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RESEARCH ARTICLE

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Specialists and generalists fulfil important and complementary functional roles in ecological processes

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Abstract

1. Species differ in their resource use and their interactions with other species and, consequently, they fulfil different functional roles in ecological processes. Species with specialized functional roles (specialists) are considered important for communities because they often interact with species with which few other species interact, thereby contributing complementary functional roles to ecological processes. However, the contribution of specialists could be low if they only interact with a small range of interaction partners. In contrast, species with unspecialized functional roles (generalists) often do not fulfil complementary roles but their contribution to ecological processes could be high because they interact with a large range of species.
2. To investigate the importance of the functional roles of specialists versus generalists, we tested the relationship between species' degree of specialization and their contribution to functional-role diversity for frugivorous birds in Andean seed-dispersal networks. We used two measures for the specialization of birds—one based on the size, and one based on the position of their interaction niche—and measured their effect on the birds' contribution to functional-role diversity and their functional complementarity, a measure of how much a species' functional role is complementary to those of the other species.
3. In all networks, there were similar log-normal distributions of species' contributions to functional-role diversity and functional complementarity. Contribution to functional-role diversity and functional complementarity increased with both increasing niche-position specialization and increasing niche size, indicating that the composition of functional roles in the networks was determined by an interplay between specialization and generalization. There was a negative interaction

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between niche-position specialization and niche size in both models, which showed that the positive effect of niche-position specialization on functional-role diversity and functional complementarity was stronger for species with a small niche size, and vice versa.

4. Our results show that there is a continuum from specialized to generalized functional roles in species communities, and that both specialists and generalists fulfil important functional roles in ecological processes. Combining interaction networks with functional traits, as exemplified in this study, provides insight into the importance of an interplay of redundancy and complementarity in species' functional roles for ecosystem functioning.

KEYWORDS

Andean seed dispersal, ecosystem function, foraging niche, frugivory, interaction networks, plant–bird mutualism, redundancy, traits

1 | INTRODUCTION

The functioning of ecosystems is governed by an interplay of many ecological processes. In particular, the different processes paramount for maintaining species communities, such as pollination and seed dispersal, often involve mutualistic interactions between different trophic levels, for example, between plants and animals. Interaction networks describe the resource use and functional roles of species in ecological processes such as seed dispersal, pollination and predation (Bascompte & Jordano, 2014). In the context of these ecological processes, species differ in the way they exploit the available resources, both in the set of resources they use (differences in the niche position) and in the range of the resources they use (differences in niche size). Resource specialists—species that preferentially use a certain type of resource (Jorge et al., 2014)—often show adaptations that allow them to exploit resources that no or few other species can use, or to use these resources more efficiently than other species (Levine & HilleRisLambers, 2009). As a result, these specialists often fulfil functional roles that are complementary to those of other species. Complementarity in functional roles is considered one of the main mechanisms underlying the relationship between diversity and the functioning of ecosystems (Blüthgen & Klein, 2011; Fründ et al., 2013), and specialized species are therefore considered particularly important for ecological communities (Mello et al., 2015; Mouillot et al., 2013; Violle et al., 2017).

The importance of a species for a community is, however, not only influenced by the degree to which the species differs in resource use from other species but also by the range of the resources it uses. For instance, species whose resource use differs from that of other species could be more important because they interact with species with which few other species interact (complementary resource use), but they could be less important if they only interacted with a small number of species; likewise, species with unspecialized resource use and large niches (generalists) could be considered less important if their resource use overlaps widely with those of other species (redundant resource use), but they could be more important because they interact with a large number of species (Chase & Leibold, 2003; Grime, 1998; Lyons et al., 2005; Mouillot et al., 2013; Violle et al., 2017). This ambiguity between generalists and specialists raises the important question of whether specialists contribute more to ecological processes than generalists, which, to our knowledge, has never been tested.

Two common ways of analysing the specialization of species in ecological processes and their functional roles are via interaction networks and via species' functional traits. In network ecology, species are regarded as specialists if they interact with relatively few interaction partners (Bascompte & Jordano, 2014) or if they interact with a distinct set of interaction partners that differs from those of the other species in the network (Blüthgen et al., 2006). In contrast, species are regarded as generalists if they interact rather indiscriminately with many partners. A major shortcoming of the network approach is that it is only based on the identities of the interacting species (i.e. species names) and does not take into account information about the interaction partners (e.g. information about their traits; Dehling, 2018). As a consequence, network indices can only describe a species' resource use in a network relative to the resource use of other species and as long as at least some species overlap in their interaction partners (Dehling et al., 2020), but it is impossible to describe the niches of species and compare them between species from different networks.

One way to take into account information about species when describing their specialization and their functional roles is via species' functional traits. Functional traits represent species' adaptations to their different functional roles (Tilman, 2001; Villéger et al., 2008), and indeed differences in species' functional trait combinations correspond to differences in their resource use (Coux et al., 2016; Dehling et al., 2016; Pigot et al., 2020). Since functional-trait diversity increases with increasing differences in trait combinations between species (Cadotte et al., 2011; Hooper et al., 2005), species with unusual trait combinations likely contribute most to functional-trait diversity (Su et al., 2019) and are therefore considered especially important for

the ecological process (Mouillot et al., 2013). However, while differences in species' traits are related to differences in functional roles between species and their preferences for certain resources (Dehling et al., 2016), it is currently still not possible to use functional traits alone to approximate the range of resources used by species, that is, their niche sizes (but see Cohen et al., 1993; Gravel et al., 2013; Warren & Lawton, 1987 for allometric relationships in food webs).

