

# Niche Packing and Local Coexistence in a Megadiverse Guild of Frugivorous Birds Are Mediated by Fruit Dependence and Shifts in Interaction Frequencies\*

D. Matthias Dehling,<sup>1,2,†</sup> Giulio Valentino Dalla Riva,<sup>1,3</sup> Matthew C. Hutchinson,<sup>1,4</sup> and Daniel B. Stouffer<sup>1</sup>

1. Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand; 2. Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland; 3. School of Mathematics and Statistics, University of Canterbury, Christchurch, New Zealand; 4. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544

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**ABSTRACT:** Niche packing is one of the prevailing mechanisms underlying the increase in the number of co-occurring species and the extraordinary diversity of tropical ecosystems. However, it is not yet understood whether niche packing is facilitated by higher specialization and reduced niche overlap or, rather, by diffuse competition and increased niche overlap. We combined highly resolved bird-plant interaction networks, bird phylogenies, and plant functional traits to compare dietary niche overlap and foraging frequencies among frugivorous birds at seven sites in the tropical Andes. We quantified niche overlap on the basis of the traits of the plants used by each bird and related it to the degree of niche packing at the different sites. Niche complementarity decreased with increasing niche packing, suggesting that increasingly dense niche packing is facilitated by increased niche overlap. Pairwise niche overlap was mediated by shifts in foraging frequencies away from shared resources, and it decreased with decreasing phylogenetic relatedness and increasing dependence on fruit as resource. Our findings suggest that foraging choices are a key axis of diversification in frugivorous birds and that differences in resource use frequencies are already sufficient to reduce potential competition between ecologically similar species and facilitate niche packing, especially if species differ in their dependence on particular resources.

**Keywords:** Eltonian foraging niche, interspecific competition, mutualism, niche evolution, niche overlap, seed dispersal interaction networks.

## Introduction

Niche expansion and niche packing are among the primary mechanisms underlying the increase in species numbers between two species communities (MacArthur 1965). Under niche expansion, species-rich communities use a wider niche space than species-poor communities, usually facilitated by more favorable combinations of local abiotic conditions, such as higher productivity and higher habitat heterogeneity (Pianka 1974; Lister 1976; Pagani-Núñez et al. 2019). Under niche packing, the available niche space is more densely packed in species-rich communities than in species-poor communities, potentially because high local productivity allows species to partition the available niche space finely among themselves (Klopf and MacArthur 1961; MacArthur 1965; Schoener 1971; Pigot et al. 2016). Recent comparisons of species communities along elevational and latitudinal gradients revealed that niche packing is the primary driver of increasing species richness (Pigot et al. 2016; Pellissier et al. 2018). However, the mechanism underlying niche packing—specifically, how ecologically similar species partition the available resources—remains poorly understood (Pigot et al. 2016).

There are different ways in which ecologically similar species in local communities can divide the available resources among themselves (Sale 1974). For instance, species can reduce niche overlap by specializing on a subset of the available resources, thereby avoiding resources shared with other species (“niche contraction”; Pianka 1974; Alatalo et al. 1985; Grant and Grant 2006; Harrington et al. 2009). Depending on the similarity in resource use and species’

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† Corresponding author; email: matthias.dehling@canterbury.ac.nz.

**ORCIDs:** Dehling, <http://orcid.org/0000-0002-2863-5580>; Dalla Riva, <http://orcid.org/0000-0002-3454-0633>; Hutchinson, <http://orcid.org/0000-0002-2423-4026>; Stouffer, <http://orcid.org/0000-0001-9436-9674>.

dependence on the resource, this might ultimately lead to patterns of reduced resource use overlap between ecologically similar species (Grinnell 1917; Diamond 1975; Sanderson et al. 2009), in either space (Crowell and Pimm 1976; Grant and Grant 1982; Bretagnolle et al. 1990; Quillfeldt et al. 2015) or time (Jones et al. 2020). Alternatively, ecologically similar species can alleviate competition for resources by changing the frequency with which they use certain resources within their niches (“frequency shifts”; Willis 1966; Alatalo et al. 1986). On longer timescales, frequency shifts can be followed by a switch to new resources (“niche shifts”; Morse 1974; Tylianakis et al. 2008; Fründ et al. 2010, 2013; Pringle et al. 2019), resulting in gradual niche divergence, decreasing similarity in resource use with time, and decreasing similarity in resource use with decreasing phylogenetic relatedness (Silvertown et al. 2001; Webb et al. 2002).

