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

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

1. Introduction

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

The use of trait-based and phylogenetic tree-based proxies is largely based on the idea of niche complementarity, whereby species with similar functional traits and thus partially overlapping niches are expected to perform similar, and to a

certain degree redundant, ecological roles [12,13]. This theory predicts that the functional contributions of species increase with their functional trait distinctiveness (hereafter FD) relative to other members of the community [14]. Because closely related species are expected to share similar traits, ecological redundancy is also expected to decrease with species evolutionary distinctiveness (ED), typically quantified using phylogenetic branch lengths [15]. As a result, for a given richness, assemblages containing a greater functional or phylogenetic diversity of species are expected to provide a greater variety and efficiency of ecological functions [12,15–17].

Spurred by a growing availability of phenotypic and phylogenetic data, the idea that species functional roles can be quantified on the basis of FD or ED has rapidly been incorporated into conservation biology [6–11]. However, the extent to which simple metrics of functional and phylogenetic diversity provide reliable surrogates for the functional integrity of ecosystems remains unclear for at least two key reasons [4,18,19]. First, most theory and evidence for the effects of functional diversity is based on experimentally assembled plant communities structured primarily by competition [20]. The extent to which this framework generalizes across naturally assembled ecosystems, comprising complex ecological networks of species linked by different kinds of interactions (e.g. predation and mutualism) has yet to be established [19,21]. Second, in addition to FD, species functional contributions are also expected to vary due to differences in abundance [22,23] and the possession of particular intrinsic traits, such as large body size, that may confer a disproportionate impact on ecological processes [24,25]. These effects of abundance and intrinsic traits have the potential to amplify, counteract or even reverse the positive effects of FD, but we know little about how these different factors covary across species and thus combine to determine species functional roles [26–28]. This is especially the case across large, heterotrophic organisms that are generally not amenable to experimental manipulation and where species ecological roles are difficult to quantify.

Here, we address this issue, using frugivorous birds as a model system for examining the links between FD and species functional roles. Seed dispersal by frugivorous birds is an essential process in plant recruitment, especially in tropical forests where coevolution between fruiting plants and their seed-dispersal agents is most pronounced [29,30]. Furthermore, many studies have demonstrated that the mutualistic interactions between plants and frugivorous birds are strongly structured according to several clearly defined and easily measured functional traits [31–34]. For instance, while foraging height determines which plants a bird is likely to encounter [33], morphological traits such as beak shape and body size influence the rewards and handling efficiency of feeding on different fruits [31,34]. This tight association between traits and resource use, leads to the prediction that frugivores with more distinct traits will perform more unique functional roles [21,35] and, all else being equal, will thus support a greater number of plant species within the network than those frugivores with less distinct traits [36–38].

To test the extent to which FD can provide a surrogate for frugivore functional roles, we assembled a comprehensive database of avian functional traits across a global compilation of plant–frugivore interaction networks (see the electronic supplementary material, table S1 for references of the original studies). These networks collectively describe more than 58 000 unique interaction events across 546 species of birds and allow

us to address the following key aims. First, we examine how trait and phylogenetic similarity relates to the dietary overlap between frugivores, and thus test the importance of niche complementarity, a key assumption underlying the relationship between functional diversity and function. Second, we conduct analyses examining how the functional roles of frugivores within networks are related to their FD (and ED) as well as a number of intrinsic traits for which an effect on function is expected. We quantified species functional roles according to three quantitative network metrics relevant to understanding the effects of FD, including the frequency of interactions [39], interaction specialization [40] and interaction strength—a measure of the number of plant species dependent on each frugivore [41]. Finally, because direct estimates of species abundance are not available for the networks we study, we examine the link between species FD and abundance across a global database of avian communities [42] using ED as a proxy for FD. Through this approach, we aim to provide a critical and broad-scale assessment of the use of functional traits as surrogates for the ecological functions supported by frugivorous birds.

2. Material and methods

(a) Avian seed-dispersal networks

We compiled from the literature a database of mutualistic networks describing the visitation and feeding events between birds and fruiting plants. In total, we obtained 34 networks from 25 studies distributed across all the world's continents (except Antarctica; electronic supplementary material, table S1). Of these networks, 23 are 'quantitative', recording not only the presence or the absence of interactions, but also the number of individuals visiting each plant species (i.e. visitation rate). Although interaction events are not synonymous with seed-dispersal events [43], they are the best available proxy at this scale in the absence of more detailed information on disperser effectiveness [26,39]. To ensure that we focused on species most probably functioning as seed-dispersal agents, we excluded known seed predators (species in the family Psittacidae, $n = 23$ species). The functional traits included in this study are specific to birds, and thus we also removed the small number of observations for non-avian frugivores ($n = 43$ species). Our final database included a total of 58 401 unique interaction events between 546 species of birds and 1141 species of plants (electronic supplementary material, table S1, database S1).

