehensive database of avian functional traits across a
106 global compilation of plant-frugivore interaction networks (see table S1 for references
107 of the original studies). These networks collectively describe >58000 unique
108 interaction events across 546 species of birds and allow us to address the following
109 key aims. First, we examine how trait and phylogenetic similarity relates to the
110 dietary overlap between frugivores, and thus test the importance of niche
111 complementarity, a key assumption underlying the relationship between functional
112 diversity and function. Second, we conduct analyses examining how the functional
113 roles of frugivores within networks are related to their FD (and ED) as well as a
114 number of intrinsic traits for which an effect on function is expected. We quantified
115 species functional roles according to three quantitative network metrics relevant to
116 understanding the effects of FD, including the frequency of interactions [39],
117 interaction specialisation [40] and interaction strength — a measure of the number of
118 plant species dependent on each frugivore [41]. Finally, because direct estimates of
119 species abundance are not available for the networks we study, we examine the link
120 between species FD and abundance across a global database of avian communities
121 [42] using ED as a proxy for FD. Through this approach, we aim to provide a critical
122 and broad-scale assessment of the utility of functional traits as surrogates for the
123 ecological functions supported by frugivorous birds.

124

125 **Methods**

126 (a) Avian seed-dispersal networks

127 We compiled from the literature a database of mutualistic networks describing the
128 visitation and feeding events between birds and fruiting plants. In total, we obtained
129 34 networks from 25 studies distributed across all the world's continents (except
130 Antarctica) (table S1). Of these networks, 23 are 'quantitative', recording not only the
131 presence or absence of interactions but also the number of individuals visiting each
132 plant species (i.e. visitation rate). Although interaction events are not synonymous
133 with seed-dispersal events [43], they are the best available proxy at this scale in the
134 absence of more detailed information on disperser effectiveness [26, 39]. To ensure
135 that we focused on species most likely functioning as seed dispersal agents, we
136 excluded known seed predators (species in the family Psittacidae, $n = 23$ species). The
137 functional traits included in this study are specific to birds, and thus we also removed
138 the small number of observations for non-avian frugivores ($n = 43$ species). Our final
139 database included a total of 58401 unique interaction events between 546 species of
140 birds and 1141 species of plants (table S1, database S1).

141

142 (b) Avian local abundance

143 Published seed-dispersal networks rarely contain information on species local
144 abundance. To assess how functional distinctiveness may be related to abundance, we
145 therefore downloaded count data for a global compilation of avian assemblages from
146 the online 'Ecological Register' repository (<http://ecoregister.org/>) [42]. This dataset
147 contains 166 avian assemblages, comprising 6976 count estimates from across 2344
148 species.

149 (c) Avian functional traits and phylogenetic relationships

150 For each avian species, we collected ten morphometric measurements, including
151 published estimates of mean species body mass (g) [44] and nine traits measured from
152 field collections and preserved museum skins (database S1). The nine traits measured
153 here (to the nearest 0.01 mm) were: beak length (two separate measures), beak width,
154 beak depth, gape width, tarsus length, tail length, wing length, and Kipp's distance,
155 the distance between the tip of the longest primary and the first secondary (see table
156 S2 for further details). Previous results indicate that these traits are robust proxies for
157 resource use, foraging manoeuvre and substrate [45]. Where possible, we obtained
158 measurements from at least two individuals from each sex for each species ($n = 2665$
159 specimens, mean = 5 per species). Throughout, we used the LN-transformed mean
160 species values to calculate trait distances between frugivores.

161 Phylogenetic relationships among avian species were extracted from the Jetz
162 et al [46] time-calibrated phylogeny assuming the Hackett backbone topology. To
163 account for phylogenetic uncertainty, we conducted our analysis across 100 trees
164 drawn at random from the posterior distribution.

165

166 (d) Testing for niche complementarity between frugivores

167 For each pair of species in each network we quantified an inverse measure of
168 interaction similarity using the Horn-Morisita distance (d_{HM}). For each network we
169 then calculated the Spearman rank correlation (ρ) between d_{HM} , species phylogenetic
170 patristic distance and Euclidian trait distance. We compared the observed correlation
171 to that expected under a null model of random network structure (1000 replicate
172 simulations) in which interactions between birds and plants were randomly re-
173 assigned while maintaining the exact species degree (i.e. number of partners) of each
174 node, using the 'permatfull' function in the R package Vegan [47]. We calculated the

175 standardised effect size of observed ρ values (i.e. the z-score) and quantified the
176 number of networks exhibiting a significant positive or negative z-score. We assessed
177 the overall significance of a departure from null model expectations using a t-test ($p =$
178 0.05 , two-tailed test). To ensure that our results are robust to the quality of network
179 data and null model assumptions, we repeated our analysis using only quantitative
180 networks ($n = 23$ networks, database S2). In this case, the null model maintained the
181 observed frequency of interactions for each node [48].

182

183 (e) Quantifying species functional roles

184 We quantified the roles of frugivores within the network using three complementarity
185 metrics, focusing on quantitative networks ($n = 485$ observations from 320 species),
186 which provide the most robust information on species interactions [49].

187 i) Visitation rate: the number of interactions performed by a species represents
188 a major quantitative constraint on species functional impact [26]. Although this metric
189 ignores any potential differences in the ‘quality’ of dispersal agents, these effects may
190 generally be outweighed by the large observed variation in visitation rates [39].

191 ii) Specialisation (d'): we quantified the degree of specialisation of each
192 frugivore using the standardised Kullback-Leibler distance [40]. This metric of
193 specialisation varies from 0 (generalist) to 1 (specialist), and accounts for differences
194 in visitation rates both across frugivores and plants. Specifically, frugivores that
195 deviate from a random sampling of available interaction partners by preferentially
196 interacting with otherwise rarely visited plants are deemed more specialised.