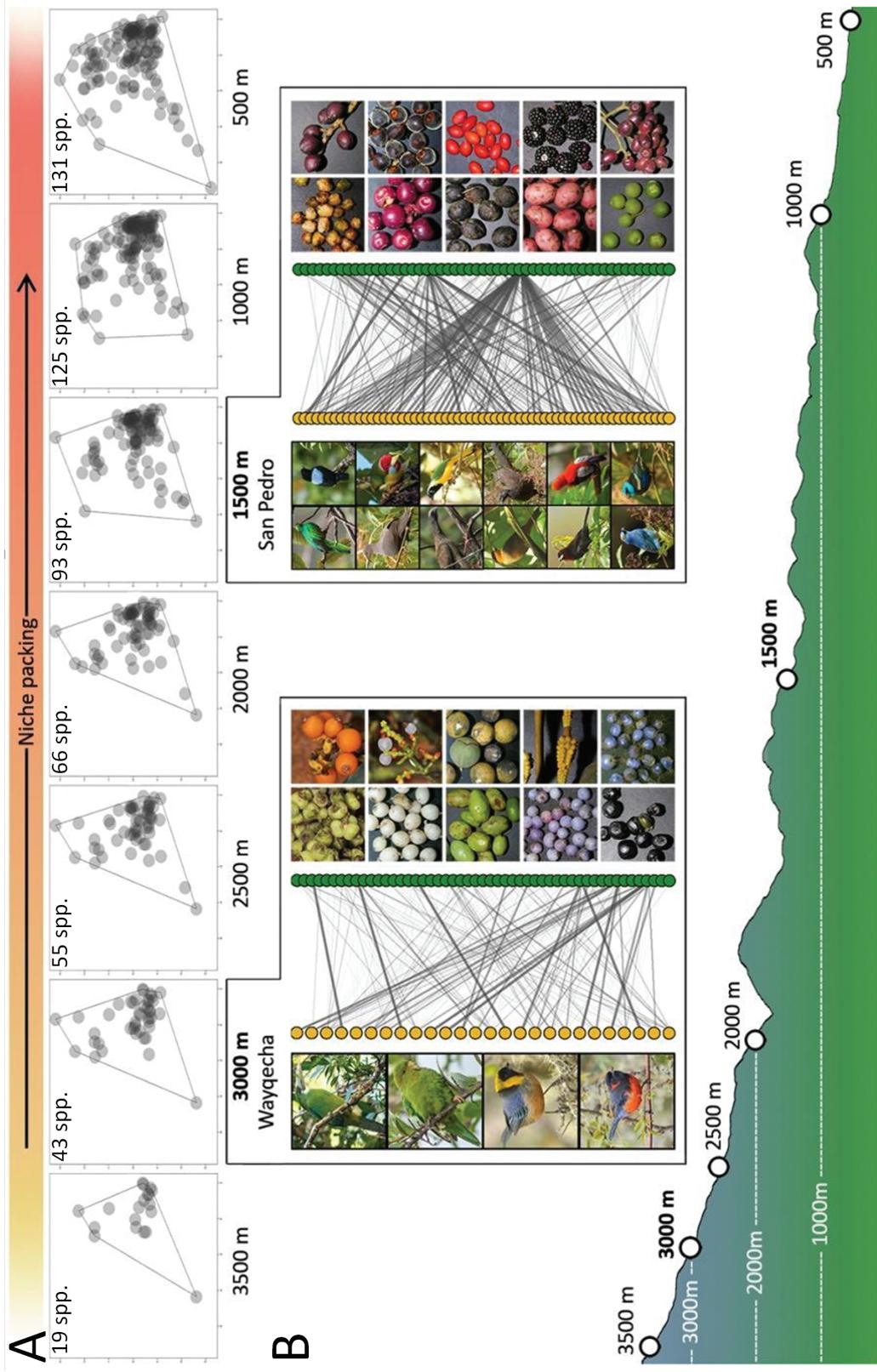
Richness gradients in the tropics are particularly well suited for studying niche packing because high productivity and long-term environmental stability should favor resource specialization and fine-scale partitioning of resources among co-occurring species (Hutchinson 1959; Schoener 1974; Pellissier et al. 2018). For instance, recent studies of bird communities along an elevational gradient in the tropical Andes of Peru revealed concurrent increases in species richness and functional trait diversity from high-elevation sites toward the more productive lower elevations (fig. 1; Dehling et al. 2014a; Pigot et al. 2016). The increase in species numbers toward lower elevations involves an increase in the density with which bird species fill the functional trait space (Dehling et al. 2014a; Pigot et al. 2016; fig. 1), consistent with the notion of an increasingly dense packing of species’ niches with increasing species richness (Klopfen and MacArthur 1961; MacArthur 1965; Schoener 1971). However, while functional trait combinations are related to species’ niche position and can therefore give insights into the differences in resource use and the distribution of these differences across a species community (Dehling et al. 2016), they are still limited in their ability to describe the range of resources that a species actually uses (i.e., the niche size of a species). It has been proposed that niche packing in species communities is facilitated either by (i) increased specialization involving smaller foraging niches and reduced niche overlap between species (niche contraction) or by (ii) reduced specialization and increased niche overlap (Klopfen and MacArthur 1961; Pigot et al. 2016), which might involve frequency shifts. Because of the limitations of quantifying overlap in resource use between co-occurring species from morphology (or other traits) alone, it has to date been impossible to assess the importance of differences in resource use as a potential mechanism underlying niche packing in species-rich communities.

One approach to studying the resource use and ecological similarity of co-occurring species is via quantitative eco-

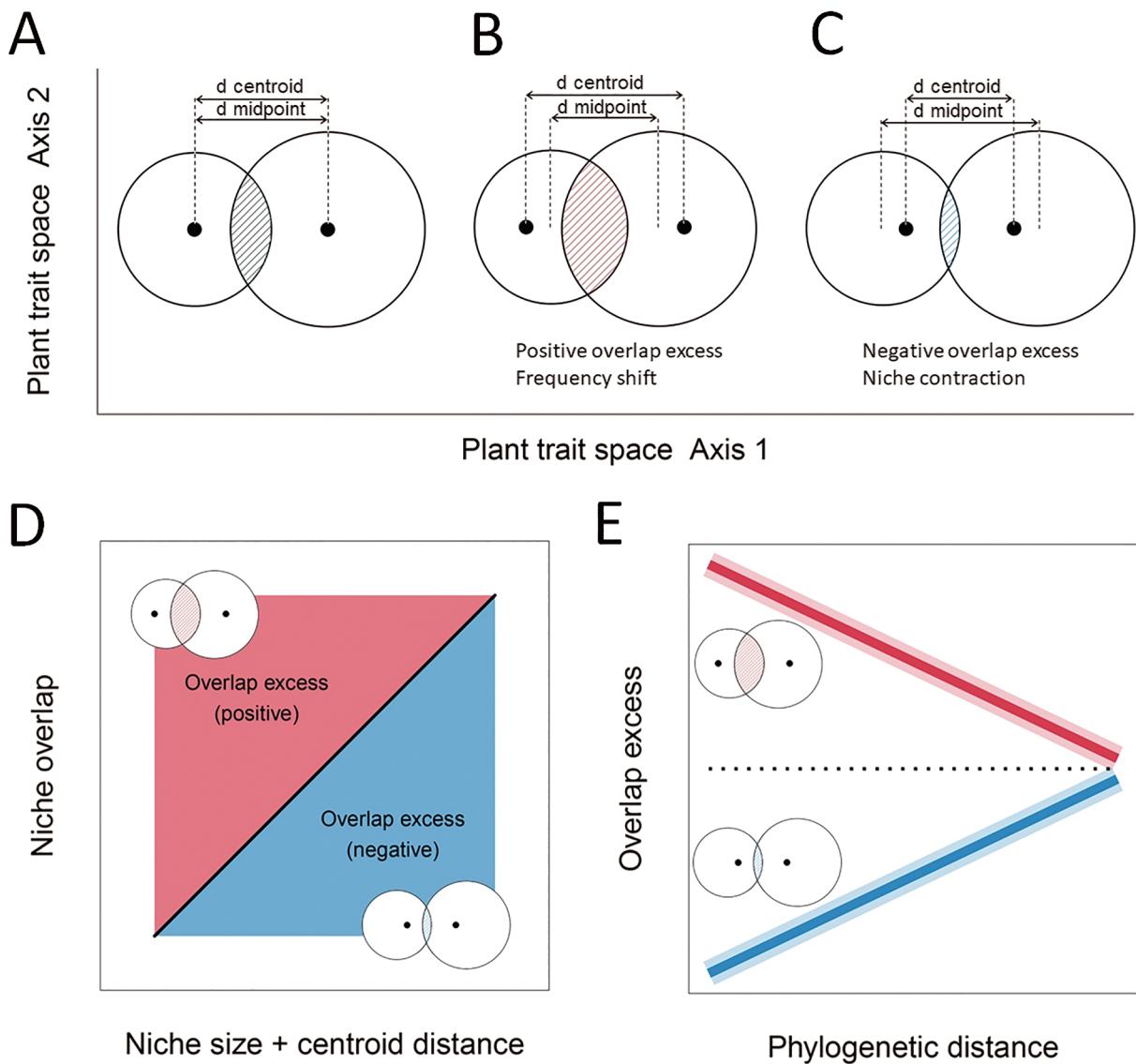
logical networks (Poisot et al. 2016; Tylianakis and Morris 2017; Dehling 2018). In particular, the recent combination of network data with functional traits has facilitated new ways to describe species’ foraging niches (Junker et al. 2013; Coux et al. 2016; Dehling and Stouffer 2018), providing new insights into seasonal (Bender et al. 2017) and local (Quitián et al. 2019; Dehling et al. 2020) variation in resource use, as well as the contribution of species to ecological processes (Peralta et al. 2020; Dehling et al. 2021a). These new approaches allow the comparison of species’ niche overlap and interaction frequencies, and they are therefore well suited for studying the mechanisms underlying niche packing in locally co-occurring species—namely, whether niche packing is facilitated by niche contraction among co-occurring species or frequency shifts away from highly used resources (fig. 2). In particular, by comparing species’ niche sizes, differences in niche overlap, and the frequency with which they use distinct resources (given by the distance between their niche centroids; fig. 2), it is possible to determine whether species overlap more (or less) in their resource use than what would be expected by chance. Moreover, a lower than expected overlap is indicative of niche contraction and possible avoidance of competition; a higher than expected overlap is indicative of frequency shifts away from shared resources (fig. 2C).

