



Similar composition of functional roles in Andean seed-dispersal networks, despite high species and interaction turnover

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Abstract. The species composition of local communities varies in space, and its similarity generally decreases with increasing geographic distance between communities, a phenomenon known as distance decay of similarity. It is, however, not known how changes in local species composition affect ecological processes, that is, whether they lead to differences in the local composition of species' functional roles. We studied eight seed-dispersal networks along the South American Andes and compared them with regard to their species composition and their composition of functional roles. We tested (1) if changes in bird species composition lead to changes in the composition of bird functional roles, and (2) if the similarity in species composition and functional-role composition decreased with increasing geographic distance between the networks. We also used cluster analysis to (3) identify bird species with similar roles across all networks based on the similarity in the plants they consume, (i) considering only the species identity of the plants and (ii) considering the functional traits of the plants. Despite strong changes in species composition, the networks along the Andes showed similar composition of functional roles. (1) Changes in species composition generally did not lead to changes in the composition of functional roles. (2) Similarity in species composition, but not functional-role composition, decreased with increasing geographic distance between the networks. (3) The cluster analysis considering the functional traits of plants identified bird species with similar functional roles across all networks. The similarity in functional roles despite the high species turnover suggests that the ecological process of seed dispersal is organized similarly along the Andes, with similar functional roles fulfilled locally by different sets of species. The high species turnover, relative to functional turnover, also indicates that a large number of bird species are needed to maintain the seed-dispersal process along the Andes.

Key words: *alpha diversity; beta diversity; ecological process; ecosystem function; ecosystem service; frugivore; functional diversity; gamma diversity; morphology; plant–bird mutualism; traits.*

INTRODUCTION

Species communities from different sites generally differ in their species composition. The composition of a local species community is determined by an interplay of abiotic factors (“environmental filters”), such as climate, habitat, or topography, and biotic factors, such as

available interaction partners or competition with other species (Pigot et al. 2016, Hanz et al. 2019), all of which vary in space themselves. As a consequence, the similarity in species composition generally decreases with increasing geographic distance between species communities, a phenomenon known as “distance decay of similarity” (Nekola and White 1999, Sojininen et al. 2007, Morlon et al. 2008, Antão et al. 2019). Comparisons of species communities with regard to their species composition and species interactions have provided insight into mechanisms underlying community assembly and

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species coexistence (Tylianakis and Morris 2017, Pellisier et al. 2018). However, little is still known about the effects of differences in local species composition on local ecological processes (but see Graham et al. 2017).

Ecological processes consist of different functional roles fulfilled by the species from a local community. In many key ecological processes (i.e., predator–prey relationships, pollination, or seed dispersal), these functional roles involve interactions with other species. The functional role of each species in the different processes is determined by the species with which it interacts (Elton 1927), and the different ecological processes in turn can be described by the respective diversity and composition of the functional roles fulfilled by the species from the local community (Dehling and Stouffer 2018). While functional diversity (functional alpha diversity) tends to be related to species richness (Petchev and Gaston 2002, Devictor et al. 2010, Safi et al. 2011), it is not known whether this holds true for the functional composition in local communities (functional beta diversity), i.e., whether increasing differences in species composition also lead to increasing differences in the composition of functional roles. For instance, if species from one community were replaced by species with different functional roles in another community, this would indicate differences in the way ecological processes are structured locally, whereas a replacement with functionally similar species would lead to a similar organization of the ecological process, i.e., a similar composition of functional roles that are simply fulfilled locally by different sets of species. Understanding differences in the functional composition of species communities will therefore lead to a better understanding of diversity patterns, especially on large spatial scales.

Comparisons of species' functional roles between species communities have been limited by the lack of suitable methods (Poisot et al. 2012, Carstensen et al. 2016, Dehling and Stouffer 2018, Pellisier et al. 2018). Approaches to describing species' functional roles in ecological processes have so far focused on analyzing either species' functional traits or patterns of species interactions in ecological networks. While functional traits can provide an idea about species' adaptations (or fitting) to environmental conditions and their resource use (Dehling et al. 2014b, 2016), they are still limited in their ability to infer pairwise species interactions related to species' functional roles in ecological processes, despite promising recent approaches (Bartomeus et al. 2016). Interaction networks, on the other hand, describe the individual interactions between species, but the common indices for describing species' roles in networks are calculated from local interaction patterns and based on species identities (i.e., species names) (Bascompte and Jordano 2014) and are therefore difficult to compare between communities that differ in species composition (Dehling 2018, Pellisier et al. 2018). Likewise, comparisons of interaction patterns and species' roles in networks have included a wide range of analyses, including

the beta diversity of species interactions (Poisot et al. 2012, Carstensen et al. 2016), the comparison of species' motif roles (Baker et al. 2015), module roles (Olesen et al. 2007, Schleuning et al. 2014, Araujo et al. 2018), as well as "structural" roles, such as measures for species' specialization and complementarity (Schleuning et al. 2012, Cirtwill et al. 2018, Dallas and Poisot 2018). All these comparisons, however, are informed by species identities, which makes them difficult to interpret ecologically (Pellisier et al. 2018).