An alternative way of describing the role of a species that combines the advantages from interaction networks and functional traits but aims to overcome the shortcomings described above is to describe the functional role of a species via the species' *interaction niche*, that is, the traits of the species with which the focal species interacts (Dehling & Stouffer, 2018). Similar to functional-trait diversity, the interaction niche is commonly measured in a multidimensional trait space (Figure 1a). By taking into account the traits of species' interaction partners (i.e. resources), this approach informs about the range of resources used (niche size) as well as the exact characteristics of these resources (niche position). Moreover, by taking into account the frequency with which a species interacts with different resources, it is possible to determine a species' preference (or *niche centroid*) within the range of resources used (Figure 1b). Applying this approach has provided new insights into the degree of specialization of species (Coux et al., 2016; Dehling & Stouffer, 2018; Peralta et al., 2020) as well as the seasonal and local variation in species' resource use (Bender et al., 2017; Dehling et al., 2020; Quitián, Santillán, Bender, et al., 2019). In addition, by comparing the differences in species' functional roles via the overlap in their interaction niches, it is possible to quantify each species' contribution to the diversity of functional roles (Figure 1c,d; Dehling & Stouffer, 2018) and the complementarity of its interaction niche and, hence, the potential importance of the species for the ecological process. The approach is therefore well-suited for testing the relationship between the specialization of a species and its contribution to ecological processes in diverse communities.

We investigated the relationship between species' resource-use specialization and their contribution to the diversity of functional roles (FD) and functional complementarity for frugivorous bird species in seed-dispersal networks in the tropical and subtropical Andes. The study area spans the region with the highest diversity of frugivorous birds worldwide (Kissling et al., 2009). In addition, Andean seed-dispersal networks are structurally similar (Bender et al., 2018; Dehling et al., 2020), which facilitates testing for general mechanisms underlying the organization of highly diverse species communities. [Correction added on 22 July 2021, after first online publication: Bender *et al.* 2018b deleted from references and Bender *et al.* 2018a changed to 2018.] For each bird species in each network, we determined the size of its interaction niche (Figure 1a) and a measure for the specialization of its interaction-niche position (Figure 1b).

Since bird species with specialized interaction-niche positions differ in their resource use from that of other species, we hypothesized that a species' contribution to FD and its niche complementarity should increase with increasing specialization of its interaction-niche position as this should lead to less overlap between its interaction niche and the interaction niches of other species.

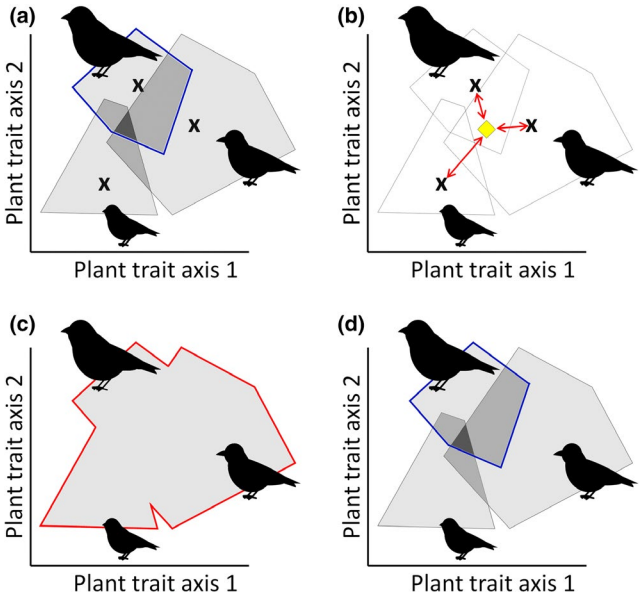

FIGURE 1 Measures to compare the resource use of species in ecological processes based on species' interaction niches. (a) The functional role of a frugivorous bird in a seed-dispersal network is described by its interaction niche: the range of trait combinations of the plants it consumes, measured in a multidimensional trait space (only two axes shown here). It is quantified as a convex hull (light-grey polygons), shown here for three bird species, and highlighted in blue for one species. The interaction-niche position of each bird is determined by the interaction centroid (shown as 'x'). It marks the mean position of all plant species consumed by a bird, weighted by the frequency with which the bird interacts with each species. (b) The specialization of a species' niche position is determined as the distance from a species' interaction centroid in plant trait space ('x') to the average centroid of all bird species in the network (*functional originality* in Dehling et al., 2016). (c) The diversity of functional roles (FD) of the bird species in a seed-dispersal network is quantified as the volume of plant trait space covered by the interaction niches of all bird species (outlined in red). (d) A species' contribution to FD and its functional complementarity are calculated by quantifying the overlap between the species' interaction niche and the interaction niches of the other bird species, here exemplified for one bird species highlighted in blue. Any part of the niche that overlaps with those of other species is divided by the number of overlapping niches. The result is the *weighted interaction niche*. A species' contribution to FD is calculated by dividing the volume of the weighted interaction niche (outlined in blue) by FD (outlined in red); functional complementarity is calculated by dividing the volume of a species' weighted interaction niche by the full volume of its interaction niche

