







RESEARCH ARTICLE

Functional Ecology



Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests

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Abstract

1. Partner choice in species interaction networks, that is, between frugivorous birds and fruiting plants, is largely determined by matching of functional traits. However, the composition of functional traits in plant communities changes along land-use gradients. Understanding how flexible consumers react to changes in the trait composition of resources is crucial to project consequences for ecosystem functions, such as seed dispersal.
2. We investigated the ability of birds to consume fruits with different sets of traits in natural and fragmented tropical montane forests across an elevational gradient. We developed a novel, trait-based approach to quantify the functional shifts of consumers between resources with different functional traits. We expected the degree of functional shifts to be associated with bird traits related to food choice, such as bill width and degree of frugivory, as well as foraging behaviour, such as wing shape and foraging stratum.
3. We sampled the plant-frugivore networks at three elevations and two habitat types (natural and fragmented forest) and measured the functional traits for each plant and bird species. We calculated the trait space of the plant community at each elevation and projected the interacting birds into it. Finally, we calculated the functional shift, which is the trait-based distance between the preferred fruit resources in the two habitat types for each bird species.
4. We found differences in the functional trait space of the fruiting plant community between natural and fragmented forests across all elevations. Birds' observed functional shifts between habitat types at each elevation were generally larger than the shifts expected by null models. Wing shape was the most important trait related to the functional shifts across the elevational gradient, whereas bill width, degree of frugivory, foraging stratum and phylogeny were not important.
5. We conclude that birds with pointed wings respond flexibly to changes in the trait composition of fruit resources, probably due to the high mobility of these species.

Our results emphasize that linking species interaction networks and functional trait analyses yield new insights into how consumer species respond to changes in biotic factors and can improve projections of how human impacts modify trophic interactions and associated ecosystem functions.

KEYWORDS

elevational gradient, functional shift, functional traits, plant–frugivore interactions, tropical montane forest

1 | INTRODUCTION

Many ecological processes involve interactions between species, such as mutualistic interactions between plants and animals (Blüthgen & Klein, 2011; Schleuning, Fründ, & García, 2015). In these interactions, partners often match according to their functional traits (Garibaldi et al., 2015; Jordano, 1987). In particular, functional traits that relate to food choice and foraging behaviour influence partner compatibility (e.g., Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; Bender et al., 2018). Mismatches in such traits between species can render some interactions impossible (forbidden link hypothesis, Jordano, Bascompte, & Olesen, 2003). Analyses of trait-based interaction rules, therefore, enable a process-based understanding of partner compatibility in ecological communities (Dehling, Töpfer, et al., 2014; Pigot, Bregman, et al., 2016; Stang, Klinkhamer, Waser, Stang, & Van Der Meijden, 2009) as well as an assessment of how flexible species respond to compositional changes in these communities (Bender et al., 2017).

Frequency and composition of traits in species communities often vary in space and time. Previous studies have shown changes in the occurrence of species traits along elevational or latitudinal gradients, such as animal body size (Bergmann's rule; see Blackburn, Gaston, & Loder, 1999; Ashton, 2002) or bill shape (Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2015). Other studies have shown seasonal differences, for instance in the presence of specific fruit (Bender et al., 2017) or leaf traits (Franco et al., 2005), or in the temporal occurrence of animals with certain sets of traits (e.g., long-tongue bees; Cane & Payne, 1993). Variation in trait composition can be associated with changes in the extent and packing of the functional space (Pigot, Trisos, & Tobias, 2016). For instance, species-rich communities at low elevations tend to be functionally over-dispersed, whereas highland communities tend to be more clustered as a consequence of environmental filtering along elevational gradients (Dehling, Fritz, et al., 2014). In addition to these natural changes in trait composition, human activities, such as land-use changes, alter the distribution of plant and animal traits in ecological communities (Burivalova et al., 2015; Menke, Böhning-Gaese, & Schleuning, 2012; Peres, 2000). Trait-mediated responses to abiotic or human-induced factors have been conceptualized in the response–trait framework for plants (Díaz et al., 2007; Suding et al., 2008) and, to a lesser extent, for animals (Luck, Lavorel, McIntyre, & Lumb, 2012),

but have largely neglected the consequences of changes in biotic factors for consumer species. Eltonian niches are particularly suitable for studying consumer responses to environmental change because they characterize the functional roles of consumer species in terms of their resource use, that is, interaction partners in ecological networks (Dehling & Stouffer, 2018). Trait-based analyses of resource–consumer relationships can thereby yield new insights into how flexible consumer species respond to changes in the trait composition of resource species.

Previous studies have used functional diversity measures (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013) to compare changes in functional trait composition between ecosystems (see Dehling, Fritz, et al., 2014; Saavedra et al., 2014; Maglianesi et al., 2015). We here present a novel trait-based measure, which quantifies *functional shifts* of consumer species between resource species differing in species traits (Figure 1). This new approach has been developed based on previous studies that projected species into the trait space of their interaction partners (Dehling et al., 2016) and quantified trait-based metrics of changes in partner associations (Bender et al., 2017). The measure of functional shift developed here is widely applicable because resource shifts in space and time are ubiquitous in nature and affect a multitude of bipartite species interactions (García, Zamora, & Amico, 2011; Mandelik et al., 2012; Memmott, Craze, Waser, & Price, 2007; Mulwa, Neuschulz, Böhning-Gaese, & Schleuning, 2013; Tellería, Ramirez, & Pérez-Tris, 2008). A trait-based approach for assessing consumer flexibility to resource variation is especially valuable for studies of highly diverse ecosystems as it facilitates generalization across species and provides a more generic and less idiosyncratic understanding of complex ecosystems. Furthermore, it fills an important conceptual gap as trait-based approaches in community ecology have so far focused on plant communities (e.g., Díaz et al., 2007; Suding et al., 2008; Lavorel et al., 2011) and have often neglected biotic effects on higher trophic levels (Schleuning et al., 2015).