197 iii) Species weighted interaction strength: The strength of the interaction
198 between frugivore species i and plant species j is calculated as the number of visits by
199 frugivore i to plant j , divided by the total number of visits to plant j [41]. A higher

200 interaction strength indicates a greater dependency of plant j on frugivore i , and the
201 sum of these values for each frugivore thus provides an integrated measure of its
202 quantitative impact on the plant community.

203

204 (f) Identifying the predictors of species functional roles

205 We examined a number of potential predictors of visitation rates, specialisation d' and
206 interaction strength. We quantified species functional trait distinctiveness (FD)
207 relative to other members of the network using three standard metrics: i) the mean
208 trait distance (MTD), ii) the mean nearest neighbor distance (MNTD), and iii) the
209 distance to the centroid of trait space (CenD). These metrics quantify different aspects
210 of distinctiveness that are expected to influence network roles in different ways. In
211 particular, while MTD and CenD quantify the departure from the average trait value
212 of a community, MNTD is more sensitive to the effects of niche partitioning between
213 the most ecologically similar species [50]. Based on phylogenetic data, we quantified
214 the evolutionary distinctiveness (ED) of species both globally (between all bird
215 species) and locally (between members of the network) using the equal splits (EDES)
216 and fair proportions (EDFP) measures [51]. We account for phylogenetic uncertainty
217 using the mean species ED value from across 100 phylogenetic trees drawn at random
218 from the Bayesian posterior distribution.

219 We compared the effects of FD and ED to a number of intrinsic traits
220 proposed to influence frugivore functional roles, including the degree of obligate
221 frugivory, average foraging height, body mass and gape width. We extracted gape
222 width measurements (mm) and body mass (g) from our dataset of morphological
223 traits. The degree of obligate frugivory (%) was obtained from an independent dataset
224 containing the percentage contribution of fruit, as well as six other food types

225 (invertebrates, vertebrates, carrion, seeds, nectar and ‘other plant material’), to
226 species’ diets [44]. We also used this dataset to calculate species foraging height as
227 the weighted mean across five ordinal levels (1 [ground], 2 [understorey], 3
228 [midstorey-lower], 4 [midstorey-upper] and 5 [canopy]). Finally, previous evidence
229 suggests that geographically rare species may be more functionally distinct [7], and so
230 we also included geographic range size, calculated by overlaying species breeding
231 extent of occurrence maps on an equal area grid (cell resolution of 110 km \approx 1° at the
232 equator) [52]. Terms exhibiting a positive skew were LN-transformed and all
233 predictors were normalised to enable a direct comparison of effect sizes.

234 Species within networks are not independent and networks from the same
235 region may share similar characteristics. We therefore modeled species functional
236 roles using linear mixed-effects models, fitted in the R package lme4, including
237 ‘region’ (typically corresponding to countries), ‘network’ and ‘species’ as random
238 effects. We also included ‘avian family’ as a random effect to ensure that any
239 significant relationships are not driven by individual clades. Finally, we accounted for
240 over-dispersion in the residuals of our model predicting visitation rates by including
241 an additional observation level random effect [53].

242 We tested the predictors of interaction strength and specialisation following
243 LN and angular transformation respectively. For visitation rate, we used a generalised
244 linear mixed model, assuming a Poisson error structure. When predicting visitation
245 rates we accounted for difference in overall sampling intensity across networks by
246 including the total number of observed interaction events as an offset term. Because
247 interaction strengths will also vary due to sampling intensity and species richness, we
248 standardised species scores relative to the maximum value observed in each network.
249 Predictor terms were assessed both in isolation and in combination using multi-model

250 averaging [54]. Specifically, we calculated the AIC of models including every
251 combination of predictors and then used model AIC weights to calculate average
252 effect sizes, significance and relative variable importance. Metrics of FD and ED
253 provide alternative measures of distinctiveness and so we fit five different model sets,
254 one for each metric. Finally, because gape width and body mass (Pearson correlation r
255 > 0.8) are strongly correlated we fit separate models for each of these variables.

256

257 (g) Quantifying the relationship between distinctiveness and abundance

258 We tested the relationship between the local abundance of species in each assemblage
259 and local ED (LN-transformed) using a generalised linear mixed effects model,
260 assuming a Poisson error structure and including ‘assemblage’, ‘species’, ‘avian
261 family’ and observation level random effects. We also calculated the correlation
262 coefficient between ED and local abundance within each avian assemblage to
263 examine how this relationship varies as a function of species richness and across
264 geographic space.

265

266 **Results**

267

268 (a) Functional trait-based complementarity of frugivore niches

269 We found that dietary distance (d_{HM}) between avian frugivores was positively
270 correlated with trait dissimilarity (figure 1, table S3). Of the 34 networks, 27 exhibited
271 a positive standardised effect that was significant in 14 cases [$p < 0.05$], strongly
272 rejecting a null model of random network structure (t-test: $t = 4.87$, $p < 0.001$).

273 Phylogenetic distance was positively associated with trait distance (33 of 34 networks
274 exhibited a positive slope, mean correlation = 0.42; table S3) and accordingly, we also

275 detected a significant positive relationship between d_{HM} and phylogenetic distance (t-
276 test: $t = 3.77$, $p < 0.001$; table S3). These results were largely robust to the type of
277 network and null model used. When we focused exclusively on quantitative networks,
278 d_{HM} remained positively correlated with both trait (t-test: $t = 3.06$, $p = 0.006$) and
279 phylogenetic distance (t-test: $t = 1.82$, $p = 0.08$), although the latter relationship was
280 marginally non-significant (table S4).