Recently, efforts have been made to integrate information on functional traits and interaction networks. For instance, when comparing the structure of entire networks, e.g., with respect to their modularity, modules are currently identified based on species identities, and species' affiliation to the different modules is then post-hoc explained by species' traits (Donatti et al. 2011, Maruyama et al. 2014, Schleuning et al. 2014), phylogeny (Martín-González et al. 2015), phenology (Bosch et al. 2009), climate (Sebastián-González et al. 2015, Dalsgaard et al. 2017), or geographic distance between communities (Araujo et al. 2018). Similarly, pairwise interactions between species are influenced by the degree of their trait-matching, both in individual traits (Stang et al. 2009, Eklöf et al. 2013, Dehling et al. 2014b) and in trait combinations (Bartomeus et al. 2016, Dehling et al. 2016). Trait-matching and the relationship between traits and structural network roles appear to be prevalent across communities (Schleuning et al. 2014, Bender et al. 2018), indicating similar mechanisms underlying the formation of interactions between species. Nevertheless, since structural network roles and interaction patterns are characterized based on species identities alone and only later related to traits, they cannot inform about the similarity in species' functional roles and in the structure underlying ecological processes between different communities. In order to compare ecological processes between sites, it could therefore be insightful if information about species' functional roles were *directly* taken into account.

An alternative way to combine information on species interactions and species' functional traits is therefore to describe interactions and species' functional roles in ecological processes directly via species' *interaction niches*, which can be described by the traits of species' interaction partners (Junker et al. 2013, Dehling and Stouffer 2018). For instance, rather than approximating the role of a pollinator via the number or identity of the plants that it pollinates and later relating this to the pollinator's functional traits (e.g., the length of its proboscis), the role can be described directly via the traits of the plants that the pollinator visits. Such a description of a species' role based on the traits of its interaction partners allows the direct comparison of species roles even between communities that differ completely in their species compositions (Dehling and Stouffer 2018). It is therefore well suited for cross-community comparisons of functional roles in ecological processes.

Taking this lens, we studied whether differences in local species composition lead to corresponding differences in the composition of functional roles in the ecological process of seed dispersal. We collected local interaction networks between frugivorous birds and fleshy-fruited plants at eight sites along the Andes in South America and compared them with regard to their composition of species, species interactions, and functional roles. First, we tested whether differences in bird species composition between the networks lead to differences in the composition of bird functional roles. Functional roles were measured from (1) functional traits, which present species' adaptations (or fitting) to their interaction partners and are therefore only an indirect measure for species' functional roles, and from (2) species' interaction niches, and (3) interaction-niche positions, both of which describe species' interaction partners directly and are therefore direct measures for species' functional roles (Dehling and Stouffer 2018). If the local seed-dispersal processes were structured similarly along the Andes, then differences in species composition should not lead to differences in the composition of functional roles.

Second, we investigated whether differences in the functional composition of the networks increased with increasing geographic distance, i.e., whether there was a distance decay of similarity in functional role composition similar to the one described for species composition (Nekola and White 1999). We tested whether differences in species composition of birds and plants, bird-plant interactions, and the three measures for functional roles increased with increasing geographic distance between the networks. We expected increasing differences in species compositions and species interactions with increasing geographic distance between the networks. However, depending on whether the seed-dispersal processes are structured similarly along the Andes, increasing geographic distance should not necessarily lead to increasing differences in the composition of functional roles.

Third, to compare the functional roles of individual frugivorous bird species directly with each other, we compiled all networks into a meta-network and then used cluster analysis to identify groups of bird species with similar functional roles, i.e., bird species that interact with similar sets of plant species. The similarity in the set of consumed plant species was assessed (i) only considering the species identity of the plant species, and (ii) also considering the functional traits of the plant species, i.e., via the similarity in the interaction niches and interaction-niche positions of the bird species. If changes in species composition between networks lead to corresponding changes in functional-role composition, we would expect a higher similarity in functional roles among the species within networks than between networks. If seed-dispersal processes were structured similarly across the Andes, we would expect to identify groups of bird species with similar functional roles across all networks.

METHODS

Data

Networks.—We sampled quantitative interaction networks between fleshy-fruited plants and frugivorous birds at eight montane forest sites along the tropical and subtropical Andes: Colombia 1 (4.717° N, 75.567° W, 2,000 m), Colombia 2 (4.700° N, 75.483° W, 2,500 m), Ecuador 1 (4.1° S, 78.96° W, 1,000 m), Ecuador 2 (3.96° S, 79.06° W, 2,000 m), Peru 1 (13.051° S, 71.536° W, 1,500 m), Peru 2 (13.168° S, 71.584° W, 3,000 m), Bolivia (16.40° S, 67.50° W, 2,500 m), Argentina (26.762° S, 65.333° W, 1,000 m). Sampling effort ranged from 300 h (Bolivia) to 960 h (Peru 1) (mean \pm SD: 606 \pm 224 h), 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), observed links between plant and bird species from 50 (Bolivia) to 398 (Peru 1) (161 \pm 111 links), and 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). In total, the networks included 11,578 interaction events between 227 plant species and 180 bird species. Additional information about the networks can be found in Appendix S1: Table S1.