To identify potential mechanisms underlying the local coexistence of ecologically similar species and niche packing in species-rich communities, we investigated the resource use of frugivorous bird species at seven sites along the tropical Andes (two sites each in Colombia, Ecuador, and Peru and one site in Bolivia) using a combination of highly resolved interaction networks and plant functional traits. These frugivorous bird communities have a similar composition in their functional roles (Dehling et al. 2020), and niche packing has been identified as the dominant mechanism underlying their community assembly (Dehling et al. 2014a, 2014b; Pigot et al. 2016). Our aim was to analyze how ecologically similar bird species divide the available resources—in particular, we tested whether observed differences in resource use are indicative of increased niche overlap and frequency shifts or, rather, reduced niche overlap involving niche contractions.

First, on the regional scale across the Andes we tested whether increasingly dense niche packing leads to an increase in niche overlap. For each bird species from each of the seven networks, we determined (i) the size of its foraging niche, as represented by the trait space of the plant species that the bird species consumes; (ii) its interaction centroid (the mean position of the plant species consumed by the bird weighted by the relative interaction frequency; Dehling et al. 2016; Dehling and Stouffer 2018; fig. 2); and (iii) its niche complementarity based on its overlap with the foraging niches of the other co-occurring bird species



**Figure 1:** Example for frugivorous bird communities and interaction networks along an elevational gradient of increasingly denser niche packing in the tropical Andes (*Kosñipata Valley*, Manú National Park, Peru). **A**, Increase of functional diversity and species richness of frugivorous birds from high elevations to the lowlands. Species richness increases faster than the size of the bird functional trait space, leading to a higher density of bird species in the bird functional trait space indicative of increasingly denser niche-packing (Dehling et al. 2014a, 2014b; Pigot et al. 2016). **B**, Interaction networks at the two Peruvian sites analyzed in this study, which are situated along an elevational gradient of increasing species richness. Wayqecha (3,000 m) includes 26 bird and 51 plant species; the network at San Pedro (1,500 m) includes 61 bird and 53 plant species. The combination of highly resolved interaction networks and data on plant traits allows the quantification of resource use overlap of the co-occurring bird species and, hence, the potential mechanisms underlying the observed niche packing in the local communities. Photos: D. Matthias Dehling.



**Figure 2:** Assessing resource use overlap of co-occurring species. *A*, The overlap between the foraging niches of two bird species in plant trait space is influenced by the sizes of their foraging niches (shown by the size of the circles) and the distance between their interaction centroids (the mean position of the plant species consumed by the bird weighted by the relative interaction frequency, shown as black dots in the circles). Niche overlap is indicated by the hatched area at the intersection between the two niches. *B*, Frequency shifts occur if species shift their interaction centroids away from each other (indicated by a larger distance between centroids than between niche midpoints) and resulting in a higher niche overlap than expected based on niche size and interaction centroid distances. *C*, Niche contraction occurs if two species reduce the use of resources in the areas where their resource use overlaps, resulting in a lower niche overlap than expected based on niche size and interaction centroid distances. Note that niche contraction does not have to be symmetrical or absolute. *D*, Linear model of the relationship of species' pairwise niche overlap versus species' niche sizes and the distance between their interaction centroids. The positive relationship is indicated by the black regression line. Positive deviations from the relationship are shown in red and indicate higher pairwise niche overlap than expected from niche size and interaction centroid distances (positive overlap excess), indicative of frequency shifts; negative deviations are shown in blue and indicate lower pairwise niche overlap than expected from niche size and interaction centroid distances (negative overlap excess), indicative of niche contraction. *E*, Expected relationship between observed overlap excess and phylogenetic distance. Closely related species should be more similar in their resource use than distantly related species. Higher than expected niche overlap (positive overlap excess) for closely related species compared with distantly related species (red line) therefore indicates that co-occurrence of closely related species—and hence niche packing—is facilitated by increasing niche overlap and shifts in interaction frequencies; lower than expected niche overlap (negative overlap excess) for closely related species compared with distantly related species (blue line) indicates that niche packing is facilitated by reduced niche overlap due to niche contraction.

(Dehling et al. 2021a). For each site, we quantified the degree of niche packing based on the number of bird species and the amount of plant trait space used by the bird community. We then tested whether niche size, nearest neighbor distance of the interaction centroids, and niche complementarity changed with increasing niche packing. Second, focusing on individual networks, we explored which factors influence niche overlap between species in highly diverse communities. We used linear models to relate species' niche overlap to their niche sizes and the distance between their interaction centroids. To identify possible mechanisms underlying foraging niche overlap and coexistence among ecologically similar species, we tested whether the residual overlap (negative or positive overlap excess, i.e., the niche overlap remaining after controlling for each species' niche size and interaction-centroid distance; fig. 2) was related to their dependence on fruit as a resource (degree of frugivory, the percentage of fruit in their diet) or the phylogenetic distance between species.