281

282 (b) The relationship between functional traits, visitation rates and 283 abundance

284 The strongest predictor of visitation rates was the degree of obligate frugivory, with
285 specialist frugivores undertaking more visits than dietary generalists (figure 2, table
286 S5). Although visitation rates increased significantly with foraging height when
287 assessed in isolation, this term was not significant in a multi-predictor model. In a
288 single-predictor model, visitation rates decreased significantly with FD according to
289 the MTD metric. However, when we accounted for the degree of obligate frugivory in
290 a multi-predictor model, all FD (except CenD) and local ED metrics were strongly
291 negatively associated with visitation rates. In contrast to local distinctiveness metrics,
292 Global ED was unrelated to visitation rates (figure 2, table S5).

293 In accordance with the patterns of visitation rates, species abundance in avian
294 assemblages was negatively associated with local ED (slope = -0.36 , $P < 0.001$, $n =$
295 6976 records). This negative relationship was globally consistent and evident across
296 88% of assemblages (figure S1).

297

298 (c) The relationship between functional traits and specialisation

299 Specialisation (d') increased with FD, an effect that was strongest when quantified
300 using the MTD metric (figure 2, table S5). d' also increased significantly with body
301 mass. This latter effect appears to arise because of the covariation between body mass
302 and MTD, because when including both terms in a multi-predictor model only MTD
303 retained its significant effect. All other intrinsic traits had low variable importance
304 scores and were not significant predictors of d' (figure 2, table S5).

305

306 (d) The relationship between functional traits and interaction strength

307 Obligate frugivory and body mass were the strongest predictors of species interaction
308 strengths, indicating that large-bodied specialist frugivores have the highest
309 quantitative impact in the network (figure 2, table S5). Although interaction strength
310 increased significantly with gape width when assessed in isolation, this term was no
311 longer significant when accounting for other covariates. Importantly, across both
312 single and multi-predictor models, interaction strength was not significantly related to
313 either FD or ED. In fact, most distinctiveness metrics exhibited a weak negative
314 association with interaction strength that was marginally non-significant in the case of
315 MTD (figure 2, table S5).

316

317 **Discussion**

318 Our analysis of the functional and phylogenetic structure of avian frugivore networks
319 provides support for trait-based niche complementary between species, a key pattern
320 thought to underpin the positive relationship between functional trait diversity and
321 ecological function. In particular, we found that closely related frugivores with similar
322 functional traits consistently interact with more similar sets of plants, while distantly
323 related birds with distinct traits exhibit relatively little overlap in resource use. In

324 accordance with this, our analysis showed that frugivores with distinct traits also tend
325 to be more functionally specialised, interacting with plants that are less frequently
326 visited by other members of the community. The importance of functional trait
327 matching in structuring interactions within plant-frugivore networks is well
328 established [31-34, 55] [56], and our analysis across multiple networks, regions and
329 ecosystems, further highlight the utility of functional traits as general predictors of the
330 overlap and specialisation of these mutualistic interactions.

331 The pattern of niche complementarity that we report here is expected to lead to
332 a positive relationship between FD and species functional contributions, because
333 species with distinct traits should be less ecologically redundant [21]. We found that
334 functionally distinct birds do tend to feed on less frequently visited plants, suggesting
335 that species *per capita* impacts may indeed increase with FD. However, our analysis
336 also shows that this does not translate into stronger interaction strengths and thus
337 higher quantitative impact at the species level because functionally distinct species
338 tend to undertake fewer interactions overall (i.e. have lower visitation rates). As a
339 result, on average, plants were no more dependent on interactions with functionally
340 distinct frugivores than they were on species with seemingly more redundant traits.
341 This lack of relationship between FD and species interaction strength was true
342 regardless of the metric used to calculate FD or whether we employed ED as a proxy
343 for trait distinctiveness.

344 One possible explanation for the decline in visitation rates with FD is the
345 occasional inclusion in the networks of distinct and distantly related species from
346 other trophic guilds that rarely feed on fruit. However, this is unlikely to explain our
347 results, because we found that the negative effects of FD on visitation rates actually
348 became stronger when we statistically accounted for the degree of obligate frugivory

349 and other intrinsic species traits. Visitation rates are expected to strongly reflect
350 underlying differences in species abundance [39] and thus an alternative explanation
351 is that the decline in visitation rates with FD is driven by a lower abundance of
352 distinct species within local assemblages. Here, using phylogenetic relatedness as a
353 proxy for trait similarity, we reveal this trend in birds at a global scale by showing
354 that locally evolutionary distinct species consistently occur at lower densities than
355 those species coexisting with many close relatives. Thus, our results suggest that the
356 quantitative impacts of frugivores are independent of FD, because the positive effects
357 of reduced ecological redundancy are nullified by a corresponding decrease in
358 abundance.

359 A lower abundance of species with distinct functional traits has been
360 demonstrated in assemblages of plants and reef fish [7, 57] and a similar trend of
361 declining visitation rates with FD has also recently been reported for insect pollinators
362 in New Zealand [50]. The processes driving these trends are unclear, but trait-
363 dependent environmental selection provides a likely candidate [58]. In particular, we
364 speculate that if certain trait combinations are unfavorable in the local environment,
365 then these trait values will be represented by both few individuals and species. While
366 this negative relationship between abundance and trait distinctiveness is not included
367 in traditional biodiversity-ecosystem function theory [12], our results suggest that it
368 may be sufficient to decouple FD from the functional impacts of frugivores within
369 seed-dispersal networks.