2 | MATERIALS AND METHODS

2.1 | Networks

We sampled interaction networks between frugivorous birds and fleshy-fruited plants at seven sites along the tropical and subtropical Andes: two networks each from Ecuador and Peru, and one each from Bolivia, Colombia and Argentina. All networks were sampled repeatedly throughout an entire year to capture seasonal differences in plant phenology. At

each site, we established transects and recorded all fruiting plant species. Interactions were recorded if a frugivorous bird visited a focal plants species and consumed its fruit. Sampling effort ranged from 300 hr (Bolivia) to 960 hr (Peru1) (mean ± *SD*: 606 ± 224 hr); network size from 19 plant × 22 bird species (Bolivia) to 52 plant × 61 bird species (Peru 1) (30 ± 13 × 38 ± 14 species); observed links between plant and bird species from 50 (Bolivia) to 398 (Peru 1) (161 ± 111 links); observed interaction events (number of distinct visits to a plant species) from 241 (Bolivia) to 4,988 (Peru 1) (1,447 ± 1,539 visits). All networks combined included 205 plant species and 162 bird species across 11,090 interaction events (additional details in Table S1, see also Bender et al., 2018). Parrots were excluded from the Argentinian and Colombian networks because the only observed interactions presented cases of seed predation. Original data on the seven seed-dispersal networks are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.wm37pvmn5 (Dehling et al., 2021). [Correction added on 22 July 2021, after first online publication: Final sentence updated to give Dryad details.]

2.2 | The interaction niche of bird species

We described the functional role of a bird species in the seed-dispersal networks by its interaction niche, which is determined by the trait combinations of the plant species that it consumes (Dehling & Stouffer, 2018). For all plant species in the networks, we collected (in the field) four morphological traits known to influence the interaction between fleshy-fruited plants and frugivorous birds (Bender et al., 2018; Dehling et al., 2014): fruit diameter, fruit length, plant height and crop mass (i.e. mean number of fruits per plant × mean fruit mass). We log- and z-transformed traits to approximate normality, and then used Principal Coordinates Analysis to project the plant species from all sites into one common four-dimensional plant trait space where they were arranged according to the Euclidean distances between their trait combinations (Villéger et al., 2008). For each bird species in each network, we then determined the interaction niche in plant trait space as the convex hull that includes all plant species with which the bird interacts (Figure 1a; Dehling & Stouffer, 2018). Based on results from previous studies on these plant–bird networks (Bender et al., 2018; Dehling et al., 2020), it appears that species forage on continuous ranges of traits, that is, the niches of species resemble multivariate normally distributed data. We therefore consider convex hulls to be useful representations of species' niches. The *interaction-niche size* of a bird species ('niche size' in the following) is given by the volume of its interaction niche in plant trait space; the *niche position* of a bird species is determined by the interaction centroid: the mean position of all plant species with which a bird interacts, weighted by the frequency of interaction (Figure 1b; Dehling et al., 2016; Dehling & Stouffer, 2018).

2.3 | Specialization of birds' functional roles in the networks: Niche size and niche position

We determined the specialization of all bird species in the networks based on the size and position of their interaction niches. Species with a larger interaction niche use plant species with a higher diversity of trait combinations, and they are therefore considered more generalized in their resource use; species with a smaller interaction niche use a smaller fraction of the available resource diversity and are therefore considered more specialized (Bascompte & Jordano, 2014). As a measure for niche-position specialization, we used *functional originality*, the distance between a species' interaction centroid and the average interaction centroid of all bird species in plant trait space (Dehling et al., 2016; Figure 1b). Species are considered more specialized; the more distant their interaction centroids are from the average interaction centroid (increasing niche-position specialization). Please note that since interaction networks are usually sampled for a single ecological process (e.g. pollination, seed dispersal), the roles of species are necessarily compared only with regard to this particular process, not with regard to a species' full resource use. The specialization of a species' functional role in the process of seed dispersal (whether it uses a wide range of fruit or how much the set of fruits it uses differs from the sets of other species) is measured only relative to the other species in the network. This potentially confusing overlap in terminology when referring to a species' specialization with regard to its full resource versus its specialization with regard to the resource use in a particular ecological process has been acknowledged in the network literature (e.g. Dalsgaard et al., 2017; Dehling, 2018). Please also note that while in this study we focus on the specialization of one of the trophic levels (birds), it would also be possible to measure the specialization and contribution for the other trophic level (plants) in an independent analysis (Dehling & Stouffer, 2018).

2.4 | Species' contribution to the diversity of functional roles (FD)

We quantified the diversity of the birds' functional roles (FD_{roles}, simply 'FD' in the following) in the seed-dispersal networks via the diversity of their interaction niches, calculated as the total volume of plant trait space covered by the interaction niches of all bird species from a network (Figure 1c; Dehling & Stouffer, 2018). FD measures the range of unique functional roles fulfilled by a set of species, and any region of the plant trait space covered by the interaction niche of more than one species is therefore counted only once (Dehling & Stouffer, 2018). To calculate the contribution of an individual species to FD, it is therefore necessary to quantify the potential redundancy between the functional roles of bird species, that is, how much each species' interaction niche overlaps with those of the other species in the network. For that, we divided the volume of any part of a species' interaction niche that overlaps with the interaction niches of other species by the number of overlapping species. We called this the *weighted interaction niche* (Dehling & Stouffer, 2018). The weighted interaction niches of all species add up to the value of FD. The *relative contribution to FD* is then calculated as the fraction between the weighted interaction niche and FD, and it is bounded between 0 and 1 (Figure 1d; Dehling & Stouffer, 2018). To visualize differences in species' contribution to

the diversity of functional roles, we determined the distribution of species' contributions to FD for each network. There were a small number of bird species that occurred in more than one network. However, since virtually none of the plants occurred in more than one network and since specialization is always measured relative to the other species in the respective networks, we treated all species from all sites as independent.