We here quantify functional shifts in diverse communities of frugivorous birds and investigate the ability of birds to switch between morphologically distinct fruit resources between natural and fragmented forests along an elevational gradient in the tropical Andes (Figure 1). Frugivorous birds are major seed dispersers in tropical forests and are essential for forest regeneration, consuming fleshy fruits and dispersing them away from the mother plant

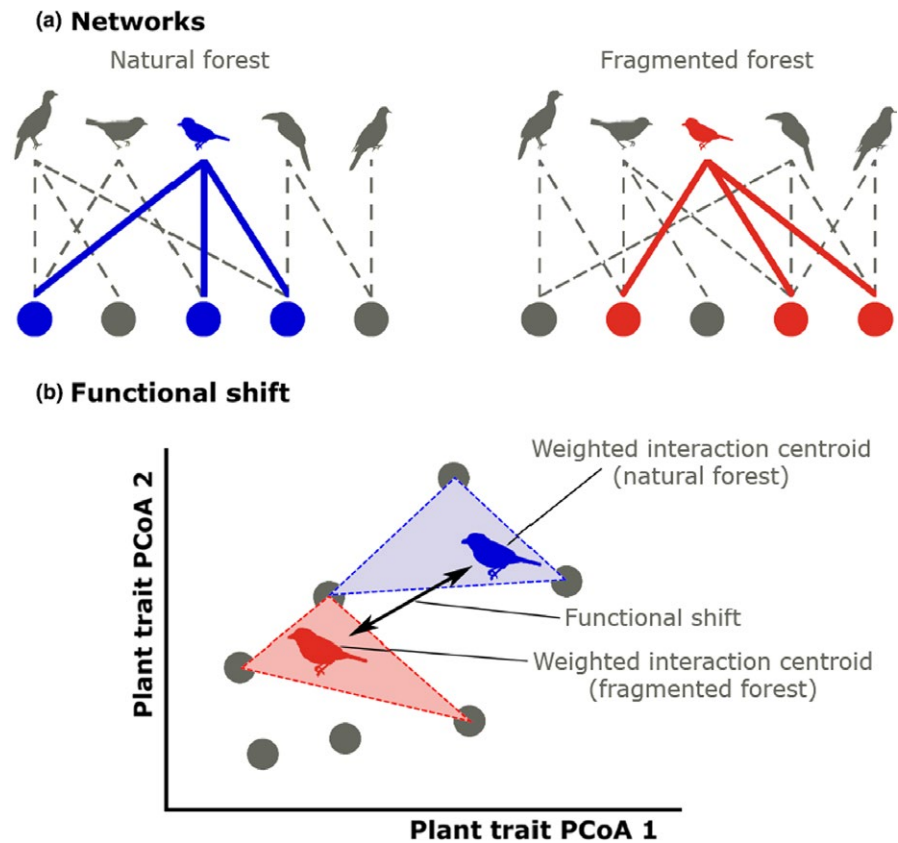


FIGURE 1 Variation in plant-frugivore interaction networks between natural and fragmented forest and the derived measure of functional shift. (a) Interactions between plants and frugivorous birds vary between natural and fragmented forests. The same bird species are present in both habitat types, but changes in the plant community in fragmented forests could cause a (partial) switching to other fruit resources. (b) Functional shift measures the change in fruit choice of a bird species between natural and fragmented forests. It is calculated as the Euclidean distance between the weighted interaction centroids for each bird species between both habitat types

(Howe & Smallwood, 1982). Functional bird traits determine the ability of frugivorous birds to exploit different types of fruit resources (Dehling, Töpfer, et al., 2014). For instance, fruit choice can be constrained by size matching because small-billed species cannot consume large fruits (Galetti et al., 2013; Levey, 1987), and the degree of frugivory has been shown to be associated with fruit choices of frugivorous birds (Carlo, Collazo, & Groom, 2003; Loiselle & Blake, 1990; Schleuning et al., 2011). Furthermore, foraging behaviour has been shown to influence fruit choice, that is, as a function of wing morphology (Bender et al., 2018) or the preferred foraging stratum (Schleuning et al., 2011). In addition to functional traits, the phylogenetic relatedness might influence the functional roles of bird species in seed-dispersal networks (Bender et al., 2017; Dehling, Fritz, et al., 2014; Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007; Schleuning et al., 2014). So far, there is a lack of knowledge on how flexible frugivorous bird species react to changes in the functional trait composition of fruiting plant communities. Understanding which bird species respond more (or less) flexible to changes in fruit resources is, however, crucial to project consequences of environmental change, such as human-induced forest fragmentation, for animal-mediated seed dispersal.

In this study, we first quantify the degree of functional shift that frugivorous birds perform between natural and fragmented forest along a tropical elevational gradient covering three elevational levels (1,000, 2,000 and 3,000 m). Then, we explore whether bird functional traits and phylogenetic relationships are related to the ability of frugivorous birds to perform a functional shift between natural

and fragmented forest. First, we expected a large proportion of birds to perform functional shifts in response to changing fruit resources between natural and fragmented forest, because many frugivorous birds are relatively flexible in their fruit choice and tend to feed on a large variety of fruit types (Bender et al., 2017). We expected that functional shifts to other fruit resources would be more pronounced in bird communities at low than at high elevations because of niche expansion and a higher prevalence of species with extreme traits in lowland communities (Dehling, Fritz, et al., 2014; Pigot, Trisos, et al., 2016). Second, we expected frugivore flexibility to be related to specific functional bird traits. In particular, we expected that birds with large bills, a high degree of frugivory, pointed wings and canopy foraging would be more flexible to respond to changes in fruit traits (Blendinger et al., 2015; Eshiamwata et al., 2006; Neuschulz, Brown, & Farwig, 2013; Schleuning et al., 2011; Wheelwright, 1985). Consequently, we also expected that closely related species would exhibit similar capacities to functional shift in plant-frugivore networks (Bender et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study area and design