370 Although species interaction strengths were generally unrelated to metrics of
371 functional diversity, we detected a significant effect of intrinsic functional traits,
372 notably obligate frugivory, body size and gape width. Previous studies have suggested
373 that obligate frugivores play an important role as ‘network connectors’ because of

374 their nutritional requirement to feed on multiple different fruits [59]. In contrast, our
375 analysis shows that frugivory is unrelated to interaction specialisation, and that the
376 stronger interaction strengths of obligate frugivores is instead likely due to their
377 higher feeding rates. The positive contributions of body size and gape width to
378 interaction strength also make sense. While plants producing small fruits can be
379 dispersed by a wide variety of birds, only large-bodied frugivores with wide gapes are
380 able to disperse the fruits of large-seeded plants [31]. The primary importance of
381 large-gaped frugivores for seed-dispersal has previously been shown [60] and our
382 analysis extends this finding across different avian assemblages, highlighting the
383 status of large-gaped species as what might be termed ‘network keystones’.
384 Furthermore, large-bodied specialist frugivores also appear highly sensitive to human
385 pressures, being the first to disappear following habitat degradation [25], suggesting
386 that even the loss of only a few frugivore species may have a disproportionate impact
387 on the maintenance of seed-dispersal services.

388 Metrics used as surrogates for ecosystem function in conservation biology
389 generally only consider the functional and phylogenetic diversity of species and rarely
390 account for species abundance or intrinsic functional traits (e.g. [8-11]). This is
391 because, at such broad spatial and taxonomic scales, information on abundance is
392 generally unavailable while the relationships between intrinsic traits and ecosystem
393 functions are generally unclear. However, abundance and intrinsic traits are known to
394 exert major constraints on species functional effects [22, 27, 28], and our results
395 suggest that standard functional and phylogenetic diversity metrics ignoring these
396 aspects of assemblage structure may misrepresent the diversity of interactions
397 supported by avian frugivores [61], and within ecological networks more generally
398 [50].

399 These conclusions are subject to a number of caveats. First, we have focused
400 on how functional traits relate to the present day quantitative impacts of species
401 within networks. In contrast, the functional resilience of networks is likely to also
402 depend on network topological plasticity and the ability of species interactions to be
403 ‘re-wired’ following extinction [62]. It seems likely that species with distinct traits are
404 generally less functionally substitutable than those with more redundant phenotypes,
405 although this remains conjecture until further empirical evidence has been compiled
406 from ‘re-wiring’ events. Second, birds mediate a number of critical ecological
407 processes beyond seed dispersal, including pollination, predation and nutrient
408 recycling [63]. Our results therefore do not preclude the possibility that a positive
409 effect of functional distinctiveness on function may emerge when considering
410 multiple ecological processes (i.e. multi-functionality) [17]. Finally, our meta-analysis
411 examining the quantitative component of seed-dispersal networks assumed that higher
412 interaction strengths translate into larger functional impacts [26, 39], which may not
413 always be the case given the potential for interspecific variation in the effectiveness of
414 avian dispersal agents [43].

415 Broad-scale comparative analyses of how functional traits and phylogenetic
416 metrics relate to the functional roles of species provide an important perspective in
417 helping to translate the results of detailed experimental studies to reliably predict, and
418 thus mitigate, the consequences of species loss in natural ecosystems. However, these
419 efforts remain preliminary and the robustness of any conclusions drawn at this scale
420 will depend on the quality and relevance of the ecological data used to quantify
421 species functional roles. Our analysis using data on frugivore-plant interaction
422 intensities confirms a general pattern of trait-based niche complementarity across
423 networks, but nonetheless suggests that functional trait diversity may provide a

424 relatively weak surrogate for frugivore functional roles. A more detailed examination
425 of the links between functional diversity, abundance, and ecological processes is a key
426 priority for future research.

427

428

429 **Acknowledgements**

430

431 We thank Nico Alioravainen, Monte Neate-Clegg and Samuel Jones for assisting in
432 the collection of trait data, Chris Cooney, Robert Heathcote, Ally Phillimore, Uri
433 Roll, Chris Trisos, Anthony Waldron and Nasim Zargar for their helpful advice and
434 discussion and Nathalie Seddon and three anonymous reviewers whose comments
435 greatly improved the manuscript. This study was funded by a Natural Environment
436 Research Council research grant (JAT), VICI grant (RE) and a VENI fellowship (AP).

437

438 **Data accessibility statement**

439 The data used in this study has been deposited in Data Dryad database S1

440

441 **Author contributions**

442 AP devised the research, TB, CS, BD compiled data, AP performed the analyses, AP,
443 RE and JAT wrote the paper.

444

445 **Competing Interests**

446 There are no competing interests.

447

448 **Ethics Statement**

449 NA

450

451

452

453 **References**

454

455 [1] Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A.,
 456 Borger, L., Bennett, D.J., Choimes, A., Collen, B., et al. 2015 Global effects of land
 457 use on local terrestrial biodiversity. *Nature* 520, 45-+. (doi:Doi 0.1038/Nature14324).

458 [2] Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,
 459 Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., et al. 2012 Biodiversity loss and
 460 its impact on humanity. *Nature* 486, 59-67. (doi:Doi 10.1038/Nature11148).

461 [3] Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A. & Ferrier, S.
 462 2016 Has land use pushed terrestrial biodiversity beyond the planetary boundary? A
 463 global assessment. *Science* 353, 288–291.

464 [4] Mace, G.M., Reyers, B., Alkemade, R., Biggs, R., Chapin, F.S., Cornell, S.E.,
 465 Diaz, S., Jennings, S., Leadley, P., Mumby, P.J., et al. 2014 Approaches to defining a
 466 planetary boundary for biodiversity. *Global Environ Chang* 28, 289-297. (doi:DOI
 467 10.1016/j.gloenvcha.2014.07.009).

468 [5] Seddon, N., Mace, G.M., Naeem, S., Pigot, A.L., Cavanagh, R., Mouillot, D.,
 469 Tobias, J.A., Vause, J. & Walpole, M. 2016 Biodiversity in the Anthropocene:
 470 prospects and policy. *Proc Biol Sci*.

471 [6] Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C.,
 472 Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoidi, L., et al.
 473 2013 Integrating abundance and functional traits reveals new global hotspots of fish
 474 diversity. *Nature* 501, 539-+. (doi:Doi 10.1038/Nature12529).