2.5 | Functional complementarity

We measured how much a species' functional role was complementary to those of other species by relating a species' contribution to FD to its niche size. For each bird species in each network, we divided the volume of its weighted interaction niche (calculated in the previous step) by the full volume of its interaction niche (Figure 1d). The complementarity of a species' interaction niche thus measures which fraction of a species' interaction niche is complementary to the niches of the other species. Complementarity is highest if a species' interaction niche does not overlap with the niches of any other species but decreases with increasing overlap between a species' interaction niche with the niches of other species. To visualize differences in species' functional complementarity, we determined the distribution of functional-complementarity values for each network.

2.6 | Relationship between species' specialization and their contribution to FD and functional complementarity

To relate a species' specialization to its contribution to FD and its functional complementarity in the seed-dispersal networks, we fitted generalized linear mixed-effects models with niche size and niche-position specialization as predictors and site as a variable (or 'random') factor (random slope and random intercept) in R 3.6 (R Core Team, 2019) and STAN (Stan Development Team, 2018). We also tested whether the different measures for specialization influenced each other by including an interaction term between niche size and niche-position specialization in the models. For the models with relative contribution to FD as response variable, we used a logit link with a beta prior for the response, as contribution to FD is bound between 0 and 1 but in practice cannot reach either value; for models with functional complementarity as response variable, we used a logit link with a log-normal prior for the response because values for functional complementarity commonly reached 1. We calculated R^2 values following Gelman et al. (2018). In the model, the slope describes how much the response changes relative to a change in the predictor (in standard deviations). Since we used a Bayesian approach, we regarded relationships to be supportive of our expectations (i.e. significant) if the confidence interval of the slope did not include zero. To consider nonlinear relationships, we repeated the analyses with a generalized additive mixed model (GAMM, Figure S1). Since species' specialization, contribution to FD and complementarity are always measured relative to the other species in the respective local network, we treated all species from all networks as independent.

3 | RESULTS

3.1 | Contribution to FD and functional complementarity

In all networks, there was a similar log-normal distribution of species' contributions to the diversity of functional roles (Figure 2a). Most species contributed little to the local FD, and the median contribution ranged from 0.008 (Argentina) to 0.025 (Peru 2; Figure 2a). The species with the highest contributions in the individual networks were *Turdus rufiventris* (0.39, Argentina), *Aulacorhynchus coeruleicinctis* (0.23, Bolivia), *Mionectes striaticollis* (0.10, Colombia), *Tangara schrankii* (0.11, Ecuador 1), *Aulacorhynchus prasinus* (0.11, Ecuador 2), *Rupicola peruvianus* (0.17, Peru 1) and *Buthraupis montana* (0.15, Peru 2).

The distribution of species' functional complementarity generally showed a broader variation across the networks (Figure 2b), with median complementarity ranging from 0.114 (Peru 1) to 0.478 (Bolivia). Bird species with both a high contribution to FD and a high functional complementarity belonged to the families Turdidae (*Turdus*), Ramphastidae (*Aulacorhynchus*, *Andigena*), Cracidae (*Penelope*, *Chamaepetes*), Cotingidae (*Rupicola*) and Thraupidae/Passerellidae (*Thraupis*, *Chlorospingus*).

3.2 | Relationship between species' resource specialization and their contribution to FD

A species' contribution to FD increased with increasing niche size and with increasing niche-position specialization ($R^2 = 0.90$, 89% CI = [0.88, 0.92], Figure 3, Table S2). The relationship was stronger for niche size (slope = 1.14 [0.91, 1.38]) than for niche-position specialization (slope = 0.45 [0.21, 0.69], Figure 3a,b). Results obtained with the GAMM were very similar (Figure S1). The findings are therefore in accordance with the expectation that species that use a wider range of resources contribute more to the diversity of functional roles, and also with the expectation that species contribute more to the diversity of functional roles if they use resources that few other species use.

There was a negative interaction between niche size and niche-position specialization (slope = −0.14 [−0.23, −0.04], Figure 3c,d), indicating that the positive relationship between niche-position specialization and contribution to FD was stronger for species with smaller niche sizes, and the positive relationship between niche size and contribution to FD was strongest for species with an unspecialized niche position. In line with that, a species' niche size was negatively correlated with the specialization of its niche position (slope = −0.74 [−1.04; −0.43], Figure S2). This suggests that there is a continuum from generalization to specialization along which species can maximize their contribution to FD.