We recorded interaction networks of frugivorous birds and fleshy-fruited plants in and around the Podocarpus National Park and the San Francisco reserve in southern Ecuador. The forest within Podocarpus National Park and San Francisco reserve remains mostly

undisturbed (Homeier, Werner, Gradstein, Breckle, & Richter, 2008). The area around the park is highly disturbed with forest fragments embedded in an agricultural matrix consisting mainly of cattle pastures (see Table S1, Supporting information, Tapia-Armijos, Homeier, Espinosa, Leuschner, & De La Cruz, 2015). The study area is located in a tropical montane forest at three different elevations (1,000 m a.s.l., 4° 6' S, 78° 58' W; 2,000 m a.s.l., 3° 58' S, 79° 4' W; and 3,000 m a.s.l., 4° 6' S, 79° 10' W, Homeier et al., 2008). The climate is characterized as humid tropical climate (Kotteck, Grieser, Beck, Rudolf, & Rubel, 2006) with two seasons, a more humid (May–July) and a less humid (September–November) season. Mean annual temperature ranges from 19.4°C in the lowlands to 9.4°C in the highlands, and mean annual precipitation ranges from 2,000 mm in the lowlands to 4,500 mm in the highlands (Moser et al., 2007). The most abundant fleshy-fruited plants consumed by the frugivores across all forest types belonged to the family Melastomataceae, specifically to the genus *Miconia*. At 1,000 m, the most common genera consumed in the natural forest were *Schefflera* (Araliaceae) and *Cecropia* (Urticaceae) and in fragmented forest *Myrsine* (Primulaceae) and *Cecropia* (Urticaceae). At 2,000 m, the most common genera consumed in the natural forest were *Cecropia* (Urticaceae) and *Isertia* (Rubiaceae) and in the fragmented forest *Cecropia* (Urticaceae) and *Viburnum* (Adoxaceae). At 3,000 m, birds consumed mainly species of the genera *Erica* (Ericaceae) and *Schefflera* (Araliaceae) in the natural forest and *Ocotea* (Lauraceae) and *Allophylus* (Sapindaceae) in the fragmented forest.

2.2 | Observations of plant–bird interactions

We sampled plant–frugivore networks at six study sites covering all three elevations (1,000, 2,000 and 3,000 m) and two habitat types (natural and fragmented forest, see Quitián, Santillán, Espinosa, et al., 2018). Every study site comprised three plots, resulting in a total of 18 study plots. Each plot was sampled once in the more humid and once in the less humid season per year over two years (2014 and 2015). During each observation period, we observed each plot for 25 hr on four consecutive days between dawn and noon. Each study plot was observed for a total of 100 hr, resulting in 300 hr for every study site and 1,800 hr for all 18 study plots. We recorded plant–frugivore interaction events by direct observations with binoculars within a 30 x 100 m transect within each plot. We walked freely through the plot and observed each fruiting plant species for a similar amount of time (Quitíán, Santillán, Espinosa, et al., 2018). The study plots ran along steep slopes, which enabled the observation of frugivore activity in the canopy. Only legitimate seed dispersal events were considered; therefore, only interactions with swallowed, pecked or transported fruits of a fruiting plant were recorded. Seed predation events were excluded from the analysis (<1% of the observed interactions).

In order to quantify resource switching between natural and fragmented forests, we selected the subset of bird species that occurred in both interaction networks (i.e., natural and fragmented forest) at each elevation (i.e., 63 species out of 133 species from

all interaction networks). We then excluded those birds that were recorded just in a single interaction event in either of the two forest types. Consequently, plant species considered in this analysis were those ones consumed by the subset of birds for each habitat type at each elevation. This resulted in a total number of 52 bird species feeding on 83 plant species that we used for all subsequent analyses. Most bird species were present at only one elevation; only four out of the 52 species were recorded at two different elevations.

2.3 | Functional trait measurements

We collected four corresponding functional traits of key importance for avian frugivory (see Dehling, Fritz, et al., 2014) for each fleshy-fruited plant and bird species. We used the morphological trait pairs fruit length/width and bird bill length/width related to size matching, as well as fruit mass and bird body mass related to energy provisioning and requirements. We additionally quantified plant height and Kipp's index (also known as hand-wing index; Moermond & Denslow, 1985; Wheelwright, 1985; Dehling, Fritz, et al., 2014). Kipp's index is calculated by Kipp's distance (i.e., the distance from the tip of the first secondary to the wing tip) divided by wing length and is related to avian foraging and flight performance. We measured traits of all fleshy-fruited plant species based on plant individuals sampled on the study plots. We measured 15 fruits per plant species to obtain an average measure for fruit mass, length and width. The height of every individual fruiting plant was estimated in the field to calculate the average height of each fruiting plant species. Bill and wing traits of birds were measured on four specimens, two females and two males, per species in museum collections (Natural History Museum, Berlin, Germany; Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; Zoological Research Museum Alexander Koenig, Bonn, Germany; Zoological Museum of the University of Copenhagen, Denmark). Bird body mass was compiled from Dunning (2007). Prior to analyses, we log-transformed plant and bird traits to obtain a normal distribution, except for Kipp's index and plant height, since both followed a normal distribution. Additionally to these morphological traits, we recorded functional traits from a published database, EltonTraits 1.0 (Wilman et al., 2014), and recorded the degree of frugivory (0%–100% fruit in diet, with an accuracy of 10%) and the preferred foraging stratum (0%–100% of canopy foraging as, with an accuracy of 10%).