(b) Avian local abundance

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

(c) Avian functional traits and phylogenetic relationships

For each avian species, we collected 10 morphometric measurements, including published estimates of mean species body mass (g) [44] and nine traits measured from field collections and preserved museum skins (electronic supplementary material, database S1). The nine traits measured here (to the nearest 0.01 mm) were: beak length (two separate measures), beak

width, beak depth, gape width, tarsus length, tail length, wing length and Kipp's distance, the distance between the tip of the longest primary and the first secondary (see the electronic supplementary material, table S2 for further details). Previous results indicate that these traits are robust proxies for resource use, foraging manoeuvre and substrate [45]. Where possible, we obtained measurements from at least two individuals from each sex for each species ($n = 2665$ specimens, mean = 5 per species). Throughout, we used the log (ln)-transformed mean species values to calculate trait distances between frugivores.

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

(d) Testing for niche complementarity between frugivores

For each pair of species in each network, we quantified an inverse measure of interaction similarity using the Horn–Morisita distance (d_{HM}). For each network, we then calculated the Spearman rank correlation (ρ) between d_{HM} , species phylogenetic patristic distance and Euclidian trait distance. We compared the observed correlation to that expected under a null model of random network structure (1000 replicate simulations) in which interactions between birds and plants were randomly re-assigned while maintaining the exact species degree (i.e. number of partners) of each node, using the 'permatfull' function in the R package Vegan [47]. We calculated the standardized effect size of observed ρ -values (i.e. the z -score) and quantified the number of networks exhibiting a significant positive or negative z -score. We assessed the overall significance of a departure from null model expectations using a t -test ($p = 0.05$, two-tailed test). To ensure that our results are robust to the quality of network data and null model assumptions, we repeated our analysis using only quantitative networks ($n = 23$ networks; electronic supplementary material, database S2). In this case, the null model maintained the observed frequency of interactions for each node [48].

(e) Quantifying species functional roles

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

- (i) Visitation rate: the number of interactions performed by a species represents a major quantitative constraint on species functional impact [26]. Although this metric ignores any potential differences in the 'quality' of dispersal agents, these effects may generally be outweighed by the large observed variation in visitation rates [39].
- (ii) Specialization (d'): we quantified the degree of specialization of each frugivore using the standardized Kullback–Leibler distance [40]. This metric of specialization varies from 0 (generalist) to 1 (specialist), and accounts for differences in visitation rates both across frugivores and plants. Specifically, frugivores that deviate from a random sampling of available interaction partners by preferentially interacting with otherwise rarely visited plants are deemed more specialized.
- (iii) Species weighted interaction strength: the strength of the interaction between frugivore species i and plant species j is calculated as the number of visits by frugivore i to plant j , divided by the total number of visits to plant j [41]. A higher interaction strength indicates a greater dependency of plant j on frugivore i , and the sum of

these values for each frugivore thus provides an integrated measure of its quantitative impact on the plant community.

(f) Identifying the predictors of species functional roles

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

We compared the effects of FD and ED to a number of intrinsic traits proposed to influence frugivore functional roles, including the degree of obligate frugivory, average foraging height, body mass and gape width. We extracted gape width measurements (mm) and body mass (g) from our dataset of morphological traits. The degree of obligate frugivory (%) was obtained from an independent dataset containing the percentage contribution of fruit, as well as six other food types (invertebrates, vertebrates, carrion, seeds, nectar and 'other plant material'), to species' diets [44]. We also used this dataset to calculate species foraging height as the weighted mean across five ordinal levels (1, ground; 2, understorey; 3, midstorey; 4, canopy and 5, aerial). Finally, previous evidence suggests that geographically rare species may be more functionally distinct [7], and so we also included geographical range size, calculated by overlaying species breeding extent of occurrence maps on an equal area grid (cell resolution of $110 \text{ km} \approx 1^\circ$ at the equator) [52]. Terms exhibiting a positive skew were ln-transformed and all predictors were normalized to enable a direct comparison of effect sizes.

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

We tested the predictors of interaction strength and specialization following log and angular transformation, respectively. For visitation rate, we used a generalized linear mixed model, assuming a Poisson error structure. When predicting visitation rates, we accounted for difference in overall sampling intensity across networks by including the total number of observed interaction events as an offset term. Because interaction strengths will also vary due to sampling intensity and species richness, we standardized species scores relative to the maximum value observed in each network. Predictor terms were assessed both in isolation and in combination using multi-model averaging [54]. Specifically, we calculated the Akaike information criterion (AIC) of models including every combination of predictors and then used model AIC weights to calculate average effect sizes, significance and relative variable importance. Metrics of FD and ED provide alternative measures of distinctiveness and so we fit five different model sets, one for each metric. Finally, because gape width and body mass