475 [7] Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-
 476 Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., et al. 2013 Rare
 477 Species Support Vulnerable Functions in High-Diversity Ecosystems. *Plos Biol* 11.
 478 (doi:ARTN e1001569 DOI 10.1371/journal.pbio.1001569).

479 [8] Thuiller, W., Pironon, S., Psomas, A., Barbet-Massin, M., Jiguet, F., Lavergne, S.,
 480 Pearman, P.B., Renaud, J., Zupan, L. & Zimmermann, N.E. 2014 The European
 481 functional tree of bird life in the face of global change. *Nat Commun* 5. (doi:Artn
 482 3118 Doi 10.1038/Ncomms4118).

483 [9] Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin,
 484 B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. 2009 Loss of functional diversity
 485 under land use intensification across multiple taxa. *Ecol Lett* 12, 22-33. (doi:DOI
 486 10.1111/j.1461-0248.2008.01255.x).

487 [10] Edwards, D.P., Gilroy, J.J., Thomas, G.H., Uribe, C.A. & Haugaasen, T. 2015
 488 Land-Sparing Agriculture Best Protects Avian Phylogenetic Diversity. *Curr Biol* 25,
 489 2384-2391. (doi:10.1016/j.cub.2015.07.063).

490 [11] Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A.,
 491 Bruscin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., et al. 2014
 492 Using ecological thresholds to evaluate the costs and benefits of set-asides in a
 493 biodiversity hotspot. *Science* 345, 1041-1045. (doi:DOI 10.1126/science.1255768).

494 [12] Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. 1997 The
 495 influence of functional diversity and composition on ecosystem processes. *Science*
 496 277, 1300-1302. (doi:DOI 10.1126/science.277.5330.1300).

497 [13] Diaz, S. & Cabido, M. 2001 Vive la difference: plant functional diversity matters
 498 to ecosystem processes. *Trends Ecol Evol* 16, 646-655. (doi:Doi 10.1016/S0169-
 499 5347(01)02283-2).

500 [14] Petchey, O.L. & Gaston, K.J. 2006 Functional diversity: back to basics and
 501 looking forward. *Ecol Lett* 9, 741-758. (doi:DOI 10.1111/j.1461-0248.2006.00924.x).

502 [15] Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. 2008 Evolutionary history and
503 the effect of biodiversity on plant productivity. *P Natl Acad Sci USA* 105, 17012-
504 17017. (doi:DOI 10.1073/pnas.0805962105).

505 [16] Loreau, M. & Hector, A. 2001 Partitioning selection and complementarity in
506 biodiversity experiments. *Nature* 412, 72-76. (doi:Doi 10.1038/35083573).

507 [17] Hector, A. & Bagchi, R. 2007 Biodiversity and ecosystem multifunctionality.
508 *Nature* 448, 188-U186. (doi:Doi 10.1038/Nature05947).

509 [18] Srivastava, D.S. & Vellend, M. 2005 Biodiversity-ecosystem function research:
510 Is it relevant to conservation? *Annu Rev Ecol Evol S* 36, 267-294. (doi:DOI
511 10.1146/annurev.ecolsys.36.102003.152636).

512 [19] Gravel, D., Albouy, C. & Thuiller, W. 2016 The meaning of functional trait
513 composition of food webs for ecosystem functioning *Philos Trans R Soc Lond B Biol
514 Sci* 371, 20150268.

515 [20] Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S.,
516 Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., et al. 2005 Effects of biodiversity
517 on ecosystem function: a consensus of current knowledge. *Ecol Monogr* 75, 3-35.

518 [21] Poisot, T., Mouquet, N. & Gravel, D. 2013 Trophic complementarity drives the
519 biodiversity-ecosystem functioning relationship in food webs. *Ecol Lett* 16, 853-861.
520 (doi:Doi 10.1111/Ele.12118).

521 [22] Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. 2015
522 Abundance of common species, not species richness, drives delivery of a real-world
523 ecosystem service. *Ecol Lett* 18, 626-635.

524 [23] Fauset, S., Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A., Brienen,
525 R.J.W., Feldpausch, T.R., Lopez-Gonzalez, G., Malhi, Y., ter Steege, H., et al. 2015
526 Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* 6. (doi:Artn 6857
527 Doi 10.1038/Ncomms7857).

528 [24] Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. &
529 Srivastava, D.S. 2004 Extinction and ecosystem function in the marine benthos
530 *Science* 306, 1177-1180.

531 [25] Bregman, T., Lees, A., MacGregor, H., Darski, B., Moura, N., Aleixo, A.,
532 Barlow, J. & Tobias, J. 2016 Biodiversity, functional traits, and the collapse of
533 ecosystem processes linked to resilience in human-modified tropical forests. *Proc
534 Biol Sci*.

535 [26] Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R.,
536 Klein, A.M., Kremen, C., M'Gonigle, L.K., Rader, R., et al. 2015 Delivery of crop
537 pollination services is an insufficient argument for wild pollinator conservation. *Nat
538 Commun* 6. (doi:Artn 7414 10.1038/Ncomms8414).

539 [27] Mokany, K., Ash, J. & Roxburgh, S. 2008 Functional identity is more important
540 than diversity in influencing ecosystem processes in a temperate native grassland. *J
541 Ecol* 96, 884-893. (doi:DOI 10.1111/j.1365-2745.2008.01395.x).