Morphological traits.—For all plant and bird species in the networks, we collected morphological traits known to influence the interactions between fleshy-fruited plants and frugivorous birds (Dehling et al. 2014b, Bender et al. 2018). For each bird species, we sampled bill width, bill length, and wing shape (i.e., Kipp's index, the pointedness of the wing) from museum specimens. Kipp's index is measured on the folded wing and describes the fraction between the distance from the tip of the first secondary feather to the wing tip, and the full length of the folded wing. We obtained data on bird body mass from Dunning (2007). For each plant species, we sampled fruit diameter, fruit length, plant height, and crop mass (i.e., mean number of fruits per plant \times mean fruit mass) in the field. Prior to the analyses, all traits were log-transformed to approach normality and homoscedasticity, and then z -transformed.

Functional roles of bird species

We characterized the functional role of a bird species in three different ways: indirectly, via (1) the morphological **functional traits** related to its foraging behavior, and directly, via (2) its resource use or **interaction niche**, which is described for each bird species by the range of trait combinations of the plant species that it consumes (Dehling and Stouffer 2018), and (3) the interaction preference within its interaction niche, i.e., its **interaction-niche position** (Dehling et al. 2016). For (1), we used principal coordinates analysis (PCoA) to project all bird

species from all sites into a common four-dimensional bird trait space (spanned by the bird traits mentioned above) where they were arranged according to the similarity in their trait combinations. The trait combination of a bird species—and, hence, its position in the bird trait space—represents the species' morphological adaptation or fitting to its resource use, which is an indirect representation of its functional role in the seed-dispersal process (Dehling et al. 2014b). For each network, we then calculated the local alpha diversity of bird trait combinations as functional richness, that is, the volume of a convex hull that includes all locally co-occurring bird species in bird trait space (Fig. 1a; Villéger et al. 2008). For (2), we described the interaction niche of each bird species in the seed-dispersal networks by the range of trait combinations of the plant species that it consumes (cf. “process-related niche” in Dehling and Stouffer 2018). Analogous to (1), we used PCoA to project all plant species from all sites into a common four-dimensional plant trait space (spanned by the plant traits mentioned above) where they were arranged according to the similarity in their trait combinations. For each bird species, we then determined the interaction niche as the convex hull in plant trait space that includes all plant species consumed by that bird species in the local network (Dehling and Stouffer 2018; Fig. 1c). For each network, we calculated the local alpha diversity of species' interaction niches as the volume of the trait space covered by the interaction niches of all bird species from a network, ignoring the overlap in individual niches (Fig. 1c; cf. FD_{base} in Dehling and Stouffer 2018). Finally, (3) for each bird species in the networks, we calculated the *interaction centroid*, which is the mean position of the plant species with which a bird interacts in plant trait space, weighted by the frequency of the interactions (Fig. 1c; Dehling et al. 2016). The interaction centroid hence takes into account the number of interactions between bird and plant species and represents a bird's weighted foraging preference or interaction-niche position in plant trait space. Differences in niche position between species can be used as a coarse, but robust, representation of the differences between their functional roles (Dehling et al. 2016).

Differences in the composition (beta diversity) of the interaction networks

We compared the interaction networks based on differences in their composition (beta diversity). We quantified pairwise differences in species composition, composition of species interactions, and composition of bird functional roles (measured from bird functional traits, interaction niches, and interaction-niche positions) between all networks. We quantified beta diversity as Jaccard dissimilarity using *vegan* 2.5 (Oksanen et al. 2018) in R 3.4.4 (R Core Team 2018). We calculated differences in the species composition of bird species (**β bird species**) and of plant species (**β plant species**) between

networks based on the number of bird and plant species, respectively, present in only one vs. both networks. Likewise, we calculated differences in the composition of bird-plant interaction (**β interactions**) based on the number of distinct interacting bird-plant pairs in one vs. both networks. Note that β bird species, β plant species, and β interactions only consider species' identities, not their traits.

Analogous to that, we calculated differences in the composition of bird functional-trait combinations between networks (**β bird traits**) based on the volume of bird trait space covered by the convex hulls of the bird species from one vs. both networks (Fig. 1b; Villéger et al. 2013). Similarly, we calculated differences in the composition of bird interaction niches (**β niche**) between the networks based on the volume of plant trait space covered by the interaction niches of the bird species from one vs. both networks (Fig. 1d; Dehling and Stouffer 2018). Since the interaction niche is described by its size and its position, β niche is influenced by changes in the interaction-niche sizes and positions between the species from two communities. To assess only the changes in the composition of interaction-niche positions of bird species (**β niche position**), we calculated the differences in interaction-niche positions between two networks as the sum of the minimum distances between the niche positions of the birds from one network and the niche positions of the birds from the other network (Fig. 1e; Dehling et al. 2014a). β niche position describes the cumulative distances between the functionally most similar species and is therefore another measure for the differences in the composition of functional roles (Dehling et al. 2014a).

Comparisons

Changes in bird species composition vs. changes in the composition of bird functional roles.—In our first comparison, we tested if changes in bird species composition between the networks lead to corresponding changes in the composition of bird functional roles (measured from bird functional traits, interaction niches, and niche positions). We used Mantel correlations (*vegan* 2.5; Oksanen et al. 2018), and tested if the pairwise differences in bird species composition (β species) between networks were related to pairwise differences in functional-role composition (β bird traits, β niche, and β niche position).