If niche packing involved a reduction in resource overlap (niche contraction) or the exclusion of species with similar resource use, we hypothesized that (i) there would be similar or higher niche complementarity with increasing niche packing and (ii) there would be smaller overlap excess between closely related species (fig. 2E). Alternatively, if niche packing was characterized by shared resource use, we expected that (i) niche complementarity would decrease with increasing niche packing and (ii) closely related species would overlap more than expected based on their niche size and interaction centroids (i.e., larger overlap excess; fig. 2E). We also expected that species with a high dependence on fruit would be less likely to share resources with other species, leading to a decrease in overlap excess with increasing degree of frugivory.

## Methods

### Data

**Interaction Networks.** We used species interaction networks between frugivorous birds and fleshy-fruited plants sampled at seven sites along the tropical Andes: two networks each from Colombia, Ecuador, and Peru and one from Bolivia (Dehling et al. 2014a, 2014b; Saavedra et al. 2014; Muñoz et al. 2017; Quitián et al. 2019). The former six were situated along elevational gradients, with increasing bird and plant species richness toward lower elevations. Along the Peruvian gradient, niche packing has been identified as the dominant mechanism underlying community assembly (Pigot et al. 2016; fig. 1). All networks were sampled repeatedly throughout an entire year to capture seasonal differences in plant phenology, and sampling of interactions followed a common methodology. Specifically, transects were established at each site, and all fruiting plant

species within the transects were identified. Interactions were recorded if a frugivorous bird visited a focal plant species and consumed its fruit. Sampling effort ranged from 300 h (Bolivia) to 960 h (Peru 1; mean  $\pm$  SD:  $606 \pm 224$  h), network size from 19 plant  $\times$  22 bird species (Bolivia) to 52 plant  $\times$  61 bird species (Peru 1;  $30 \pm 13 \times 38 \pm 14$  species), observed links between plant and bird species from 50 (Bolivia) to 398 (Peru 1;  $161 \pm 111$  links), and observed interaction events (number of distinct visits to a plant species) from 241 (Bolivia) to 4,988 (Peru 1;  $1,447 \pm 1,539$  visits). All networks showed a similar composition of functional roles (Dehling et al. 2020), including a similar composition of generalists and specialist species (Dehling et al. 2021a). Original data on the seven seed dispersal networks have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.wm37pvmn5>; Dehling et al. 2021a, 2021b; additional details are provided in table S1.1 [tables S1.1, S2.1, S2.2, S3.1, S3.2 are available online] and Bender et al. 2018).

**Foraging Niches and Interaction Centroids of Bird Species.** We used data on plant traits for each of the networks (Dehling et al. 2021a, 2021b) that are known to represent the use of plant species by frugivorous birds (Dehling et al. 2014b, 2016; Bender et al. 2018): fruit length, fruit diameter, plant height, and crop mass (mean crop size  $\times$  mean fruit weight, as a measure for the amount of fruit mass offered by a single plant). We log and z transformed all traits and used principal coordinates analysis to project plant species from all networks into one common four-dimensional trait space with independent axes (Villéger et al. 2008). For each bird species from each network, we used the approach of Dehling and Stouffer (2018) to calculate (1) the absolute size of its foraging niche (represented by the traits of all plant species that the bird consumed) and (2) its interaction centroid (i.e., the mean position in plant trait space of the plant species consumed by the bird, weighted by the relative interaction frequency; Dehling et al. 2016; fig. 2). In addition to the absolute niche size, we also calculated species' relative niche sizes compared with the whole community (i.e., the ratio between a species' niche size and the total resource trait space occupied by the niches of all species in the community). To account for potential differences in methodology, we measured the birds' foraging niches in three different ways. First and second, we calculated foraging niches as trait probability densities (TPDs; see Carmona et al. 2019) in two different ways: once as a cumulative trait probability density (TPDc) of the trait combinations of all plants consumed by a bird, which considers individual TPDs around each plant species and then calculates a combined volume of trait space occupied by the TPDs of the plant species consumed by a bird, and once as a mean trait probability density (TPDm), which

considers a single density based on the mean and standard deviation of the trait combinations of the plants consumed by a bird (Carmona et al. 2019). Bird species with only one observed interaction partner were assigned the minimum standard deviation of birds with more than four observed interaction partners. When calculating the volumes occupied by TPD<sub>C</sub> and TPD<sub>M</sub>, we used the default TPD proportion (0.95; Carmona et al. 2019). Third, we computed each species' niche as the convex hull in plant trait space that includes all plant species consumed by a bird species (Dehling and Stouffer 2018; R code available at [http://www.github.com/matthiasdehling/fd\\_niche](http://www.github.com/matthiasdehling/fd_niche)). Since the results obtained with the different approaches were very similar, we present only those for TPD<sub>C</sub> in the main text (results for TPD<sub>M</sub> and convex hulls are presented in supplement S2 and supplement S3, respectively; supplements S1–S3 are available online).

**Niche Packing.** To determine the total niche space used by the birds of a local network, we calculated the diversity of their foraging niches as FD<sub>base</sub> (Dehling and Stouffer 2018), which measures the volume of plant trait space covered by the foraging niches of all bird species and any regions of trait space where foraging niches overlap are counted only once. We determined the degree of niche packing at each site as the number of bird species divided by FD<sub>base</sub> and standardized the values across networks by dividing all values by the maximum observed value for niche packing.

**Niche Overlap and Centroid Distance.** For each bird species in each network, we computed resource use similarity with all co-occurring species as the overlap in their foraging niches and the distance between their interaction centroids (Dehling and Stouffer 2018; fig. 2A). First, we determined the volume of niche overlap between bird species *i* and *j* as the volume of the intersection between their foraging niches, which describes the volume of resource trait space used by the two bird species (fig. 2). Next, we quantified the relative niche overlap for species *i* by dividing the volume of its niche overlap (with species *j*) by the total volume of its foraging niche. Relative niche overlap describes the proportion of species *i*'s foraging niche that is also occupied by another, potentially competing species *j* and hence ranges between 0 (no overlap) and 1 (complete overlap). Note that the relative niche overlap of species *i* with species *j* is different from the relative niche overlap of species *j* with species *i*. To describe the difference in interaction frequencies between each pair of bird species, we calculated pairwise Euclidean distances between their interaction centroids. For each species, we also determined the Euclidean distance to the species with the most similar

interaction centroid in the network (nearest neighbor centroid distance).