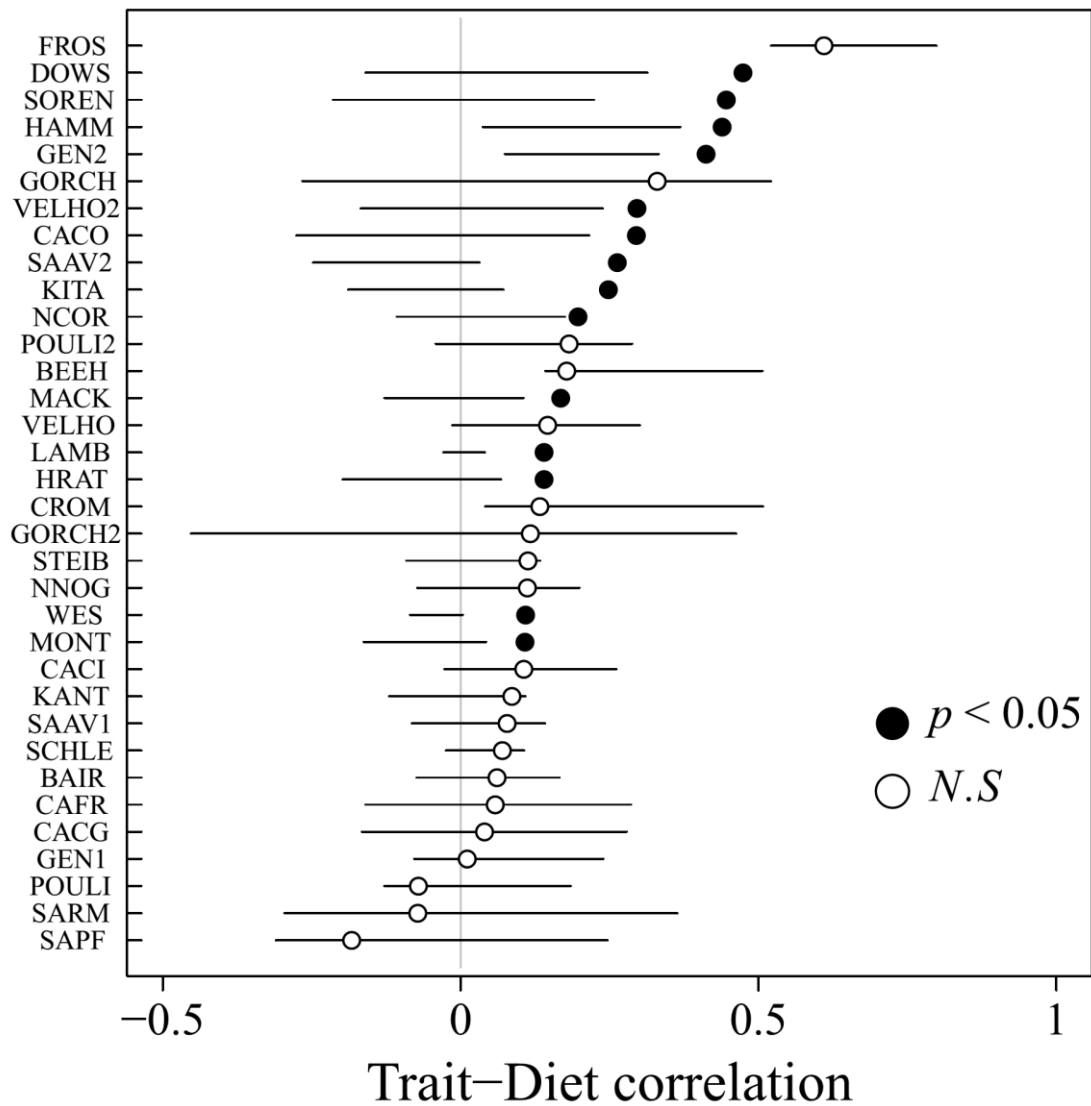
542 [28] Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C.,
543 Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., et al. 2015 Functional
544 identity and diversity of animals predict ecosystem functioning better than species-
545 based indices. *P Roy Soc B-Biol Sci* 282. (doi:Unsp 20142620
546 Doi 10.1098/Rspb.2014.2620).

547 [29] Wotton, D.M. & Kelly, D. 2011 Frugivore loss limits recruitment of large-seeded
548 trees. *Proc Biol Sci* 278, 3345-3354. (doi:10.1098/rspb.2011.0185).

549 [30] Jordano, P. 2016 Chasing Ecological Interactions. *Plos Biol* 14, e1002559.
550 (doi:doi:10.1371/journal.pbio.1002559).