2.4 | Functional diversity and trait space of the plant community

We used a principle coordinate analysis (PCoA) to project the fruiting plant species into a multidimensional trait space (Villéger, Mason, & Mouillot, 2008). We projected all plant species from both natural and fragmented forests into a single four-dimensional PCoA space based on Mahalanobis distances between species (see Dehling et al., 2016; Bender et al., 2017). To quantify plant trait diversity for each forest type and elevation, we calculated two metrics of functional diversity from the four-dimensional PCoA based on Euclidean

distances across all plants in the trait space (see Table S2, Supporting information for a correlation matrix of the four plant traits and the respective axes): functional richness (FRic) and functional dispersion (FDis). FRic is the entire volume of the niche space filled by the species in the community (Mason, Moullot, Lee, Wilson, & Setälä, 2005). FDis equals the spread of species in the functional space calculated as the weighted distance to the assemblage centroid across all species (Laliberté & Legendre, 2010). Weighting was done by the square root of the number of interactions a plant had with a bird in a given habitat and elevation; the square root transformation was chosen to down-weight the importance of plant species with many observed interaction events. Large values of FDis imply that many plant species have long distances to the community centroid of the trait space, indicating communities with many functionally extreme species (Laliberté & Legendre, 2010). We additionally calculated functional turnover (FTurn), which equals the mean of the Euclidean distances from all species in one assemblage to their functionally most similar species in the other assemblage (Dehling, Fritz, et al., 2014). FTurn estimates the dissimilarity in the functional traits of a community, for instance before and after being disturbed, and is a measure of functional β -diversity (de Bello, Lavergne, Meynard, & Leps, 2010; Ricotta & Szeidl, 2009).

2.5 | Functional shift

We calculated functional shift as a measure of a bird's ability to shift between plant resources with different traits between natural and fragmented forests (Figure 1). Large values of functional shift indicate a high flexibility of a frugivorous bird species in its choice of resource types. First, we selected all plant species a bird fed on in a given forest type and elevation. Then, we weighted the principal component values of these plant species by the interaction strength and averaged them to obtain the weighted interaction centroid for each bird species at the respective forest type and elevation (Figure 1, see Dehling et al., 2016, Bender et al., 2017). We calculated interaction strength as the ratio between the number of bird visits to a specific plant species and the total number of interaction events of the birds across all plant species (Bascompte & Jordano, 2007). We then calculated the functional shift for each bird species by calculating the Euclidean distance between the weighted interaction centroids of the bird in natural and fragmented forests for a given elevation (Figure 1).

To compare the observed to a randomly expected functional shift, we implemented a null model of species interactions. We used the Patefield algorithm, which randomizes the observed interaction events while maintaining the total interaction frequency per species (Patefield, 1981). Each network was randomized 100 times. For each elevation, we paired a randomized network for natural and fragmented forest, respectively, and calculated the functional shift for each bird species in a given network pair in the same way as for the observed networks. We then extracted the 5% and 95% quantiles of the expected functional shift for each bird species and elevation, based on the 100 randomized networks, and compared these values

to the observed functional shift of each species. We also calculated the mean functional shift of each bird species at each elevation over all 100 randomized networks. Then, for both observed and expected values, we calculated the mean functional shift over all bird species at each elevation.

2.6 | Phylogenetic signal of functional shift

We calculated the phylogenetic signal of the functional shift because we expected that phylogenetically related bird species show similar degrees of functional shifts. We first constructed a phylogenetic tree of all bird species recorded in the study area in Ecuador ($n = 261$; Quitián, Santillán, Espinosa, et al., 2018; Santillán et al., 2018), using the global bird phylogeny from Jetz, Thomas, Joy, Hartmann, and Mooers (2012). We downloaded 10,000 trees from birdtree.org using the "Hackett All Species" backbone. We combined the trees into one consensus tree using the "maximum clade credibility tree" option with median node height with the program TreeAnnotator v1.8.4. (BEAST v 1.8.1, Drummond, Suchard, Xie, & Rambaut, 2012). From the overall bird phylogeny of the study area ($n = 261$ species), we removed those species, which did not occur in interaction networks of both forest types at a respective elevation and constructed a final phylogenetic tree with the remaining subset of species ($n = 52$). Finally, we calculated the phylogenetic signal of the functional shift (log-transformed) using the lambda (Pagel, 1999) and K (Blomberg, Garland, & Ives, 2003) statistics. Lambda ranges from 0 (i.e., traits evolve independent of phylogeny) to 1 (i.e., species traits have a strong phylogenetic dependency). K ranges from 0 to infinity, with larger values indicating a stronger phylogenetic signal.

2.7 | Relationship between functional shift and functional traits

To test the relationship between functional shift (log-transformed) and bird functional traits across the elevational gradient, we fitted a Markov chain Monte Carlo generalized linear mixed model (MCMC glmm, Hadfield, 2010), which accounted for phylogenetic relatedness among bird species. As bill length and body mass were correlated with bill width (Pearson correlations, $r > 0.85$, $p < 0.001$ in both cases), we only selected bill width (log-transformed) and Kipp's index related to size matching and foraging behaviour, respectively. Both traits were unrelated (Pearson correlation, $n = 54$ species, $r = -0.11$, $p = 0.41$). In addition to bill and wing shape, we further included the degree of frugivory and the preferred foraging stratum as additional species' traits related to food choice and foraging in the full model. We accounted for phylogenetic relatedness among bird species based on the phylogenetic tree (ginverse function, Hadfield, 2010). We also added elevation (fixed factor included as a continuous predictor) and a weighting factor to the model (i.e., the geometric mean of the overall number of interactions observed per bird species in natural and fragmented forest), which gave frequently interacting bird species a larger weight in the model. We ran the MCMC glmm model for 100,000 iterations and a burn-in of 10,000. To identify the best predictive model,

we conducted a stepwise elimination of predictors, removing at each step the predictor with the largest p -value. We compared the resulting models based on the deviance information criterion (DIC; Wilson et al., 2010) and selected the final model with the lowest DIC value. All analyses were carried out with R 3.4.0 (R Development Core Team).