**Niche Complementarity.** For each bird species in each network, we calculated niche complementarity as the species' contribution to total resource use relative to its niche size (Dehling et al. 2021a). Specifically, we divided the volume of each part of a species' foraging niche that overlapped with the foraging niches of other species by the number of overlapping species ("weighted foraging niche"; Dehling and Stouffer 2018). The ratio between the volume of this weighted foraging niche and the full volume of the foraging niche represents the complementarity of a species' niche relative to the other species in the network (Dehling et al. 2021a; Dehling and Dehling 2021). If a species' foraging niche does not overlap with the niches of other species, the entire volume of the species' foraging niche is complementary to the niches of the other species; if the niche overlaps with the niches of other species, the resource use of the species is partly redundant, and only a fraction of the volume of a species' foraging niche is complementary to the foraging niches of the other species.

**Phylogenetic Relatedness of Bird Species.** We obtained 1,000 dated phylogenetic trees including all bird species from our networks from birdtree.org (Jetz et al. 2012, 2014) and calculated a consensus tree based on the phylogenetic backbone by Hackett et al. (2008). For each network, we calculated the pairwise phylogenetic distances between all bird species with the R package ape (Paradis and Schliep 2018).

**Degree of Frugivory.** Since the consequences of foraging niche overlap might also depend on the degree to which each bird species depends on fruit as a resource, we determined the degree of frugivory for each bird species in the network. For this, we used the percentage of fruit in the bird's diet as given in the EltonTraits database (Wilman et al. 2014).

#### Statistical Analyses

To identify the mechanisms underlying niche packing, we compared the resource use of frugivorous birds across all networks across the Andes; to identify mechanisms underlying the overlap in resource use in highly diverse communities, we compared similarity in foraging niches between co-occurring species within the individual networks.

First, we compared relative niche size, nearest neighbor centroid distance, and niche complementarity among the seven Andean networks on the regional scale and related them to differences in species richness and niche packing to test (i) whether the increase in species richness was facilitated by niche expansion or niche packing and

(ii) whether increasingly dense niche packing lead to either increased niche overlap or avoidance of niche overlap between species. For all variables, we used the median values for each network and compared them with the local species richness and niche packing (i.e., the ratio between species richness and total occupied niche space) using linear regression models.

Next, within each network, we analyzed the determinants of niche overlap between the co-occurring species to identify potential mechanisms underlying the niche packing in the species communities. First, for each network we fit linear regression models of species' relative niche overlap against niche size and centroid distance. We then used the residuals of these models to determine the overlap excess—i.e., the niche overlap between two species that remained after accounting for their expected overlap based on their niche sizes and interaction centroid distance (fig. 2). We used overlap excess to analyze the relationship between species' niches: a positive overlap excess represents a niche overlap between two species that is larger than expected and indicates that species' interaction frequencies (interaction centroids) are shifted away from each other; in contrast, a negative overlap excess represents a smaller than expected observed niche overlap and indicates that two species potentially exclude each other in the areas where their resource use overlaps (figs. 2C, S1; figs. S1, S2.1, S2.2, S3.1, S3.2 are available online).

To identify the mechanisms underlying niche packing within communities, we assessed the relationship between overlap excess and phylogenetic distance. Specifically, a positive overlap excess (larger than expected niche overlap) for closely related species compared with distantly related species (i.e., a negative relationship between phylogenetic distance and overlap excess) would suggest that co-occurrence of closely related species—and hence niche packing—is facilitated by a shift of interaction centroids away from shared resources (fig. 2E). Conversely, a negative overlap excess (smaller than expected niche overlap) for closely related species compared with distantly related species (i.e., a positive relationship between phylogenetic distance and overlap excess) would indicate that niche packing is facilitated by niche contraction away from shared resources (fig. 2E). Since the dependence of bird species on fruit likely represents their degree of foraging specialization and may influence their ability to switch to other resource types, we also tested the relationship between overlap excess and species' degree of frugivory. Finally, we tested whether any observed relationship between overlap excess and phylogenetic distance (i.e., niche packing) was mediated by species' degree of frugivory by including an interaction term between phylogenetic distance and degree of frugivory in the linear models.

We tested the relationship once for all networks combined in a linear mixed effects model with site as random effect (random intercept and slope). To consider potential non-independence between pairwise overlap excess values, we compared the model outcome against 1,000 models in which we randomly permuted rows and columns using the R package sna (Butts 2020).

## Results

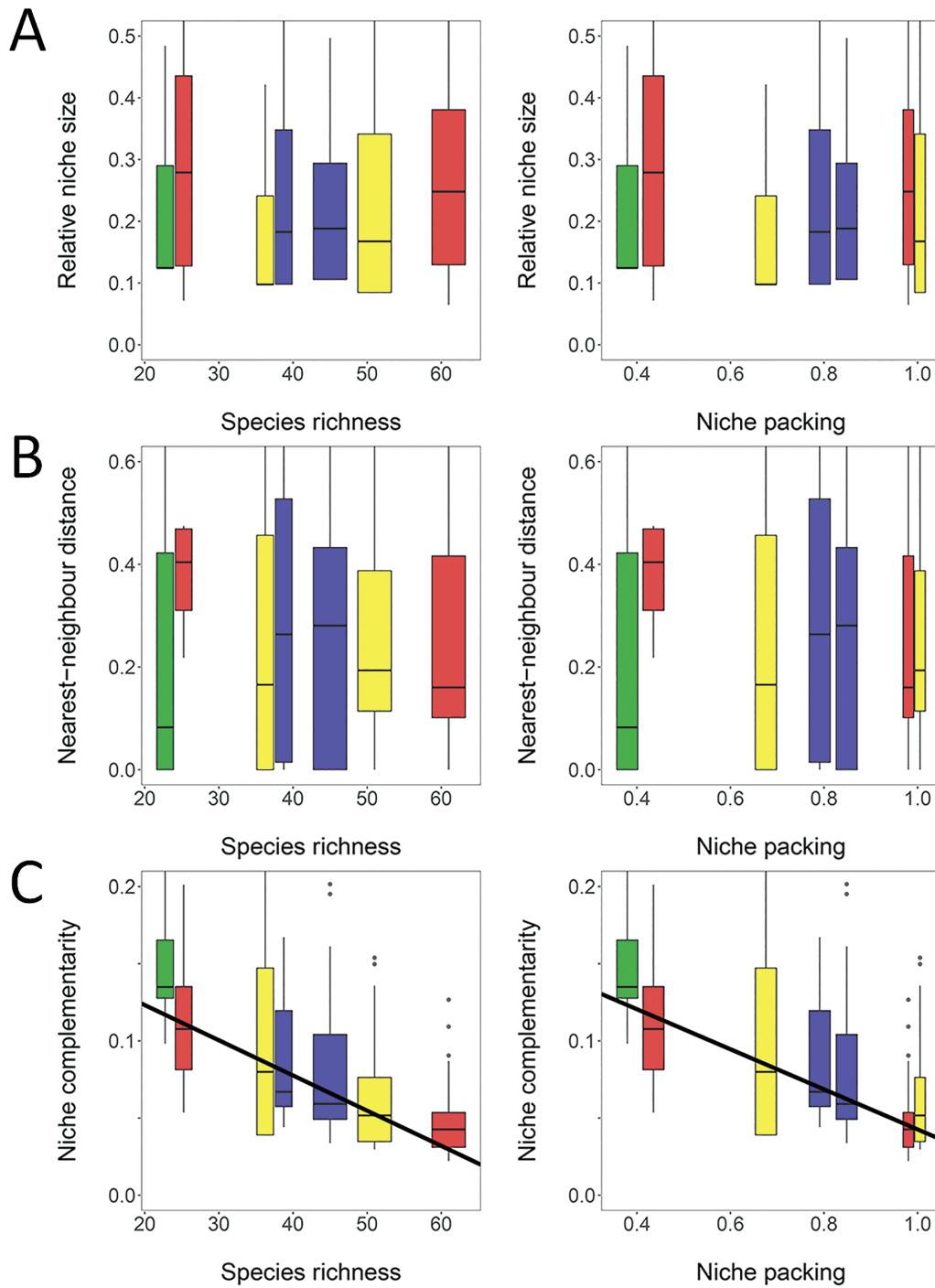
### *Comparison of Species' Niche Overlap on the Regional Scale*