- 551 [31] Wheelwright, N.T. 1985 Fruit Size, Gape Width, and the Diets of Fruit-Eating
552 Birds. *Ecology* 66, 808-818. (doi:Doi 10.2307/1940542).
- 553 [32] Jordano, P. 1987 Frugivory, External Morphology and Digestive-System in
554 Mediterranean Sylviid Warblers *Sylvia* Spp. *Ibis* 129, 175-189. (doi:DOI
555 10.1111/j.1474-919X.1987.tb03199.x).
- 556 [33] Schleuning, M., Bluthgen, N., Florchinger, M., Braun, J., Schaefer, H.M. &
557 Bohning-Gaese, K. 2011 Specialization and interaction strength in a tropical plant-
558 frugivore network differ among forest strata. *Ecology* 92, 26-36. (doi:Doi 10.1890/09-
559 1842.1).
- 560 [34] Dehling, D.M., Jordano, P., Schaefer, H.M., Bohning-Gaese, K. & Schleuning,
561 M. 2016 Morphology predicts species' functional roles and their degree of
562 specialisation in plant-frugivore interactions. *P Roy Soc B-Biol Sci* 283, 20152444.
- 563 [35] Dehling, D.M., Topfer, T., Schaefer, H.M., Jordano, P., Bohning-Gaese, K. &
564 Schleuning, M. 2014 Functional relationships beyond species richness patterns: trait
565 matching in plant-bird mutualisms across scales. *Global Ecol Biogeogr* 23, 1085-
566 1093. (doi:Doi 10.1111/Geb.12193).
- 567 [36] Bluthgen, N. & Klein, A.M. 2011 Functional complementarity and
568 specialisation: The role of biodiversity in plant-pollinator interactions. *Basic Appl*
569 *Ecol* 12, 282-291. (doi:DOI 10.1016/j.baae.2010.11.001).
- 570 [37] Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. 2006 Functional diversity of
571 plant-pollinator interaction webs enhances the persistence of plant communities. *Plos*
572 *Biol* 4, 129-135. (doi:ARTN e1 DOI 10.1371/journal.pbio.0040001).
- 573 [38] Schleuning, M., Frund, J. & Garcia, D. 2015 Predicting ecosystem functions
574 from biodiversity and mutualistic networks: an extension of trait-based concepts to
575 plant-animal interactions. *Ecography* 38, 380-392. (doi:Doi 10.1111/Ecog.00983).
- 576 [39] Vazquez, D.P., Morris, W.F. & Jordano, P. 2005 Interaction frequency as a
577 surrogate for the total effect of animal mutualists on plants. *Ecol Lett* 8, 1088-1094.
578 (doi:DOI 10.1111/j.1461-0248.2005.00810.x).
- 579 [40] Blüthgen, N., Menzel, F. & Blüthgen, N. 2006 Measuring specialization in
580 species interaction networks. *Bmc Ecol* 6, 9.
- 581 [41] Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. 2003 The nested
582 assembly of plant-animal mutualistic networks. *P Natl Acad Sci USA* 100, 9383-9387.
583 (doi:DOI 10.1073/pnas.1633576100).
- 584 [42] Alroy, J. 2015 The shape of terrestrial abundance distributions. *Science Advances*
585 1, e1500082.
- 586 [43] Schupp, E.W., Jordano, P. & Gomez, J.M. 2010 Seed dispersal effectiveness
587 revisited: a conceptual review. *New Phytol* 188, 333-353. (doi:DOI 10.1111/j.1469-
588 8137.2010.03402.x).
- 589 [44] Wilman, W., Belmaker, J., Simpson, J., de la Rosa, C. & Rivadeneira, M.M.
590 2014 EltonTraits 1.0: Species-level foraging attributes of the world's birds and
591 mammals. *Ecology* 95, 2027-2027.
- 592 [45] Pigot, A.L., Trisos, C. & Tobias, J.A. 2016 Functional traits reveal the expansion
593 and packing of ecological niche space underlying an elevational diversity gradient in
594 passerine birds. *Proc Biol Sci* 283.
- 595 [46] Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. 2012 The
596 global diversity of birds in space and time. *Nature* 491, 444-448. (doi:Doi
597 10.1038/Nature11631).
- 598 [47] Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P.,
599 McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., et al. 2016

600 vegan: Community Ecology Package. R package version 2.4-0. [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)
601 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan).
602 [48] Patefield, W.M. 1981 Algorithm AS159. An efficient method of generating $r \times c$
603 tables with given row and column totals. *Applied Statistics* 30, 91–97.
604 [49] Bluthgen, N., Frund, J., Vazquez, D.P. & Menzel, F. 2008 What Do Interaction
605 Network Metrics Tell Us About Specialization and Biological Traits? *Ecology* 89,
606 3387-3399. (doi:Doi 10.1890/07-2121.1).
607 [50] Coux, C., Rader, R., Bartomeus, I. & Tylianakis, J.E. 2016 Linking species
608 functional roles to their network roles. *Ecol Lett* 19, 762-770.
609 [51] Redding, D.W. & Mooers, A.O. 2006 Incorporating evolutionary measures into
610 conservation prioritization. *Conserv Biol* 20, 1670-1678. (doi:DOI 10.1111/j.1523-
611 1739.2006.00555.x).
612 [52] International, B. 2012 The IUCN Red List of Threatened Species. Version 2012.
613 <www.iucnredlist.org>. Downloaded December 2012.
614 [53] Rigby, R.A., Stasinopolous, M.D. & Akantziliotou, C. 2008 *Computational*
615 *Statistics & Data Analysis*.
616 [54] Burnham, K.P. & Anderson, D.R. 2004 Multimodel Inference. *Sociological*
617 *Methods and Research* 33, 261-304.
618 [55] González-Castro, A., Yang, S., Nogales, M. & Carlo, T.A. 2015 Relative
619 importance of phenotypic trait matching and species' abundances in determining
620 plant–avian seed dispersal interactions in a small insular community. *AoB plants* 7,
621 plv017.
622 [56] Schleuning, M., Ingmann, L., Strauss, R., Fritz, S.A., Dalsgaard, B., Dehling,
623 D.M., Plein, M., Saavedra, F., Sandel, B., Svenning, J.C., et al. 2014 Ecological,
624 historical and evolutionary determinants of modularity in weighted seed-dispersal
625 networks. *Ecol Lett* 17, 454-463. (doi:Doi 10.1111/Ele.12245).
626 [57] D'agata, S., Vigliola, L., Graham, N.A.J., Parravicini, V., Villéger, S., Moutham,
627 G., Frolla, P., Friedlander, A., Kulbicki, M. & Mouillot, D. 2016 Unexpected high
628 vulnerability of functions in wilderness areas: evidence from coral reef fishes. *Proc*
629 *Biol Sci*.
630 [58] Shipley, B. 2010 *From plant traits to vegetation structure: chance and selection*
631 *in the assembly of ecological communities* Cambridge, Cambridge University Press.
632 [59] Mello, M.A.R., Rodrigues, F.A., Costa, L.d.F., Kissling, W.D., Şekercioğlu,
633 Ç.H., Marquitti, F.M.D. & Kalko, E.K.V. 2014 Keystone species in seed dispersal
634 networks are mainly determined by dietary specialization. *Oikos*.
635 [60] Galetti, M., Guevara, R., Cortes, M.C., Fadini, R., Von Matter, S., Leite, A.B.,
636 Labacca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., et al. 2013 Functional
637 Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. *Science* 340,
638 1086-1090. (doi:DOI 10.1126/science.1233774).
639 [61] Plein, M., Längsfeld, L., Neuschulz, E.L., Schultheiß, C., Ingmann, L., Töpfer,
640 L., Böhning-Gaese, K. & Schleuning, M. 2013 Constant properties of plant–frugivore
641 networks despite fluctuations in fruit and bird communities in space and time.
642 *Ecology* 94, 1296-1306.
643 [62] Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanes, P. & Flores, J.D.
644 2012 Topological plasticity increases robustness of mutualistic networks. *J Anim Ecol*
645 81, 896-904.
646 [63] Sekercioğlu, C.H., Daily, G.C. & Ehrlich, P.R. 2004 Ecosystem consequences of
647 bird declines. *P Natl Acad Sci USA* 101, 18042-18047. (doi:DOI
648 10.1073/pnas.0408049101).