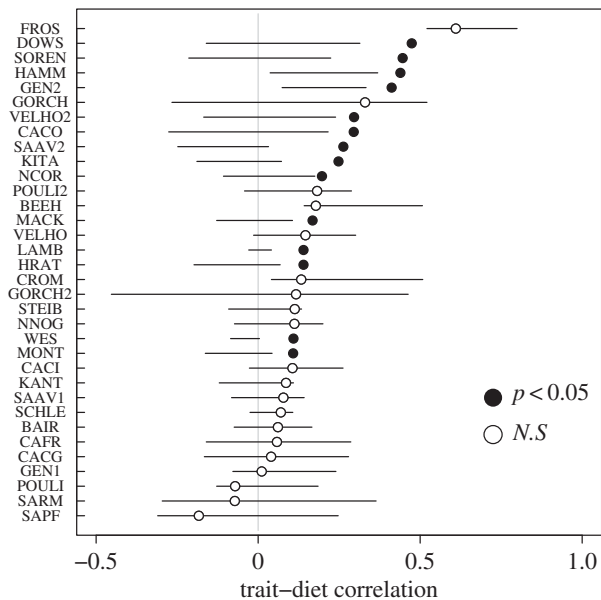


Figure 1. Functional trait-dependent structure of mutualistic seed-dispersal networks. Observed correlations between dietary d_{HM} and functional trait dissimilarity (circles) across the 34 empirical networks compared to the expectations under the null model (horizontal bars indicate 95% confidence intervals). Filled circles indicate correlations that are stronger than expected under the null model.

(Pearson correlation $r > 0.8$) are strongly correlated we fit separate models for each of these variables.

(g) Quantifying the relationship between distinctiveness and abundance

We tested the relationship between the local abundance of species in each assemblage and local ED (ln-transformed) using a generalized linear mixed-effects model, assuming a Poisson error structure and including 'assemblage', 'species', 'avian family' and observation level random effects. We also calculated the correlation coefficient between ED and local abundance within each avian assemblage to examine how this relationship varies as a function of species richness and across geographical space.

3. Results

(a) Functional trait-based complementarity of frugivore niches

We found that dietary distance (d_{HM}) between avian frugivores was positively correlated with trait dissimilarity (figure 1; electronic supplementary material, table S3). Of the 34 networks, 27 exhibited a positive standardized effect that was significant in 14 cases ($p < 0.05$), strongly rejecting a null model of random network structure (t -test: $t = 4.87$, $p < 0.001$). Phylogenetic distance was positively associated with trait distance (33 of 34 networks exhibited a positive slope, mean correlation = 0.42; electronic supplementary material, table S3) and accordingly, we also detected a significant positive relationship between d_{HM} and phylogenetic distance (t -test: $t = 3.77$, $p < 0.001$; electronic supplementary material, table S3). These results were largely robust to the type of network and null model used. When we focused exclusively on quantitative networks, d_{HM} remained positively correlated with both trait (t -test: $t = 3.06$, $p = 0.006$) and phylogenetic distance (t -test: $t = 1.82$, $p = 0.08$), although the

latter relationship was marginally non-significant (electronic supplementary material, table S4).

(b) The relationship among functional traits, visitation rates and abundance

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

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

(c) The relationship between functional traits and specialization

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

(d) The relationship between functional traits and interaction strength

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

4. Discussion

Our analysis of the functional and phylogenetic structure of avian frugivore networks provides support for trait-based

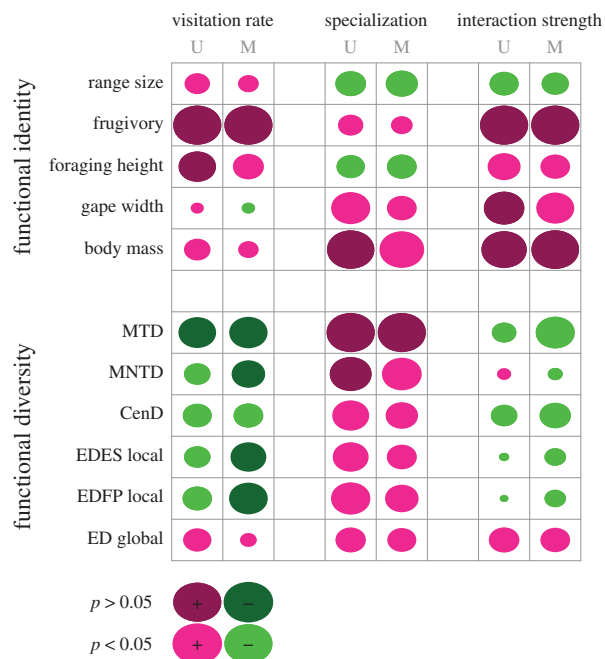


Figure 2. Functional trait and phylogenetic predictors of species network roles quantified on the basis of visitation rates, interaction specialization d' and interaction strength ($n = 485$). Results are shown for both univariate (U) and multivariate (M) models. Circle colour denotes positive (magenta) or negative (green) trends and statistical significance (dark: $p < 0.05$; light: $p > 0.05$). Circle size is proportional to the absolute effects size scaled relative to other predictors in each model.