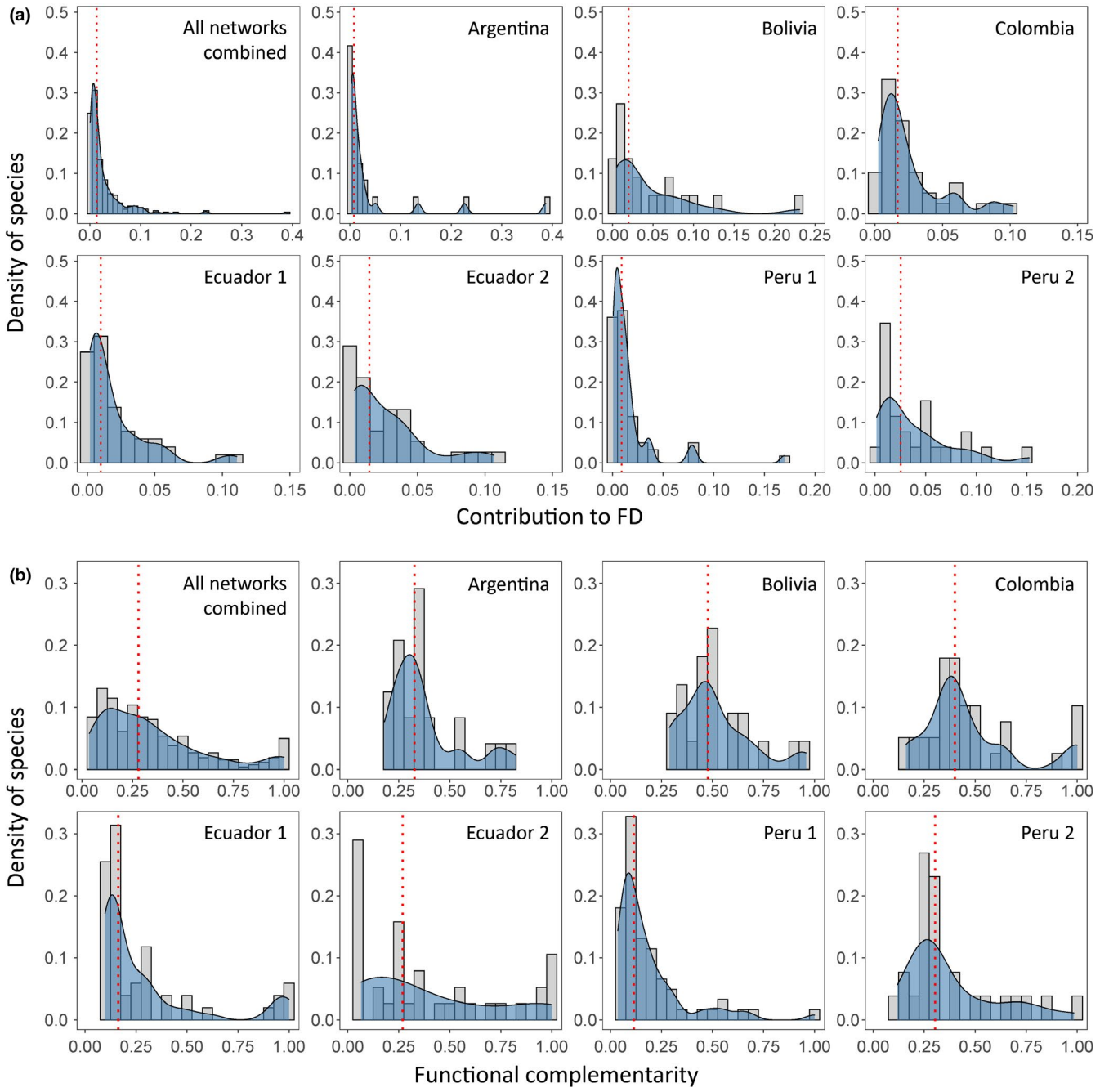

FIGURE 2 Variation in the contribution to the diversity of functional roles (FD) and functional complementarity among species across seven seed-dispersal networks along the Andes. (a) Histograms and density distribution for species' contribution to FD. Values for species contribution are shown on the *x*-axis, the density of species for each value of contribution on the *y*-axis. The red vertical line marks the median contribution observed in each network. Note the different scaling of the *x*-axes. (b) Histograms and density distribution for species' functional complementarity. Values for functional complementarity are shown on the *x*-axis, the density of species for each value of contribution on the *y*-axis. The red vertical line marks the median functional complementarity observed in each network. Values close to 0 indicate that a species' interaction niche overlaps with those of many other species; values of 1 indicate that a species' interaction niche does not overlap with those of any other species

3.3 | Functional complementarity versus niche specialization

Functional complementarity increased with increasing niche-position specialization and with increasing niche size (R^2 = 0.64 [0.59, 0.67], Figure 4, Table S3). Results obtained with the GAMM were very similar (Figure S1). The relationship was stronger for niche-position specialization (slope = 0.42 [0.19, 0.65]) than for niche size (slope = 0.17 [0.07, 0.28], Figure 4a,b). As in the model for contribution to FD, there was a negative interaction between niche size and niche-position specialization in the model (Figure 4c,d), indicating that the relationship between functional complementarity