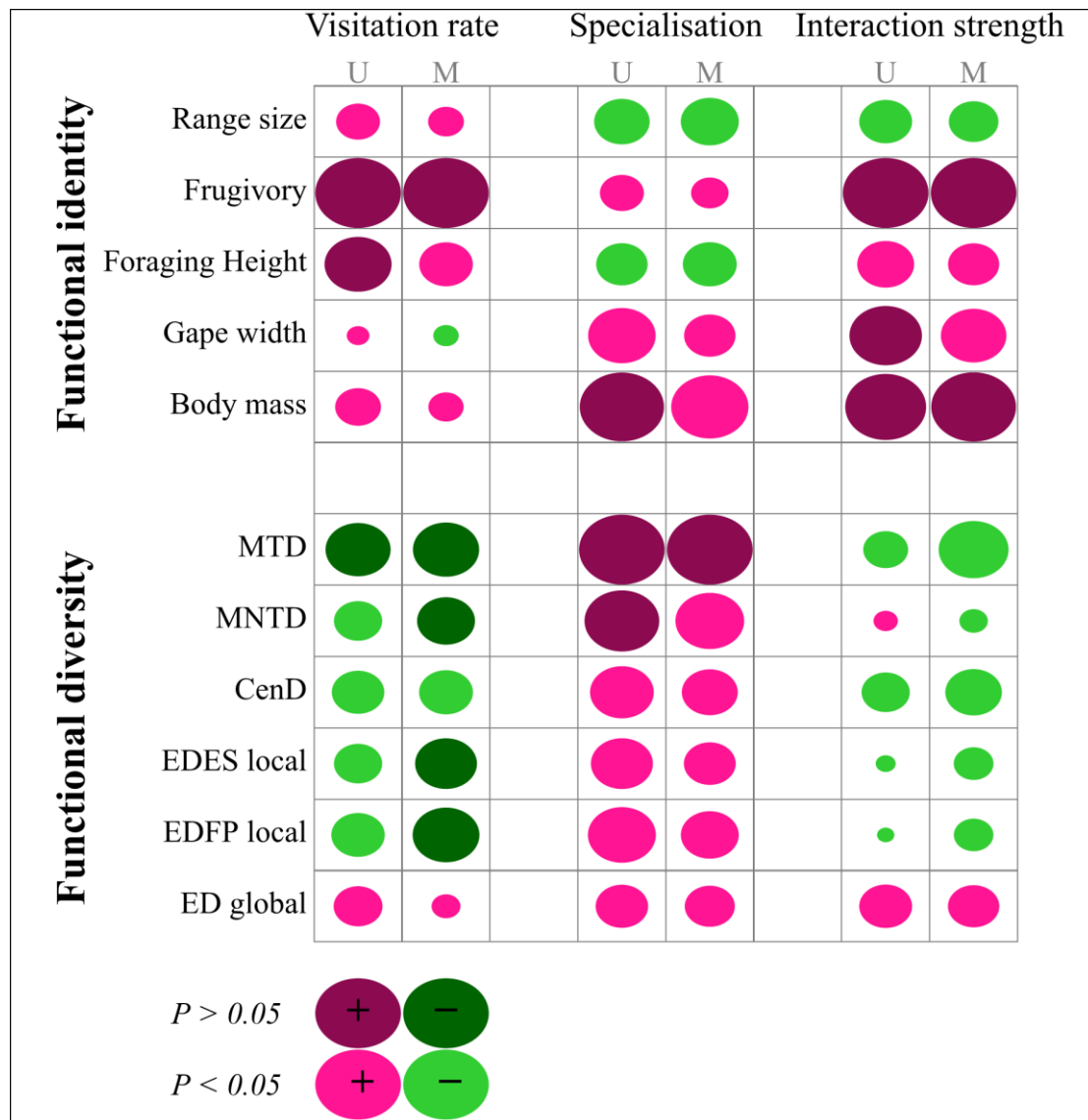
650

651 **Figure 1.** Functional trait-dependent structure of mutualistic seed-dispersal networks.652 Observed correlations between dietary d_{HM} and functional trait dissimilarity (circles)

653 across the 34 empirical networks compared to the expectations under the null model

654 (horizontal bars indicate 95% confidence interval). Filled circles indicate correlations

655 that are stronger than expected under the null model.



656

657 **Figure 2.** Functional trait and phylogenetic predictors of species network roles
658 quantified on the basis of visitation rates, interaction specialization d' and interaction
659 strength ($n = 485$). Results are shown for both univariate (U) and multivariate (M)
660 models. M1-M4 denote models of interaction strength including various combinations
661 of visitation rate and d' as predictors. Circle colour denotes positive (magenta) or
662 negative (green) trends and statistical significance (dark: $p < 0.05$; light: $p > 0.05$).
663 Circle size is proportional to the absolute effects size scaled relative to other
664 predictors in each model.

665

666