Distance decay in the similarity of network composition.—In our second comparison, we tested if increasing geographic distance between the networks leads to decreasing similarity in their composition (distance decay of similarity). We determined the pairwise geographic distances between the networks and then used Mantel correlations (*vegan* 2.5; Oksanen et al. 2018) to test if the pairwise geographic distances were related to pairwise differences in species composition (β bird

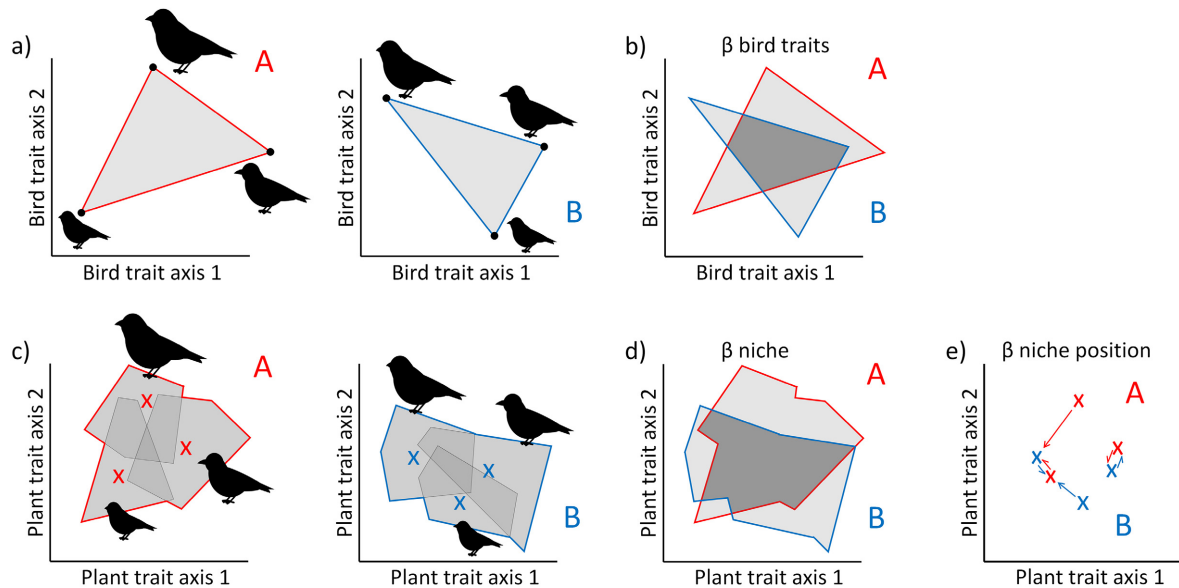


FIG. 1. Alpha and beta diversity of functional-trait combinations and interaction niches. (a) Functional-trait diversity. Community A consists of three bird species that are placed in a multidimensional trait space according to their trait combinations (only two axes shown here). The diversity of trait combinations is measured as Functional Richness, the volume of a convex hull that includes all bird species in the bird trait space (outlined in red). Community B also consists of three bird species that are placed in the same multidimensional trait space, and the diversity of trait combinations is measured as the volume of the convex hull outlined in blue. (b) Differences in the composition of trait combinations (β bird traits) between communities A and B are measured as Jaccard dissimilarity based on the volume of bird trait space covered by both communities (dark gray) vs. the volume that is covered by only one of the communities (light gray). (c) Diversity of interaction niches. The functional role of a bird species is described by its interaction niche: the range of trait combinations of the plants it consumes. The interaction niche is quantified as the convex hull in plant trait space that includes all plant species that the bird consumes in a local network. The interaction-niche position of each bird is given by the interaction centroid, the mean position of the plant species it consumes, weighted by interaction frequency (here shown as “x”). The diversity of interaction niches is quantified as the volume of plant trait space covered by the interaction niches of the species from each community, ignoring the overlap between individual niches (outlined in red for A, outlined in blue for B). (d) Differences in the composition of interaction niches (β niche) between communities A and B are measured as Jaccard dissimilarity based on the volume of plant trait space covered by both communities (dark gray) vs. the volume covered by only one of the communities (light gray). (e) Differences in the composition of functional-niche positions of A and B are measured as the sum of the shortest distances between the niche positions from A and B, indicated by the red and blue arrows.

species, β plant species), composition of species interactions (β interactions), and composition of bird functional roles (β bird traits, β niche, β niche position).

Comparison of the functional roles of individual bird species across all networks.—In addition to the comparisons of bird functional roles on the network level (i.e., on the level of the local species communities), we compared the functional roles of individual bird species directly across all networks. For this, we created a meta-network by combining the bird–plant interactions from all local networks into one large regional network of bird–plant interactions. We then identified bird species with similar functional roles in this regional meta-network. We determined the similarity in functional roles of bird species via the similarity in their interaction partners (the consumed plant species), using three different approaches. First, considering only the species identity of the consumed plants, we calculated the pairwise differences between bird species as (i) the Jaccard

dissimilarity between the sets of plant species with which each bird species interacted. Second, considering also the traits of the consumed plant species, we calculated the pairwise differences between bird species (ii) according to the extent of their niche overlap as the Jaccard dissimilarity between their interaction niches, and (iii) as the difference in their niche positions, i.e., the distance between their interaction centroids. For each of the sets of pairwise dissimilarities, we then performed a cluster analysis (method UPGMA in function hclust in vegan 2.5; Oksanen et al. 2018) to sort bird species into groups of species with similar roles. Species were sorted into the same group if they preferred similar sets of plant species (i), or if they preferred plant species with similar functional traits (ii and iii). To visualize whether the clusters identified with the three different approaches included groups of species with similar functional roles, we projected the niche positions of all bird species from the different clusters into the plant trait space.