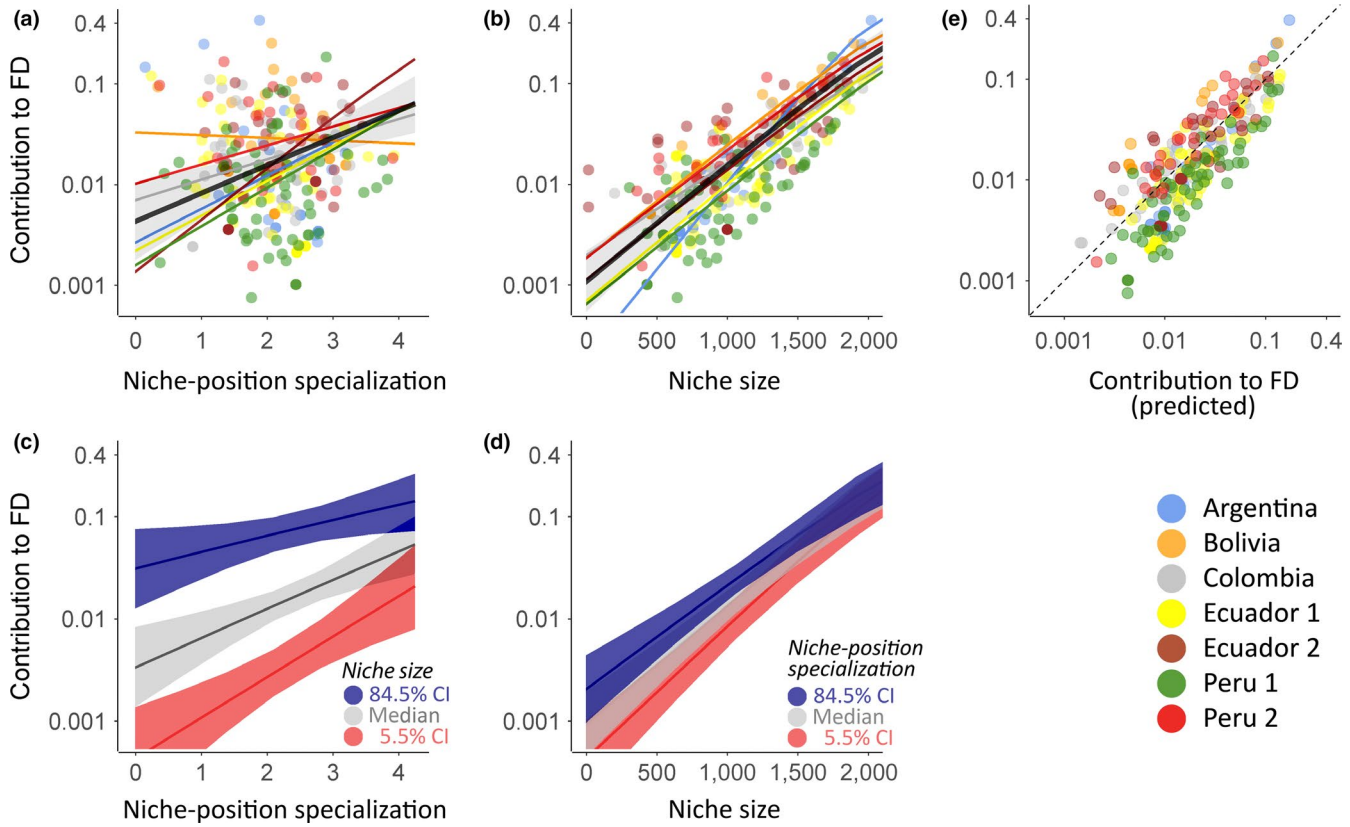

FIGURE 3 The relationship between species' resource-use specialization and their contribution to the diversity of functional roles (FD) in seed-dispersal networks from seven sites in the Andes. (a)–(d) Marginal-effects plots for estimates from a generalized mixed-effects model for the relationship between species' contribution to FD and the predictors niche-position specialization, niche size and their interaction, with site included as random factor. Mean estimates of intercept and slope for each site are shown in corresponding colours; black lines show mean and 89% confidence interval (grey) of estimates for the fixed effects. The contribution to FD increases with (a) increasing specialization of the interaction-niche position and (b) increasing niche size. (c) Marginal effects of niche-position specialization on contribution to FD for three fixed values of niche size (blue: 84.5 percentile, grey: median, red: 5.5 percentile) to illustrate the interaction between niche-position specialization and niche size. (d) Marginal effects of niche size on contribution to FD for three fixed values of niche-position specialization (blue: 84.5 percentile, grey: median, red: 5.5 percentile). (e) Observed values for species' contribution to FD against mean posterior predictions from the full model (contribution to FD ~ niche size + niche-position specialization + niche size × niche-position specialization. Colours correspond to the seven sites

and niche-position specialization was strongest for species with small niches, and the relationship between functional complementarity and niche size was strongest for species with unspecialized niche positions. Even though complementarity generally increased with increasing niche size, a few species with small niches also showed high values of functional complementarity (Figure 4b).

4 | DISCUSSION

In all networks, there were similar log-normal distributions of species' contributions to functional-role diversity and species' functional complementarity. The contribution of species to the functional-role diversity in the seed-dispersal networks appeared to be determined by an interplay between generalization and specialization, and species' contributions were highest for species with larger interaction niches—that is, species that interact with a wide range of plant species—as well as for species with specialized niche position—that is, species that interacted with plant species with which few or no other species interacted. Similarly, the complementarity of species increased with increasing niche-position specialization and increasing niche size. The observed negative interaction between species' niche size and their niche-position specialization indicated that there was a continuum from generalization to specialization along which species could maximize their contribution to FD.

The large variation in the contribution to FD and in functional complementarity among the species in each network demonstrates that there was a wide spectrum in the way in which species contributed to the seed-dispersal process, from generalists with large niches and overlapping roles to specialist frugivores with specialized and complementary roles. While seed-dispersal networks are generally considered less specialized than other networks such as pollination networks or host–parasite networks (Blüthgen et al., 2007), these differences between individual species are a reminder that not all participants in the seed-dispersal process are generalists or even redundant in their resource use. Instead, in each network, there was

