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RESEARCH PAPER

Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms across scales

D. Matthias Dehling[1]*, Till Töpfer[1,2]†, H. Martin Schaefer[3], Pedro Jordano[4], Katrin Böhning-Gaese[1,5] and Matthias Schleuning[1]

[1]*Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt (Main), Germany,* [2]*Senckenberg Naturhistorische Sammlungen Dresden, 01109 Dresden, Germany,* [3]*Department of Evolutionary Biology and Animal Ecology, Faculty of Biology, University of Freiburg, Hauptstrasse 1, 79104 Freiburg, Germany,* [4]*Integrative Ecology Group, Estación Biológica de Doñana (CSIC-EBD), Avda. Americo Vespucio s/n, Isla de La Cartuja, E41092 Sevilla, Spain,* [5]*Department of Biological Sciences, Johann Wolfgang Goethe-Universität Frankfurt, 60438 Frankfurt (Main), Germany*

*Correspondence: D. Matthias Dehling, Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt (Main), Germany.
E-mail: matthias.dehling@senckenberg.de
†Present address: Zoological Research Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany.

ABSTRACT

Aim Functional relationships between species groups on macroecological scales have often been inferred from comparisons of species numbers across space. On large spatial scales, however, it is difficult to assess whether correlations of species numbers represent actual functional relationships. Here, we investigated the functional relationship between a feeding guild (fruit-eating birds) and its resource (fleshy-fruited plants) by studying the matching of their functional traits across spatial scales, from individual interactions to regional patterns.

Location A 3000-m elevational gradient in the tropical Andes.

Methods We sampled plant–bird interactions at two sites along the elevational gradient, and using multivariate statistics (fourth-corner analysis) we identified corresponding morphological traits of birds and plants that influenced which bird species fed from which plant species. We then tested whether the functional trait diversities of the bird species assemblages matched those of the plant species assemblages along the elevational gradient.

Results Corresponding functional traits of birds and plants were closely and significantly correlated on the scale of individual plant–bird interactions. On the regional scale, the functional diversities, but not species numbers, of bird and plant assemblages correlated significantly along the elevational gradient.

Main conclusions The analysis of species interaction networks with multivariate statistics was a powerful tool for identifying relationships between functional traits of interacting species. The close functional relationships between birds and plants on the scale of individual interactions and on the regional scale show that comparisons of functional trait diversities, based on matching traits of interacting species, are better suited than correlations of species numbers to reveal the mechanisms behind large-scale diversity patterns of interacting species. The identification of functional interdependences between interacting species on large spatial scales will be important for improving predictive models of species distributions in space and time.

Keywords
Andes, elevational gradient, fleshy-fruited plants, fourth-corner analysis, frugivorous birds, functional diversity, interaction networks, Manú National Park, mutualism, seed dispersal.

INTRODUCTION

The occurrence of a species at a particular site is not only determined by its interaction with the abiotic environment but also by its interactions with other species (Soberón, 2007; Holt, 2009). The effect of trophic and mutualistic interactions on species occurrences and diversity patterns on large spatial scales has so far only been addressed in studies that compared patterns of species numbers (Hawkins & Porter, 2003; Kissling *et al.*, 2007, 2008; Jetz *et al.*, 2009; Sandom *et al.*, 2013). On large

spatial scales, however, it is difficult to assess whether an observed covariation of species richness is in fact evidence of a functional relationship between species groups or simply a parallel pattern caused by other factors, such as similar responses to climatic conditions. Hence, studies of species richness patterns have yielded inconclusive results (Hawkins & Porter, 2003; Kissling *et al.*, 2008; Jetz *et al.*, 2009).

Trophic interactions, especially if mutually beneficial, usually involve mutual adaptations between the species of the different trophic levels (Guimarães *et al.*, 2011; Sandom *et al.*, 2013). Pronounced specificity of species interactions is very rare (Johnson & Steiner, 2000), and in plant–animal mutualistic assemblages trait convergence and complementarity is the rule, resulting in interactions of low specificity (Janzen, 1980; Janzen, 1985). Accordingly, strong functional relationships between interacting groups of species should lead to increased complementarity between interacting partners and increased convergence among the species of each trophic level (Thompson, 2009; Guimarães *et al.*, 2011). The concept of functional diversity provides a powerful tool for evaluating complementarity and convergence patterns in multispecies assemblages by measuring the diversity of species functional roles, as manifested in the diversity of traits that are associated with specific ecological functions (Tilman, 2001; Violle *et al.*, 2007). Comparison of the functional diversities might therefore be a suitable way to assess the mutual dependences of species groups on large spatial scales. To our knowledge, the matching of functional traits and the covariation in functional trait diversities of interdependent groups of organisms has so far not been investigated on large spatial scales.

The study of mutualistic interaction networks is a way to assess the interdependences of interacting species (Bascompte & Jordano, 2014). Whether or not two species interact depends on the matching of their traits (Jordano, 1987; Stang *et al.*, 2009), and species interactions might already be inferred from a small number of traits (Eklöf *et al.*, 2013). If species interactions indeed depended on trait matching and trait complementarity between trophic levels, the diversity of interactions should also be manifested in the diversity of traits in species assemblages.