Relative niche size—the proportion of niche space used by each species—was not related to species richness ( $R^2 = 0.06, P = .60$ ) or niche packing ( $R^2 = 0.01, P = .82$ ) of the local networks (fig. 3A), which is in line with the notion that an increase in species richness does not lead to species-level niche contraction (i.e., the use of a reduced range of resources to avoid niche overlap with other species). Nearest neighbor centroid distance—the proximity to the species with the most similar niche—was not related to species richness ( $R^2 = 0.02, P = .77$ ) or niche packing ( $R^2 = 0.01, P = .83$ ; fig. 3B). In contrast, niche complementarity—the degree to which a species' resource use differed from the co-occurring species—decreased with increasing species richness ( $R^2 = 0.89, P = .001$ ) and increasing niche packing ( $R^2 = 0.95, P < .001$ ) in the local networks (fig. 3C), which aligns with the expectation of increased resource use overlap between ecological similar species with increasing niche packing.

### *Determinants of Niche Overlap in the Individual Networks*

At all sites, relative niche overlap—the proportion of a species' niche that overlaps with the niche of another species—increased with niche size and decreased with increasing distance between species' interaction centroids (table 1). Intuitively, species experienced greater niche overlap with species that had larger niches and smaller niche overlap with species whose interaction centroids was more distant from their own centroid. Niche overlap between species was also negatively related to their phylogenetic distance ( $t = -3.6, P < .001$ ).

Overlap excess—the niche overlap that remained after accounting for niche size and centroid distance—decreased with increasing phylogenetic distance (table 2; fig. 4), supporting the hypothesis that niche packing in these communities is facilitated by higher than expected resource use overlap among closely related species and shifts in the interaction frequencies of those species away from shared resources. Overlap excess also decreased with increasing degree of



**Figure 3:** Differences in niche overlap of frugivorous birds among seven seed dispersal networks from seven sites along the tropical Andes (two sites each from Colombia [blue], Ecuador [yellow], and Peru [red] and one site from Bolivia [green]) with different levels of species richness and niche packing (number of species per volume of resource trait space used by the birds). *A*, Relative niche sizes (the ratio between a bird species' niche size and the total volume of used resources in plant trait space) against species richness ( $R^2 = 0.06, P = .60$ ) and niche packing ( $R^2 = 0.01, P = .82$ ). *B*, Nearest neighbor distances between species' niche centroids against species richness ( $R^2 = 0.02, P = .77$ ) and niche packing ( $R^2 = 0.01, P = .83$ ). *C*, Species' niche complementarity (the contribution of a species to the overall resource use in the network relative to the size of its foraging niche) against species richness and niche packing. Complementarity is highest for species' whose foraging niche does not overlap with those of other species, and it decreases with increasing niche overlap with other species. Niche complementarity decreased with increasing species richness ( $R^2 = 0.89, P = .001$ ; black line) and increasing niche packing ( $R^2 = 0.95, P < .001$ ; black line).

**Table 1:** Linear regression models of the relationship between relative niche overlap and two predictors, niche size and the distance between species' interaction centroids, in co-occurring frugivorous bird species at seven sites along the tropical Andes (two sites each from Colombia, Ecuador, and Peru and one site from Bolivia)

|                   | Niche overlap    |       |       |
|-------------------|------------------|-------|-------|
|                   | Estimate         | t     | P     |
| <b>Peru:</b>      |                  |       |       |
| 3,000 m:          |                  |       |       |
| Niche size        | .0001 ± .000002  | 31.3  | <.001 |
| Centroid distance | -.136 ± .009     | -14.9 | <.001 |
| 1,500 m:          |                  |       |       |
| Niche size        | .0001 ± .000001  | 70.5  | <.001 |
| Centroid distance | -.092 ± .003     | -34.6 | <.001 |
| <b>Colombia:</b>  |                  |       |       |
| 2,500 m:          |                  |       |       |
| Niche size        | .0001 ± .000002  | 34.9  | <.001 |
| Centroid distance | -.217 ± .007     | -32.8 | <.001 |
| 2,000 m:          |                  |       |       |
| Niche size        | .0001 ± .000002  | 33.9  | <.001 |
| Centroid distance | -.222 ± .007     | -33.0 | <.001 |
| <b>Ecuador:</b>   |                  |       |       |
| 2,000 m:          |                  |       |       |
| Niche size        | .0001 ± .000003  | 21.4  | <.001 |
| Centroid distance | -.294 ± .007     | -43.5 | <.001 |
| 1,000 m:          |                  |       |       |
| Niche size        | .0001 ± .000001  | 49.7  | <.001 |
| Centroid distance | -.176 ± .005     | -31.9 | <.001 |
| <b>Bolivia:</b>   |                  |       |       |
| 2,000 m:          |                  |       |       |
| Niche size        | .00004 ± .000003 | 15.4  | <.001 |
| Centroid distance | -.192 ± .013     | -14.9 | <.001 |

frugivory (table 2; fig. 4), corroborating the idea that species that depend less on fruit as a resource overlap more in their foraging niches. Finally, there was an interaction between phylogenetic distance and degree of frugivory: overlap excess was highest for closely related species with a low percentage of fruit in their diet and lowest for distantly related species with a high percentage of fruit in their diet (fig. 4), indicating that closely related species in this system are

more likely to co-occur when they are less dependent on fruits as resource.