RESULTS

Changes in bird species composition vs. changes in the composition of bird functional roles

For our first comparison, we tested whether differences in species composition were related to differences in the compositions of functional roles (measured from traits, niches, and niche positions) in the eight communities. Differences in species composition of birds (β bird species) were positively correlated with differences in the composition of bird traits (β bird traits, Mantel $R = 0.45$, $P = 0.002$), but not of bird interaction niches (β niche, Mantel $R = -0.272$, $P = 0.878$) or bird niche positions (β niche position, Mantel $R = 0.08$, $P = 0.432$) (Fig. 2). This shows that changes in the composition of bird species in the networks did not lead to changes in the composition of functional roles.

Distance decay in the similarity of network composition

For our second comparison, we tested whether differences between communities increased with increasing geographic distance. With increasing geographic distance, dissimilarity between communities increased with regard to species composition (β bird species, Mantel $R = 0.41$, $P = 0.027$; β plant species, Mantel $R = 0.52$, $P = 0.004$) and species interaction (β interactions, Mantel $R = 0.38$, $P = 0.014$), but not with regard to the functional roles of bird species (β bird traits, Mantel $R = 0.23$, $P = 0.126$; β niche, Mantel $R = -0.02$, $P = 0.550$; β niche position, Mantel $R = 0.30$, $P = 0.08$) (Fig. 3). This shows that species and their interactions were continuously replaced between communities, whereas the composition of functional roles remained similar.

Comparisons of the functional roles of individual bird species across all networks

For our third comparison, we identified bird species with similar functional roles across all networks based on the similarity in (i) the species identity of the plants they consumed, (ii) their interaction niches, and (iii) their interaction-niche positions. When birds were grouped based on the similarity in the species identities of the plant species they consumed, bird species were sorted into eight clusters that corresponded almost perfectly to the original eight networks (Fig. 4a). Some bird species could not be assigned to any cluster because they did not share interaction partners with other species (Fig. 4a). In contrast, when birds were grouped based on the similarity of their interaction niches and niche positions (i.e., taking into account the traits of the plant species with which the birds interacted), bird species were sorted into clusters of species with similar functional roles composed of species from across all networks (Fig. 4b, c). The separation was clearer for the clusters based on the similarity in niche positions than for the clusters based on similarity in niche overlap (Fig. 4b, c).

The differences between the approaches were also striking when we projected the clusters into the plant trait space. The clusters based on the similarity in the species identities of consumed plant species overlapped greatly in trait space, and each cluster included almost the entire range of bird functional roles (Fig. 4d). The clusters based on similarity in niche overlap were separated more clearly and composed of species from across all networks, but they were generally small (Fig. 4e). In contrast, clusters based on similarity in niche position were clearly separated and, most importantly, they were composed of species from across all networks (Fig. 4f).

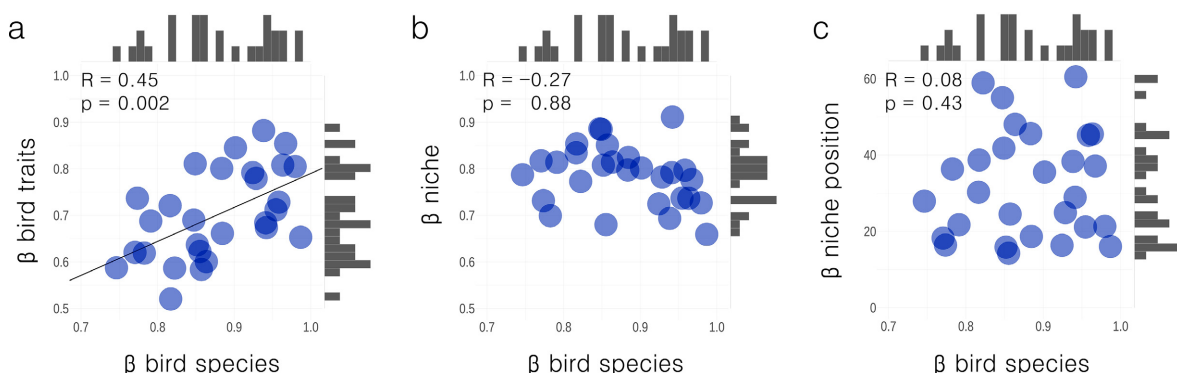


FIG. 2. Differences in bird species composition vs. three measures for differences in functional role composition (β bird traits, β niche, β niche position) in eight bird–plant networks along the Andes. Differences in species composition (β bird species) are calculated as Jaccard dissimilarity based on species present in one vs. both networks. Similarly, changes in the composition of (a) functional traits (β bird traits), and (b) interaction niches (β niche) of bird species are calculated as Jaccard dissimilarity based on the volume in multidimensional functional-trait spaces occupied by the species from one vs. both networks. Changes in the composition of (c) interaction-niche positions of birds (β niche position) are calculated as the sum of the shortest distances from the niche positions of the species from one network to the niche positions of the species from the other network (Dehling et al. 2014a). See methods for details. Significant Mantel correlations (Pearson) are indicated by a regression line.