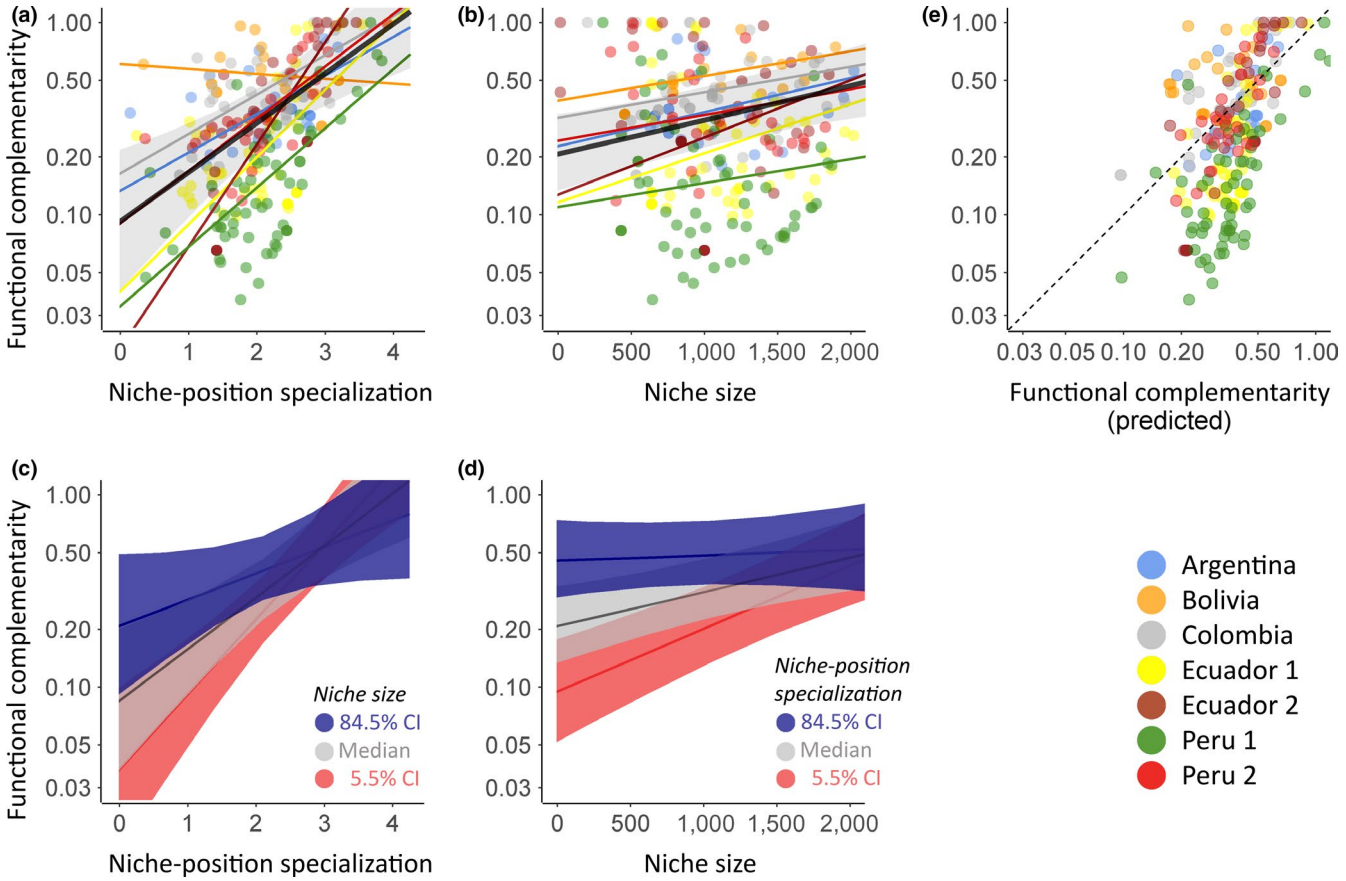

FIGURE 4 The relationship between species' resource-use specialization and their functional complementarity in seed-dispersal networks from seven sites in the Andes. (a)–(d) Marginal-effects plots for estimates from a generalized mixed-effects model for the relationship between species' functional complementarity and the predictors niche-position specialization, niche size and their interaction, with site included as random factor. Mean estimates of intercept and slope for each site are shown in corresponding colours; black lines show mean and 89% confidence interval (grey) of estimates for the fixed effects. Functional complementarity increases with (a) increasing niche-position specialization and (b) increasing niche size. (c) Marginal effects of niche-position specialization on functional complementarity for three fixed values of niche size (blue: 84.5 percentile, grey: median, red: 5.5 percentile) to illustrate the interaction between niche-position specialization and niche size. (d) Marginal effects of niche size on functional complementarity for three fixed values of niche-position specialization (blue: 84.5 percentile, grey: median, red: 5.5 percentile). (e) Observed values for functional complementarity against mean posterior predictions from the full model (functional complementarity ~ niche size + niche-position specialization + niche size × niche-position specialization). Colours correspond to the seven sites

a set of species whose functional roles comprised a very large part of the diversity of functional roles and could probably not be replaced by the other species in the network. The differences also underline that not all species contribute to a local ecological process to the same extent: many species overlapped with many other species and therefore contributed relatively little to FD, whereas a relatively small number of species had very high contributions to the diversity of functional roles. At the same time, even species with small interaction niches (and, hence, a small contribution to FD) showed a high functional complementarity, that is, they fulfil functional roles that no or only few other species fulfil. This is in line with recent findings that, while functional-trait diversity generally increases with increasing number of species, the increase does not have to be strictly proportional (Lamanna et al., 2014; Santillán et al., 2019). To the contrary: the expectation of similar contributions to FD from all species could mask the impact of the species that contribute the most to the diversity of functional roles and at the same time overestimate the impact of species that only opportunistically participate in a process.