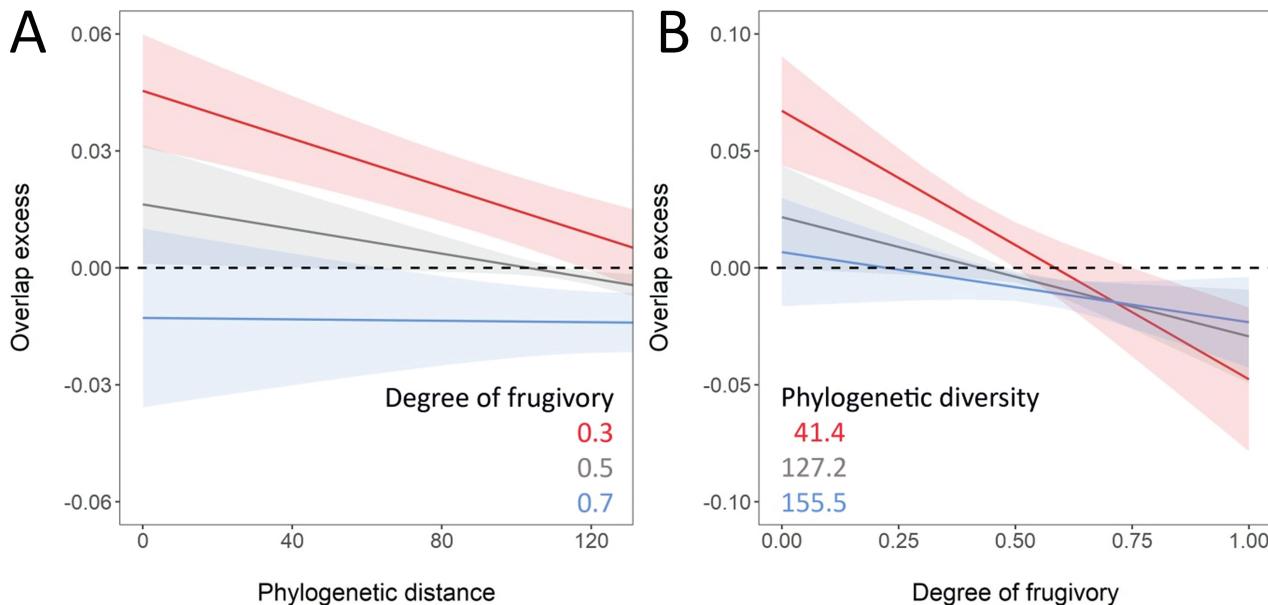
## Discussion

Across seven bird-plant interaction networks from the tropical Andes, we found that niche complementarity, but not relative niche size, decreased with increasing species richness and niche packing, which is in line with the

**Table 2:** Linear mixed effects model of the relationship between overlap excess and pairwise phylogenetic distance, degree of frugivory, and the interaction between phylogenetic distance and degree of frugivory in co-occurring frugivorous bird species at seven sites along the tropical Andes (two sites each from Colombia, Ecuador, and Peru and one site from Bolivia), with site as random effect (random intercept and slope)

|                                   | Overlap excess (residual niche overlap) |       |       |
|-----------------------------------|-----------------------------------------|-------|-------|
|                                   | Estimate                                | z     | P     |
| Phylogenetic distance             | -.0005                                  | -3.65 | <.001 |
| Degree of frugivory               | -.146                                   | -4.01 | <.001 |
| Phylogenetic distance × frugivory | .0007                                   | 2.90  | <.001 |

Note: Overlap excess describes the amount of niche overlap between two species not accounted for by their niche sizes and the distance between their interaction centroids; degree of frugivory is measured as the percentage of fruit in a bird's diet.



**Figure 4:** Relationship between overlap excess (the amount of niche overlap between two species after accounting for the size of their niches and the distance between their interaction centroids) and the phylogenetic distance between the overlapping species (A) and the degree of frugivory (the percentage of fruit in a bird's diet; B) at seven sites along the tropical Andes. A, Marginal effects of phylogenetic distance on overlap excess. Estimates for slope and 95% confidence interval are shown for three fixed values of degree of frugivory (25%, 50%, and 75% quantile). B, Marginal effects of degree of frugivory on overlap excess. Estimates for slope and 95% confidence interval are shown for three fixed values of phylogenetic distance (25%, 50%, and 75% quantile).

notion that increased niche packing involves higher overlap in species' foraging niches. Similarly, our network-level analyses showed that, across all sites, overlap excess in foraging niches was influenced by the phylogenetic relatedness of the birds and the degree to which species depended on fruit as a resource: overlap excess was highest for closely related species with a lower percentage of fruit in their diet, and it was lowest for distantly related species with higher dependence on fruit as a resource. The high overlap in resource use between closely related species in all networks corroborated the finding that niche packing was facilitated by increased niche overlap (overlap excess) and divergent resource selection (frequency shifts) rather than niche contraction.

Niche packing and the number of overlapping species increased with increasing species richness in the networks, in line with an increasingly denser niche packing as species richness increases toward lower elevations (Dehling et al. 2014a; Pigot et al. 2016) and toward sites with higher productivity (Pellissier et al. 2018). Importantly, species in the networks showed no reduction in their relative niche sizes or in their nearest neighbor centroid distance, indicating that the higher species richness toward lower elevations was not primarily driven by community-level niche expansion (i.e., the use of a wider range of resources by the bird

community; Lister 1976; Pagani-Núñez et al. 2019) or by niche contraction on the species scale (i.e., use of a reduced resource range by individual species to avoid niche overlap with other species; Pianka 1974; Alatalo et al. 1985). Instead, networks with higher species richness and denser niche packing showed a higher number of overlapping species and lower niche complementarity among the species, which indicates that niche packing involves increased niche overlap between ecologically similar species.

Across all networks, overlap excess was higher for closely related species (i.e., higher niche overlap than expected from centroid distance and niche size, indicative of a shift of interaction centroids away from shared resources) and decreased with increasing phylogenetic distance. The high overlap in resource use between closely related species in all networks suggests that niche packing in these communities was facilitated by increased niche overlap but divergent resource selection (i.e., shifts in interaction frequencies; Willis 1966; Alatalo et al. 1986) rather than niche contraction away from shared resources. Even though species used very similar sets of resources, they appeared to reduce the likelihood of resource competition by altering the frequency with which they use specific food items. This suggests that coexistence in ecologically similar species with widely overlapping niches can be

facilitated by behavioral shifts in the frequency with which resources are used.