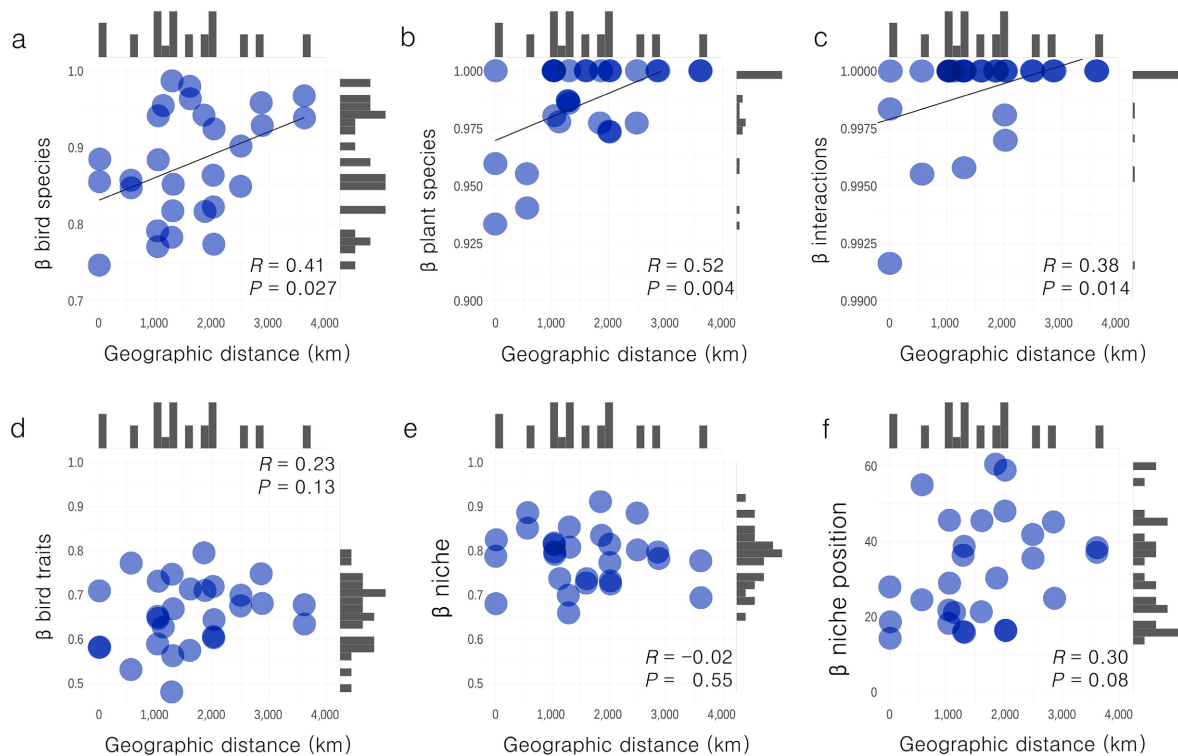


Fig. 3. Relationship between geographic distance and six measures for compositional changes (β bird species, β plant species, β interactions, β bird traits, β niche, β niche position) in eight bird–plant networks along the Andes. Differences in species composition of (a) bird species (β bird species), (b) plant species (β plant species), and (c) bird–plant interactions (β interactions) are calculated as Jaccard dissimilarity based on the species and interactions, respectively, present in one vs. both networks. Similarly, differences in the composition of (d) functional traits (β bird traits), and (e) interaction niches (β niche) of birds are calculated as Jaccard dissimilarity based on the volume in multidimensional functional-trait spaces occupied by the species from one vs. both networks. Changes in the composition of (f) interaction-niche positions (β niche position) are calculated as the sum of the shortest distances from the niche positions of the species from one network to the niche positions of the species from the other network (Dehling et al. 2014a). See methods for details. Significant Mantel correlations (Pearson) are indicated by a regression line. The small variation in β plant species and β interactions is caused by the high turnover of plant species between the networks.

The positions of plant species, and hence the niche positions of birds, were determined by combinations of plant traits that showed distinct trends along the axes of the trait space (Appendix S1: Fig. S1), showing that the bird species in the different clusters preferred distinct sets of plant trait combinations. For instance, cluster 6 mostly included small to medium-sized birds with small beaks, such as tanagers (*Anisognathus*, *Chlorochrysa*, *Chlorornis*, *Chlorospingus*, *Cyanerpes*, *Diglossa*, *Ramphocelus*, *Tangara*) and finches (*Chlorophonia*, *Euphonia*) that preferred medium to large trees that offered small fruits, cluster 1 mostly included medium-sized tanagers (*Iridosornis*, *Pipraeidea*, *Thraupis*) and flycatchers (*Elaenia*, *Lophotriccus*, *Mionectes*) that preferred rather low trees that offered medium-sized fruits in small quantities, and cluster 7 included relatively large-bodied, obligate frugivorous birds, such as toucans (*Aulacorhynchus*), conditigs (*Cephalopterus*), quetzals (*Pharomachrus*), and thrushes (*Turdus*) that preferred medium-sized to tall trees that offered large fruits in vast quantities (Fig. 4, Appendix S1: Fig. S1).