3 | RESULTS

The trait spaces of the plant communities differed between natural and fragmented forest across all three elevations (Figure 2, see Table S2). At all elevations, functional richness was lower in the natural than in the fragmented forest. Functional dispersion was lower in the natural than in the fragmented forests at low and high elevations, but was higher in natural than in fragmented forests at mid-elevations. Across the elevational gradient, species and functional richness as well as functional turnover decreased, whereas functional dispersion was highest at mid and lowest at high elevations (Figure 2).

At all elevations, observed values of functional shifts were on average larger than those expected from Patefield null models (mean values at community level; 1,000 m: observed 1.19 vs. expected 0.93; 2,000 m: observed 0.83 vs. expected 0.48; 3,000 m: observed 1.17 vs. expected 0.81). Overall, we found that functional shifts of about 30% of the bird species ($n = 16$) were significantly larger than expected from the null model (see Table S3, Supporting information for observed and expected functional shift values for each species). Species with a larger observed functional shift than expected included Russet-backed oropendola (*Psarocolius angustifrons*, Icteridae), Band-tailed pigeon (*Patagioenas fasciata*, Columbidae) and Flame-faced tanager (*Tangara parzudakii*, Thraupidae). In contrast, only 10% of the species ($n = 6$) had a functional shift significantly lower than expected, that is, Yellow-throated bush-tanager (*Chlorospingus flavigularis*, Passerellidae) and Inca jay (*Cyanocorax yncas*, Corvidae).

Overall, we did not find a significant phylogenetic signal in functional shift ($\lambda = 0.7$, $p = 0.5$; $K = 0.24$, $p = 0.01$, Figure 3), that is, closely

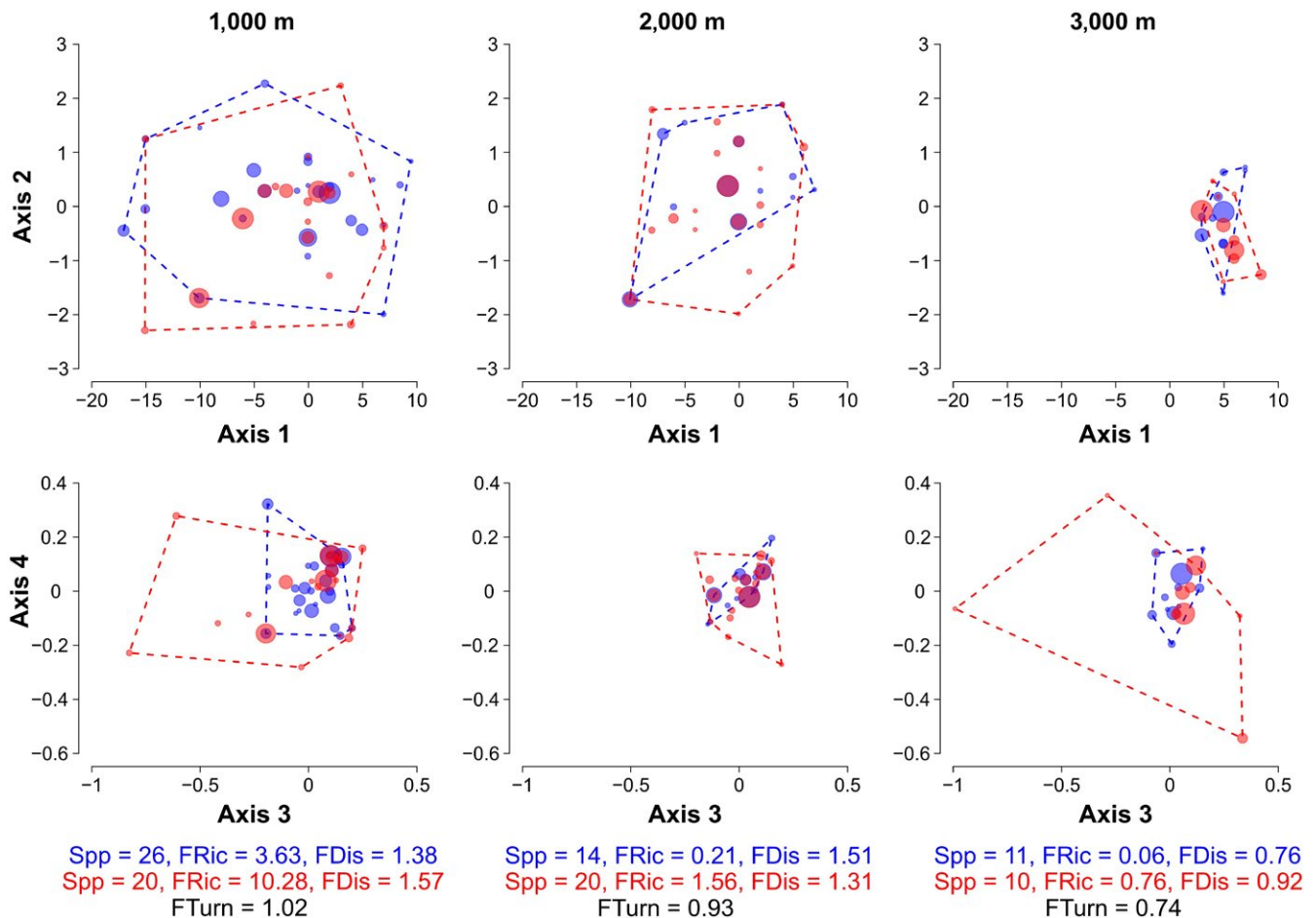
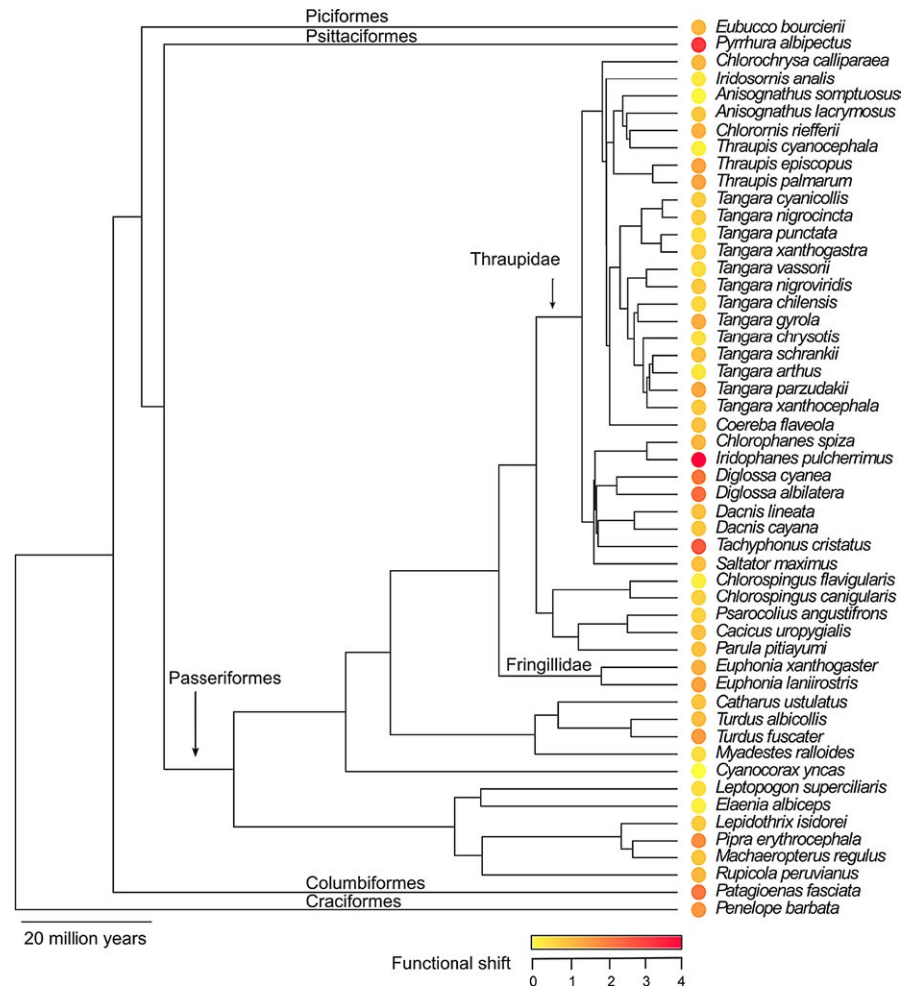