Our results corroborate the idea that niche packing does not involve all species to the same extent (Gómez et al. 2010; Colorado and Rodewald 2015), and it was influenced by both phylogenetic relatedness and the degree to which species depended on fruit as a resource. In general, overlap excess was highest for species with a low dependence on fruit as a resource (opportunistic frugivores) and lowest for species from phylogenetically distinct lineages that depended more on fruit as resource (obligate frugivores), such as Galliformes (*Penelope*, *Ortalis*), Trogoniformes (*Pharomachrus*, *Trogon*), and Piciformes (Ramphastidae, *Andigena*, *Aulacorhynchus*). Hence, species that depend more on a resource were less likely to share resources with other species than species that largely feed on other resources (Zamora 2000; Dehling et al. 2014b). The “permissible degree of niche overlap” (Pianka 1974) under which coexistence—and hence niche packing—is possible appears to be lower for obligate frugivores than for opportunistic frugivores.

The large overlap excess observed in opportunistic frugivores compared with obligate frugivores might be related to population dynamics of birds and dispersal strategies of plants. Many opportunistic frugivores in our study sites forage in mixed-species flocks that can consist of several dozens of species (Munn 1985; Merkord 2010), providing the safety of a flock where local abundances of individual bird species are low (Powell 1985; Graves and Gotelli 1993). For predator avoidance and flock cohesion, it is advantageous if species have a similar morphology (Sridhar et al. 2012; Colorado and Rodewald 2015), which could in turn result in the use of relatively similar resources (Dehling et al. 2016). Similarly, many plant species visited by these flocks (e.g., the many species of Melastomataceae in our system) tend to produce large quantities of small fruits to attract a large number of opportunistic dispersers. Given the low local abundances of individual seed disperser species, it is therefore advantageous for the plants to be visited by a large number of species (Howe 1993). Hence, while competition can promote divergence (Schluter 1994), in our system divergence could be limited because it is more advantageous for opportunistic frugivores to forage in a flock than to have a unique resource; likewise, it could be more advantageous for opportunistic plant species to have many potential dispersers than to have unique dispersers. The availability of fruit differs seasonally, and competition might be alleviated in times when fruit are superabundant and more intense when resources are scarce (Terborgh and Diamond 1970; Fleming 1979) and species become more similar in their resource use (Bender et al. 2017). However, while some mixed-species flocks include clusters of ecologically similar species (Gómez et al. 2010; Colorado and Rodewald 2015), others can show competitive exclusion

on the level of individual flocks (Graves and Gotelli 1993). Unfortunately, interaction networks are usually not sampled in sufficient detail to show the resource use of species on the level of individual flocks. Fine-scale differences in flock composition or foraging patterns (MacArthur 1958; Robinson and Holmes 1982) could therefore additionally favor the local co-occurrence in our communities.

Niche shifts and shifts in the frequencies with which resources are used can both lead to resource partitioning and reduced potential for competition between coexisting species, facilitating the coexistence and affecting the evolutionary trajectories of species in diverse ecological assemblages (Alatalo et al. 1986; Losos et al. 1998). The decrease of overlap excess with increasing phylogenetic distance in our networks might suggest that shifts in the frequencies of resource use are the initial step underlying species diversification that are then later followed and manifested in proper niche shifts (Grant and Grant 1982). On the other hand, our networks do not present closed communities of species that all evolved in sympatry. Rather than an evolutionary trajectory, the relationship between niche overlap excess and phylogenetic relatedness could therefore also reflect a state of community assembly: species that evolved in different places were able to establish themselves in the local community because their niches were sufficiently different from those of the resident species or they could shift the frequency with which they used different resources sufficiently to “fit” into the community (Janzen 1985). Such an addition to the local seed dispersal system might likewise include local species that evolve to use suitable fruits opportunistically (Thompson 2005). In that sense, the relationship between phylogenetic relatedness and niche overlap represents one of several possible combinations in which species could co-occur locally.

Our results go beyond a relationship between phylogenetic relatedness and niche overlap (Fraser et al. 2018; Sydenham et al. 2018). In investigating the excess overlap rather than overlap itself, we examined the way in which closely related species modify their resource use in response to the presence of ecologically similar species—do species overlap more with each other’s niches than we would expect, presumably competing weakly for resources, or is a boundary drawn between each species’ foraging niche that limits competition and yields lower than expected niche overlap? In the communities of primarily frugivorous birds along the tropical Andes, we found that increased niche overlap, indicative of diffuse resource competition, appears to be the norm. As described, this result accords with the population and social structure of these assemblages as well as the evolutionary incentives of seed dispersal. However, it remains to be tested whether the same holds true for other consumer-resource systems in which the potential for intense resource competition is greater. For example, large

mammalian carnivores will often exclude co-occurring guild members from resources (e.g., lion dominance over smaller carnivores in African savanna ecosystems; Swanson et al. 2014) and resource-poor environments may require dietary specialization in consumers (e.g., seed size-based separation in Darwin's finches; Grant and Grant 2006), and it is possible that in these cases niche packing may be characterized more by niche contraction and lower than expected overlap. As we have demonstrated in frugivorous birds, we expect that the signatures of niche packing within guilds will offer insights to the behavioral and ecological underpinnings of coexistence.

Our study shows that many species with almost identical foraging niches can coexist in local species communities, especially if they differ in their dependence on the shared resource. This suggests that similarity in resource use is not always a good indicator for potential competition between species, especially if information about the dependence of a species on a particular resource is missing. This becomes even more important if resource use is inferred indirectly from species' morphological traits or phylogeny (Pigot et al. 2016; Goodale et al. 2020; Munkemüller et al. 2020). Studies that aim to incorporate species interactions and interspecific competition into models of species distributions and community assembly should therefore consider the dependence of a species on a particular resource. The integration of traits and interaction networks presents a suitable tool for such analyses.

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### Statement of Authorship

D.M.D. and G.V.D.R. conceived the study and methodology; all authors contributed to conceptualization and

development of methods; D.M.D. collected and analyzed the data; D.M.D. prepared the first draft of the manuscript and all figures, with contributions from M.C.H.; and all authors contributed to reviewing and editing.

### Data and Code Availability

Data and code used are available from sources cited in the article. Additional code to analyze niche overlap is available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2fqz612qf>; Dehling et al. 2021c).

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