DISCUSSION

Changes in bird species composition between seed-dispersal networks were not mirrored by corresponding changes in bird functional roles: while the composition of bird functional traits changed together with the turnover of bird species in the networks, the composition of interaction niches and interaction-niche positions remained similar despite the constant and almost complete replacement of bird and plant species throughout the Andean forests. Likewise, while there was a distance decay of similarity regarding the species composition of birds, plants, and bird–plant interactions in the networks, there was no distance decay of similarity with regard to the composition of bird functional roles. Finally, the comparison of the functional roles of individual bird species via the cluster analysis of the meta-network corroborated the high species turnover between the networks, but once we considered species' interaction niches, it also revealed the presence of species with similar functional roles in all networks across the Andes.

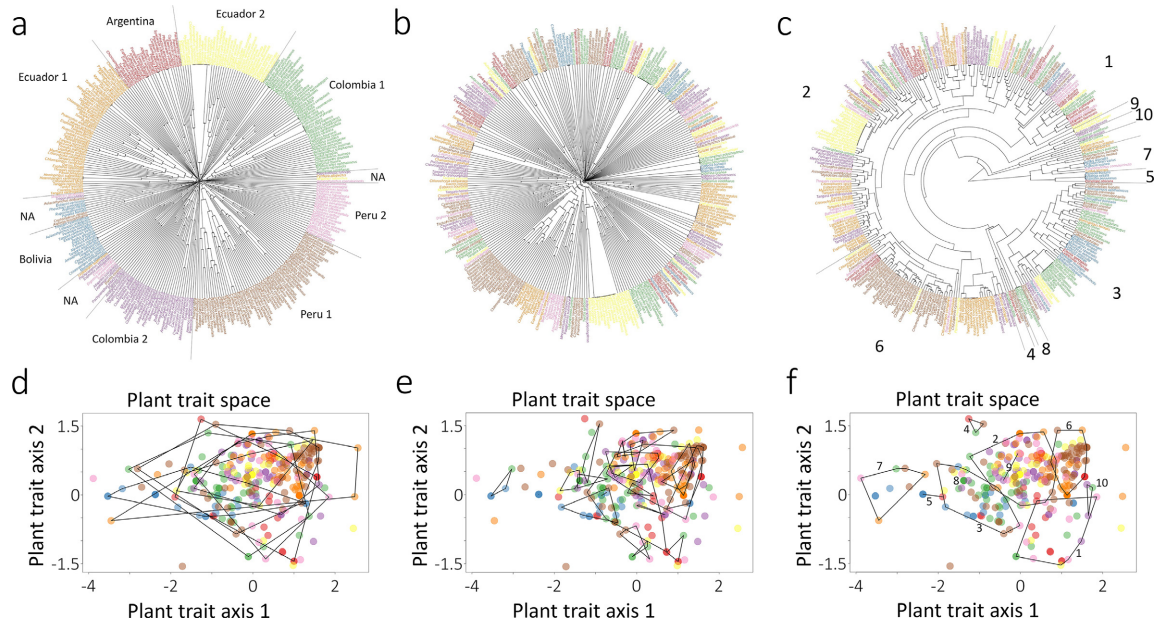


FIG. 4. Identification of bird species with similar functional roles across all networks via cluster analysis of a meta-network. Colors refer to the eight original networks along the Andes. (a) Hierarchical Cluster Analysis (UPGMA) based on the Jaccard dissimilarity in the species composition of interaction partners of birds (i.e., the sets of plant species consumed by each bird species). Species are sorted into clusters that almost perfectly represent the original eight networks. (b) Hierarchical Cluster Analysis (UPGMA) based on the Jaccard dissimilarity in interaction niches (niche overlap) of bird species in plant trait space. Clusters are composed of bird species with similar functional roles across all networks that are separated close to the base of the dendrogram. (c) Hierarchical Cluster Analysis (UPGMA) based on the difference in niche positions of bird species (centroid distances) in plant trait space. Species are sorted into 10 clusters composed of species with similar functional roles across all networks. When the niche positions of bird species are projected into the plant trait space, (d) the clusters based on differences in the species composition of interaction partners overlap widely, (e) clusters based on niche overlap are small and not well separated, but (f) the 10 clusters based on differences in niche position are well-separated in plant trait space and composed of species from across all networks.

Our comparisons based on species identity corresponded to findings from other studies. Similar changes in species composition, and, consequently, in species interactions, have been found in mutualistic networks (Trøjelsgaard et al. 2015) as well as antagonistic networks (Dallas and Poisot 2018). Likewise, the distance decay of similarity in species composition has been found in other network comparisons (Carstensen et al. 2014, Trøjelsgaard et al. 2015), and the high species turnover between meta-network clusters in the comparison informed by species identities corresponded to the species turnover observed in other meta-networks (Emer et al. 2018). Hence, if we only considered the species identities of birds and plants, our findings might lead us to the conclusion that there were large differences in the composition of seed-dispersal networks along the Andes. However, when we considered the functional roles of species in the comparisons, it showed that the networks were much more similar in their functional composition. Despite the generality of the distance decay in similarity for species composition (Soininen et al. 2007, Antão et al. 2019) there was no distance decay in the similarity of functional roles.