FIGURE 2 Traits spaces of fleshy-fruited plants in natural (blue) and fragmented (red) forest at 1,000, 2,000 and 3,000 m a. s. l. in a tropical mountain forest in the Andes. The principal coordinate analysis is based on four plant traits (i.e., fruit length, width and weight and plant height). Each dot represents one plant species. Dot size represents the square root of the number of interaction events of the respective plant species with all frugivorous birds in the respective network. Plant species richness (Spp), functional richness (FRic) and functional dispersion (FDis) are shown for each forest type and elevation below each trait space. Functional turnover (FTurn), a measure of the functional dissimilarity between natural and fragmented forest, is shown for each elevation. The first ordination axis explained 67%, the second 25%, the third 6% and the fourth axis 2% of the variance in the data. Please note the different scales of the axes between upper and lower panel

FIGURE 3 Functional shift across the avian phylogenetic tree. Yellow dots indicate low values of functional shift, corresponding to a low degree of resource switching between natural and fragmented forests; red dots indicate high values of functional shift. Values represent means across elevations in the rare case ($n = 4$) a species appeared at two adjacent elevations



related bird species did not respond similarly to variation in fruit resources between the two habitat types. In the full MCMC model relating functional shift to the four functional bird traits, only Kipp's index was positively associated with functional shift (Figure 4a), whereas bill width, degree of frugivory and foraging stratum were not related to functional shift (see Table S4, Supporting information for the full model table). After stepwise model simplification, we obtained two models with a similar support and $\Delta\text{DIC} < 2$ (see Table S5, Supporting information for model selection table). The most parsimonious of these two models only contained Kipp's index that was positively associated with functional shift (Table 1, Figure 4a). Although these relationships were tested for a subset of species (52 bird species that occurred in both habitat types), the trait distribution of Kipp's index was representative for the entire frugivore community in the study area (Figure 4b).

4 | DISCUSSION

We found pronounced differences in the functional trait spaces of the consumed fruiting plants between natural and fragmented forests across all three elevations. About one third of all bird species showed a higher flexibility in their fruit choice than expected by Patefield null models and was able to switch between plants of

different traits in natural and fragmented forests. Wing shape was the most important bird trait determining the flexibility of birds to switch fruit resources between natural and fragmented forests, whereas other functional traits and phylogeny were not associated with functional shift. This finding suggests that foraging behaviour was more important for avian flexibility in fruit selection than traits related to food choice.