All networks showed similar distributions of species' contribution to FD and complementarity. This is in line with previous studies that showed that there is a similar composition in functional roles in all networks, despite large differences in species composition (Dehling et al., 2020). Most species contributed little to local FD; and few contributed much. A few bird species, mostly from the families of toucans (*Aulacorhynchus*, *Andigena*), cotingas (*Rupicola*), tanagers (*Buthraupis*, *Thraupis*) and guans (*Chamaepetes*, *Penelope*) showed combinations of both high contributions to FD and high functional complementarity and therefore contributed most to the seed-dispersal process in the local networks. These species tend to be obligate frugivores, and they appear to be particularly important for the corresponding plant species and, hence the functioning of the ecological process in the local species communities (Bastazini

et al., 2019; Vizentin-Bugoni et al., 2020). At the other extreme, there were a large number of species that contributed little to FD. However, several of the species nevertheless showed high values for complementarity, indicating that their niches showed little or even no overlap with those of other species. This demonstrates that species with low contributions to FD are not necessarily redundant or replaceable, because even species with comparably small niches can contribute functional roles to the ecological process that are fulfilled by few or even no other species.

In addition, even the species with low complementarity and low contribution might be relevant for the ecological process, even though their effect on the process might be more difficult to detect. While the loss of species with specialized functional roles can have obvious impacts on species communities, for example, a reduction in fruit size due to the loss of large frugivores (Galetti et al., 2013), the effects of losing redundancy on the functioning of ecological processes are less well known and more difficult to assess (Gaston & Fuller, 2008). Redundancy in species' functional roles is often considered an insurance against species extinctions or fluctuations of species' abundances in time (Allan et al., 2011; Naeem, 1998). However, the functioning of ecological processes also depends on the number of individuals that fulfil certain functional roles, that is, on abundance itself (Quitián, Santillán, Espinosa, et al., 2019; Winfree et al., 2015), and these individuals can be composed of different but functionally similar species. Given that many species in tropical networks have low local abundances that are limited by factors other than the availability of food (Hubbell, 2013), the loss of species with apparently redundant roles or even the reduction in the number of individuals fulfilling these roles could have detrimental effects on plant communities (Dee et al., 2019; Gaston & Fuller, 2008; Janzen, 2001; Rosenberg et al., 2019; Valiente-Banuet et al., 2015). Unfortunately, interaction networks are usually not sufficiently well-resolved to investigate the effect of the number of individuals per species that participate in the network. Consideration of species abundances in future studies of ecological processes via interaction networks could therefore lead to a better understanding of the quality, as well as quantity, of functional roles required for the functioning of ecological processes in a local community—that is, the match between the functional roles that need to be fulfilled and the local number of species and individuals that fulfil them.

Related to that, even if bird species appear to be redundant because they feed on the same plant species, they could still be complementary with regard to the outcome of their interactions, for instance because they differ in the way they disperse the seeds of the plants. Each plant species attracts a certain set of dispersers and all these dispersers together provide a distinct dispersal kernel for each plant species (Sorensen et al., 2020). The loss of any of the dispersers will necessarily alter the dispersal kernel, with potentially detrimental effects for the regeneration of forests after natural or anthropogenic disturbances (García & Martínez, 2012; Schleuning et al., 2020). Taking into account differences in the outcome of interactions (Blendinger, 2017; Muñoz et al., 2017; Simmons et al., 2018) might therefore lead to additional insights into the complementarity or redundancy of co-occurring species (Allan et al., 2011; Blüthgen & Klein, 2011; Kang et al., 2015; Pillar et al., 2013).

In addition, the contribution of bird species to the seed-dispersal process could change seasonally according to the range of available resources. While the specialization of species' niche positions relative to the other species in a network was shown to be similar in different seasons (Bender et al., 2017), the relative contribution could differ depending on seasonal differences in the presence of bird species in the networks. The latter might especially prove to be true if—instead of quantifying the contribution of birds to the dispersal of plants—we considered the other trophic level and measured the contribution of plants to maintaining the diversity of frugivorous bird species in different seasons or in times of resource scarcity.

Finally, measuring the contribution of birds to the seed dispersal of plants is only one way to quantify the potential contribution of bird species to the functioning of plant communities. For instance, instead of using plant traits that influence the interaction between bird and plant species, we could use plant traits that are related to other ecological processes fulfilled by the plants. Using the data on bird–plant interactions from the observed seed-dispersal networks, we could then quantify the contribution of each bird species to the ecological process fulfilled by the plants that the bird disperses.

In the present study, we compared resource use and overlap between co-occurring bird species and showed that both generalists and specialists can contribute important functional roles to seed-dispersal processes. Understanding the required balance in the functional roles fulfilled by generalists and specialists is a challenging topic for future studies in network ecology that will lead to new insights into the relationship between diversity and ecosystem functioning. In this regard, the combination of interaction networks and functional traits to quantify the overlap of species' functional roles in a local ecological process, as exemplified in our study, is a powerful approach to provide insight into the importance of the interplay between redundancy and complementarity for the functioning of ecological processes.

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AUTHORS' CONTRIBUTIONS

D.M.D. and D.B.S. conceived the ideas and designed the study; D.M.D., P.G.B., M.C.M., M.Q., F.S. and V.S. collected the data; D.M.D. analysed the data and wrote the manuscript; all authors commented on conceptual ideas and manuscript drafts, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Original data on the seven seed-dispersal networks are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wm37pvmn5 (Dehling et al., 2021). [Correction added on 22 July 2021, after first online publication: First sentence deleted from this section.]

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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