The similarity in the composition of functional roles suggests that seed-dispersal networks along the Andes

are organized in a similar way. Each network appeared to be composed of a similar mix of plant species with different dispersal strategies and the corresponding types of avian seed dispersers (Howe and Smallwood 1982), ranging from plants that produce a large number of small fruit that attract many different bird species to plants that produce large fruit that attract a smaller number of large, obligate frugivorous bird species (Fig. 4, Appendix S1: Fig. S1). While species interactions appear to be labile in space when only species identities are considered (cf. Carstensen et al. 2016), they appear to be more consistent when we instead consider species' functional roles. Likewise, networks are sometimes regarded as non-random samples of a regional "metaweb" (Ricklefs 1987, Dunne 2006, Poisot et al. 2012, Gravel et al. 2019). The contrasting patterns of turnover and distance decay observed for species composition vs. functional-role composition suggest that the underlying mechanism for such non-random samples is the continuous replacement of species with similar functional roles between local networks, that is, despite changes in species composition, there are similar functional roles in the networks that are locally fulfilled by ecologically equivalent species in a similar manner (Root 1967, Zamora 2000).

The high species turnover between the networks despite similar composition of functional roles suggests rather strong limits to the geographic distribution of individual bird and plant species. Geographic ranges of species and, consequently, the assembly of local species communities are influenced by a combination of abiotic and biotic factors, including climate, topography, and geographic barriers, as well as interspecific relationships (Pigot et al. 2016, Hanz et al. 2019). Especially along elevational gradients in mountain ranges, such as in this study, these factors change quickly over small spatial extents. As a result, many vertebrate species in tropical mountains have notoriously small ranges (McCain 2009), resulting in the continuous replacement of species between local networks and the distance decay of similarity in species composition observed in this study.

The high species turnover between networks also has implications for the conservation of the seed-dispersal process on the regional scale. With a high local turnover of species (high beta diversity), a higher number of species on the regional scale (high gamma diversity) are needed to fulfil the functional roles in the respective local species communities (Cardinale et al. 2011, Isbell et al. 2011, Winfree et al. 2018). This is even true for processes in which a small number of dominant species contribute most to the process (Winfree et al. 2018). The high species turnover despite similar functional roles observed in our networks suggests that maintaining the seed-dispersal process along the Andes requires a high regional gamma diversity of seed dispersers. Given that species from different parts of the Andes are adapted to different environmental conditions, conservation of a high regional diversity of ecologically similar species could also act as insurance against species extinctions in local communities under expected altered environmental conditions and corresponding range shifts of species in the future (Sakschewski et al. 2016, Bender et al. 2019, Nowak et al. 2019).

Our study showed that comparisons of interaction networks and species communities can differ substantially depending on whether we consider species identities or species' functional roles. Incorporating information about species' functional roles into analyses and comparisons of interaction networks could lead to new insights into the mechanisms underlying the composition and structure of ecological networks, ecological processes, and species communities. For instance, because of the large species turnover between the networks, only our functional-role approach to meta-networks revealed that species with similar functional roles were present in the different networks along the Andes. Consideration of species' functional roles instead of species identities could, hence, lead to new insights into the structure of meta-networks and the effect of disturbances such as fragmentation on the maintenance of ecological processes (Emer et al. 2018, Marjakangas et al. 2020). While, in this study, we used data from mutualistic networks to assess functional roles of birds

based on their interaction partners, the general approach can also be applied to other types of interactions (e.g., antagonistic networks) as well as to the comparison of roles that are not typically depicted in networks and to relationships between species and the environment (Dehling and Stouffer 2018). For instance, the approach can be used to describe species' functions that are difficult to assess indirectly via species' traits (e.g., physiological and metabolic processes) or to describe the environmental conditions under which species can exist, i.e., their Grinnellian niches (Dehling and Stouffer 2018). Taking into account species' functional roles could prove to be especially useful for comparisons of networks and ecological processes between sites that have few or no species in common, e.g., in comparisons on large spatial scales, across habitats, and in regional meta-networks (Araujo et al. 2018, Dugger et al. 2019). However, while the method we used allows the direct comparison of all species that contribute to an ecological process, independent of their taxonomic relationships, most networks have so far been sampled for single taxa in the upper trophic level (e.g., bird-plant or bat-plant networks). In order to compare ecological processes on large spatial scales where similar functional roles might be fulfilled by different taxa, we need to sample species interactions for all species that contribute to the processes (Dehling and Stouffer 2018).

CONCLUSIONS

Our study exemplifies a new way to compare species communities via species' functional roles in ecological processes. This approach is especially useful for comparisons of communities that have few or no species in common, for instance in comparisons on large spatial scales or across habitats and taxa. Our study also highlights the importance of biodiversity for maintaining functional roles in ecological processes at the community and regional scale.

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