At all elevations, the average functional shifts in the observed networks were larger than those expected by Patefield null models. We found a high capacity of functional shift for species across different phylogenetic lineages. Our findings suggest that many frugivorous bird species have a high capacity to switch to other types of fruit resources. Dietary plasticity, that is, the ability to switch to other types of fruits or even other resource types, seems to be a widespread ecological phenomenon in frugivorous birds (Carnicer, Jordano, & Melián, 2009; Tellería, Blázquez, De La Hera, & Pérez-Tris, 2013). This is also supported by a previous study, which found a high flexibility in response to temporal fluctuations in fruit resources across phylogenetic lineages (Bender et al., 2017). Our findings were also consistent across the elevational gradient. Although plant species richness and functional diversity showed a decreasing trend towards higher elevations, we found no differences in functional shift between lowland and

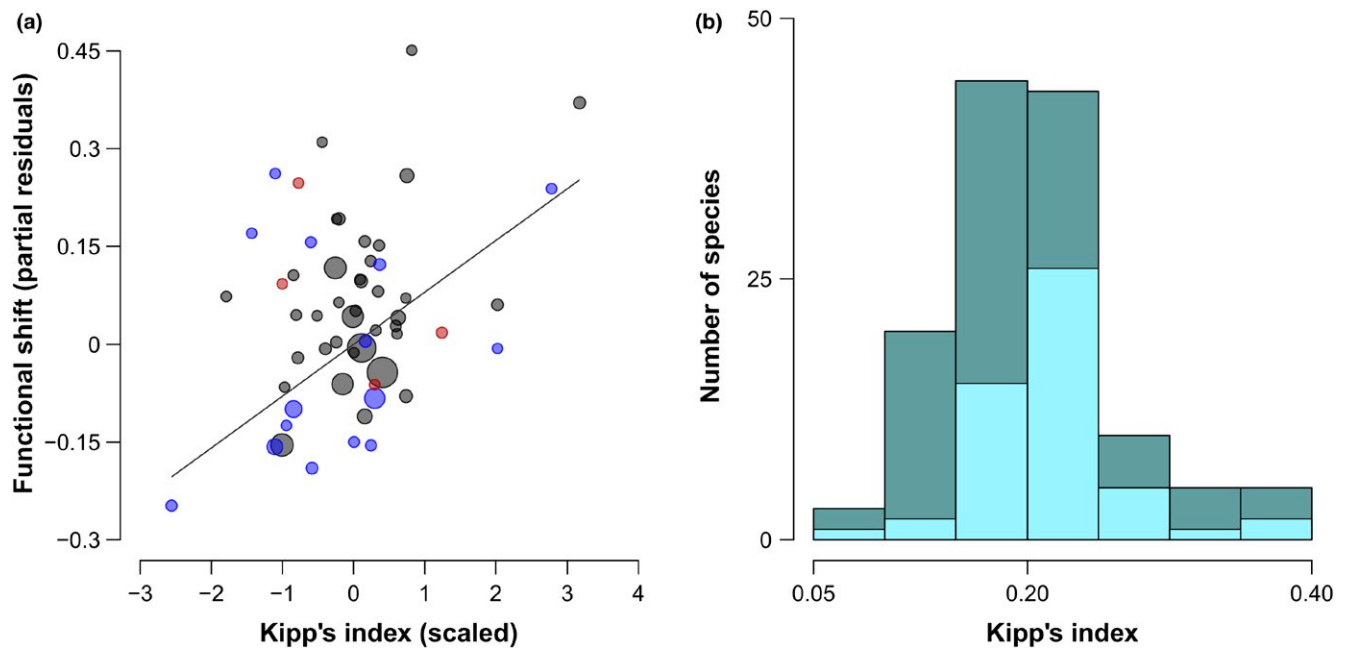


FIGURE 4 (a) Relationships between functional shift and Kipp's index (scaled) based on a generalized linear mixed effects model (MCMC glmm, Hadfield, 2010). Points represent partial residuals of the log-transformed functional shift for each of the 52 bird species occurring in natural and fragmented forests across all elevations. Point size is weighted by the square root of the product of the number of bird interactions in natural and fragmented forest (i.e., larger point size for a higher number of interactions). Black points indicate bird species at 1,000 m, blue 2,000 m, red 3,000 m a. s. l. (b) Histogram illustrating how representative the subset of species ($n = 52$, species that occur in both natural and fragmented forests) is in comparison with the overall species pool (recorded at all elevations, $n = 133$ species) in relation to Kipp's index

TABLE 1 Functional shift between plant resources in natural and fragmented forests as a function of Kipp's index (scaled). Estimates, 95% confidence intervals (CI) and p -values are based on a generalized linear mixed effects model using the MCMC glmm library (Hadfield, 2010). Not shown, but also included were a random effect for a correlation matrix based on the phylogenetic tree, and a weighting factor proportional to the geometric mean of the overall number of interactions observed per bird species in natural and fragmented forest. Significant p -values are shown in boldface

	Hedge's d	Lower 95% CI	Upper 95% CI	p MCM C
Intercept	0.25	0.20	0.29	<0.001
Kipp's index	0.08	0.02	0.14	0.01

highland bird communities. This suggests that similar mechanisms influence avian foraging across the different elevational levels although niche expansion and packing are higher in lowland than highland bird communities (Pigot, Trisos, et al., 2016). Variation in the functional structure of plant and bird communities, however, does not necessarily translate into differences in the structure of interaction networks (Plein et al., 2013). Although trait matching is a general phenomenon in plant–frugivore networks across the entire Andean range (Bender et al., 2018), our findings suggest that trait-based interaction rules do not represent strict constraints in partner choices, but allow species to adapt their fruit choices, at

least to a certain extent. We found that species identities of plants and birds changed almost entirely across the elevational range. Nevertheless, the trait-based approach revealed no systematic differences in functional shift among elevations, which underlines the ability of this approach to identify general patterns across ecological communities. Because flexibility in resource choice is widespread in seed dispersal (Chapman et al., 2004; Wendeln, Runkle, & Kalko, 2000) and pollination interactions (Fontaine, Collin, & Dajoz, 2008), the here proposed approach might be useful to test the trait-based flexibility of plant–animal interactions also in other mutualistic interaction systems. Furthermore, it could also be used to analyse the spatial or temporal variability of other types of resource–consumer interactions, such as plant–herbivore (Dyer et al., 2007; Novotny, Bremerk, & Cizek, 2002) or host–parasite interactions (Morris, Gripenberg, Lewis, & Roslin, 2014).