niche complementary between species, a key pattern thought to underpin the positive relationship between functional trait diversity and ecological function. In particular, we found that closely related frugivores with similar functional traits consistently interact with more similar sets of plants, while distantly related birds with distinct traits exhibit relatively little overlap in resource use. In accordance with this, our analysis showed that frugivores with distinct traits also tend to be more functionally specialized, interacting with plants that are less frequently visited by other members of the community. The importance of functional trait matching in structuring interactions within plant–frugivore networks is well established [31–34,55,56], and our analysis across multiple networks, regions and ecosystems further highlights the use of functional traits as general predictors of the overlap and specialization of these mutualistic interactions.

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

calculate FD or whether we employed ED as a proxy for trait distinctiveness.

One possible explanation for the decline in visitation rates with FD is the occasional inclusion in the networks of distinct and distantly related species from other trophic guilds that rarely feed on fruit. However, this is unlikely to explain our results, because we found that the negative effects of FD on visitation rates actually became stronger when we statistically accounted for the degree of obligate frugivory and other intrinsic species traits. Visitation rates are expected to strongly reflect underlying differences in species abundance [39] and thus an alternative explanation is that the decline in visitation rates with FD is driven by a lower abundance of distinct species within local assemblages. Here, using phylogenetic relatedness as a proxy for trait similarity, we reveal this trend in birds at a global scale by showing that locally evolutionary distinct species consistently occur at lower densities than those species coexisting with many close relatives. Thus, our results suggest that the quantitative impacts of frugivores are independent of FD, because the positive effects of reduced ecological redundancy are nullified by a corresponding decrease in abundance.

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

Although species interaction strengths were generally unrelated to metrics of functional diversity, we detected a significant effect of intrinsic functional traits, notably obligate frugivory, body size and gape width. Previous studies have suggested that obligate frugivores play an important role as ‘network connectors’ because of their nutritional requirement to feed on multiple different fruits [59]. By contrast, our analysis shows that frugivory is unrelated to interaction specialization, and that the stronger interaction strengths of obligate frugivores are instead probably owing to their higher feeding rates. The positive contributions of body size and gape width to interaction strength also make sense. While plants producing small fruits can be dispersed by a wide variety of birds, only large-bodied frugivores with wide gapes are able to disperse the fruits of large-seeded plants [31]. The primary importance of large-gaped frugivores for seed-dispersal has previously been shown [60] and our analysis extends this finding across multiple avian assemblages, highlighting the status of large-gaped species as what might be termed ‘network keystones’. Furthermore, large-bodied specialist frugivores also appear highly sensitive to human pressures, being the first to disappear following habitat degradation [25], suggesting that even the loss of only a few frugivore species may have a disproportionate impact on the maintenance of seed-dispersal services.

Metrics used as surrogates for ecosystem function in conservation biology generally only consider the functional and

phylogenetic diversity of species and rarely account for species abundance or intrinsic functional traits (e.g. [8–11]). This is because, at such broad spatial and taxonomic scales, information on abundance is generally unavailable while the relationships between intrinsic traits and ecosystem functions are generally unclear. However, abundance and intrinsic traits are known to exert major constraints on species functional effects [22,27,28], and our results suggest that standard functional and phylogenetic diversity metrics ignoring these aspects of assemblage structure may misrepresent the diversity of interactions supported by avian frugivores [61], and within ecological networks more generally [50].

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

the case given the potential for interspecific variation in the effectiveness of avian dispersal agents [43].

Broad-scale comparative analyses of how functional traits and phylogenetic metrics relate to the functional roles of species provide an important perspective in helping to translate the results of detailed experimental studies to reliably predict, and thus mitigate, the consequences of species loss in natural ecosystems. However, these efforts remain preliminary and the robustness of any conclusions drawn at this scale will depend on the quality and relevance of the ecological data used to quantify species functional roles. Our analysis using data on frugivore–plant interaction intensities confirms a general pattern of trait-based niche complementarity across networks, but nonetheless suggests that functional trait diversity may provide a relatively weak surrogate for frugivore functional roles. A more detailed examination of the links between functional diversity, abundance and ecological processes is a key priority for future research.

Data accessibility. The data used in this study have been deposited in Data Dryad database S1 [64].

Authors’ contributions. A.L.P. devised the research; T.B., C.S. and B.D. compiled data; A.L.P. performed the analyses and A.L.P., R.S.E. and J.A.T. wrote the paper.

Competing interests. There are no competing interests.

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