We found that wing shape was the only trait that was significantly associated with the degree of functional shift across bird species. Species with a large Kipp's index (i.e., pointed wings), such as Russet-backed oropendola (*Psarocolius angustifrons*), Golden-collared honeycreeper (*Iridophanes pulcherrimus*) and Band-tailed pigeon (*Patagioenas fasciata*), were among those species with the largest values in functional shift. Birds with pointed wings are associated with the forest canopy and might efficiently move over long distances (Moermond & Denslow, 1985; Savile, 1957; Senar, Leonart, & Metcalfe, 1994), whereas species with rounded wings (e.g., Yellow-throated bush-tanager, *Chlorospingus flavigularis*)

usually have smaller home ranges (Westcott & Graham, 2000) and mostly navigate through the understorey (Keast, 1996). Our findings suggest that species' foraging behaviour, rather than size constraints, is the major determinant of functional shift. It is likely that species with large foraging distances have, in general, a high capacity to switch between different types of resources (Piersma, Pérez-Tris, Mouritsen, Bauchinger, & Bairlein, 2005)—or that dietary generalists require a high mobility to fulfil their dietary needs (Saracco, Collazo, & Groom, 2004). This notion is consistent with our finding that species that appear to have a high mobility are more flexible than less mobile species. In a previous study, we found a positive association between functional flexibility over time and the temporary specialization on specific types of fruit resources (Bender et al., 2017). This suggests that frugivorous birds with a high mobility follow a nuanced strategy of foraging, which comprises the selection of specific fruit types as well as plastic switches to other fruit types, depending on fruit availability. In contrast, short-ranging species with rounded wings appear to be more constrained and less selective in their fruit choice (Bender et al., 2018). Differences in functional shift between frugivores may not only depend on bird traits, but also on the availability of fruit resources in a bird's foraging habitat. Abundance and diversity of fruits have been shown to be higher in the canopy than in the understorey (Schaefer, Schmidt, & Wesenberg, 2002), which leads to an increase in generalization of plant–frugivore interactions in the canopy (Schleuning et al., 2011). Canopy foragers, which usually have pointed wings (Levey & Stiles, 1992; Moermond & Denslow, 1985), might, therefore, have a larger fruit trait space at their disposal and, thus, have a higher likelihood to perform shifts to fruit resources with different sets of traits. However, we found no association between the preferred avian foraging stratum and functional shift, which suggests that avian foraging was more important for functional shift than differences in fruit availability between forest layers.

In contrast to our expectations, bill width and degree of frugivory were not related to the responses of frugivores to trait differences of the fruiting plant community between natural and fragmented forests. Frugivores with a wide range of bill sizes shifted to plants of different traits in fragmented forests, suggesting that even species with small bills have the opportunity to switch to other fruit types. One explanation for this interesting finding is that small-fruited plants are generally more abundant than large-fruited plant species in tropical forests, both in the canopy and in the forest understorey (Seidler & Plotkin, 2006; Wheelwright, 1985). In our study system, fruits in natural forest were on average larger than in fragmented forest (community weighted mean of fruit width; 0.61 cm in natural vs. 0.49 cm in fragmented forests). The large amount of plant species with small fruits offered in the fragmented forests could explain why even birds with a small bill width were able to switch to other fruit resources in fragmented forest. This could explain why size matching between plants and birds was not associated with the flexibility of birds to switch to other resource types. Surprisingly, we also found no association between the degree of frugivory and functional shift. Degree of frugivory has been shown to be one of

the strongest drivers of species' functional roles in ecological networks (Moran & Catterall, 2010; Moran, Catterall, Green, & Olsen, 2004; Schleuning et al., 2011). One explanation for the lack of an effect on functional shift could be that different mechanisms drive responses of species with an obligate vs. opportunistic fruit diet. We expected that obligate frugivores were more flexible in fruit choice, consistent with previous studies on specialization that have shown that obligate frugivores usually cover a wide spectrum of fruit traits (Blendinger et al., 2015). On the other hand, opportunistic frugivores are also likely to show plastic responses to food availability as they frequently switch between different resource types (Carnicer et al., 2009). Hence, plastic responses to food availability are expected for species with a high and a low degree of frugivory. Overall, we show that the flexibility of avian frugivores to consume fruit resources of different types is high and related to avian foraging behaviour. Because resource–consumer interactions are ubiquitous in nature, it is crucial to quantify consumers' flexibility to adapt to changes in resource availability. The trait-based approach of calculating functional shifts in resource use, developed in this study, is a way to quantify this flexibility independent of species identity and is applicable to all types of bipartite trophic interactions, such as pollination, herbivory or predator–prey interactions. We conclude that the implementation of this new measure, functional shift, will be useful to detect how flexibly consumer species react to biotic changes in resource availability. Quantifying functional shifts in communities may provide an important extension of the concepts in trait-based community ecology that often focused on plant responses so far.

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AUTHORS' CONTRIBUTIONS

M.Q., V.S., K.B.-G., M.S. and E.L.N. conceived and designed the study; M.Q. and V.S. collected the data; J.H. identified the botanical samples; M.Q. analysed the data; M.Q., M.S. and E.L.N. led the writing of the manuscript with editorial advice from I.M.A.B., C.I.E., J.H. and K.B.-G.

DATA ACCESSIBILITY

All data used in this manuscript have been uploaded to the Senckenberg Data and Metadata Repository and are accessible using the following <https://doi.org/10.12761/SGN.2018.10268> (Quitián, Santillán, Bender, et al., 2018b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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