Here, we tested for the first time whether the traits of interacting species groups are consistently related across spatial scales, from the matching of species traits in individual interactions to the matching of functional trait diversities of species assemblages on the regional scale. We investigated these functional relationships for a feeding guild (fruit-eating birds) and its resource (fleshy-fruited plants) along a tropical elevational gradient. Climatic conditions and habitats vary greatly over small spatial extents along elevational gradients, which makes them excellent systems for studying diversity patterns (Sanders & Rahbek, 2012). Frugivorous birds and fleshy-fruited plants are well suited for this study because most tropical woody plants produce fleshy fruits with seeds that are dispersed by birds (Howe & Smallwood, 1982), and many tropical birds are highly dependent on fruit as food resource (Kissling *et al.*, 2009). Several combinations of morphological traits of birds and plants are known to influence the fruit choice of frugivorous birds, and correspondingly the fruit display of plants (Moermond &

Denslow, 1985). The most important traits for bird species are probably beak size and gape width because they restrict the maximum size of fruits that can be handled and/or swallowed (Moermond & Denslow, 1985; Wheelwright, 1985; Levey, 1987). The fruit choice of a bird species is further influenced by the availability of fruits. Large frugivores, for instance, depend on reliable fruit resources and should therefore prefer trees with large fruit crops (Blendinger & Villegas, 2011; Corlett & Primack, 2011). Finally, fruits are offered at different heights in the forest (Schaefer *et al.*, 2002) and birds are often adapted to foraging in certain forest strata (Clark *et al.*, 2001; Schleuning *et al.*, 2011). Bird species that forage in lower strata usually have relatively rounded wings because this increases manoeuvrability inside the forest, whereas species that forage in the canopy and fly long distances between fruiting plants above the canopy have longer and more pointed wings (Moermond & Denslow, 1985; Gill, 2007).

We studied the functional relationships between frugivorous birds and fleshy-fruited plants on two spatial scales.
1. We selected corresponding bird and plant traits and tested whether these traits influenced the frequencies of interaction between bird and plant species. For this, we used a novel approach in which we applied multivariate statistics to data from plant–bird networks collected at two elevations along the elevational gradient. We expected high interaction frequencies between species with matching functional traits.
2. We then used the same set of plant and bird traits to calculate functional diversities of bird and plant assemblages along the entire elevational gradient to test whether the trait diversities of both groups matched on a regional scale.

METHODS

We studied functional relationships between bird and plant assemblages at seven sites at every 500-m elevation along a gradient from 500 to 3500 m a.s.l. ('m' hereafter) in the Kosñipata valley in the Manú Biosphere Reserve in the Andes of south-east Peru, a global hotspot of frugivorous bird diversity (Kissling *et al.*, 2009).

Interaction networks

At two sites along the Manú gradient – Wayqecha (3000 m, upper montane rain forest) and San Pedro (1500 m, lower montane rain forest) – we sampled plant–bird interactions four times approximately every 3 months between December 2009 and September 2010. To record these interactions, we installed plots of 100 m × 30 m (six plots in Wayqecha, eight plots in San Pedro; distances between the plots were at least 200 m), and recorded all fleshy-fruited plant species therein. During each observation period, we observed every plot on five consecutive days between dawn and noon for a total of 30 h and recorded which bird species fed on which plant and the way the birds handled the fruits. Because our plots ran along steep slopes, we could also observe frugivore activity in the canopy. The total observation time was 720 h in Wayqecha and 960 h in San

Pedro, and all interactions recorded at a site were pooled for the analyses. Interaction frequencies were measured as the number of bird visits to a plant species. The Wayqecha network included 1344 interaction events of 26 bird species with 51 plant species, and the San Pedro network included 4988 interaction events of 61 bird species with 53 plant species. To assess the completeness of the networks, we calculated the expected numbers of frugivore species and interacting species pairs with Chao's richness estimators using the R package vegan (Oksanen *et al.*, 2012) and generated accumulation curves from randomly drawn subsamples of the observed interactions.

Species richness

We compiled lists of co-occurring bird species for all sites using data from Walker *et al.* (2006) and Merkord (2010), as well as data collected by D.M.D. during field work in Manú between December 2009 and September 2011 (Dehling *et al.*, 2013, 2014). We identified all bird species in the dataset that consume fruit as a main part of their diet (obligate and partial frugivores in the classification of Kissling *et al.*, 2009) but omitted ground-dwelling species (Tinamidae, Odontophoridae, Psophidae, *Mitu*) because they have other foraging and fruit-handling strategies than species that take fruit directly from the plant. The bird assemblages included 219 frugivorous species.

For plant species richness, we sampled an area of 1 ha at each site (divided into 10 plots of 20 m × 50 m) and recorded all plants with ripe fleshy fruit. To account for phenological differences, each site was sampled once in the rainy season (December to March) and once in the dry season (June to September) between December 2009 and September 2011. The plant dataset included 401 plant species.

Functional traits

For all bird and plant species recorded in the interaction networks and at the seven sites, we collected corresponding bird and plant traits that are related to avian frugivory: (1) beak length and beak width versus fruit length and fruit diameter as corresponding traits related to the matching of beak and fruit sizes; (2) body mass versus fruit crop mass as corresponding traits related to energy requirements and resource availability; and (3) pointedness of the wing versus plant height as corresponding traits related to the preferred foraging height of a bird. We measured beak length, beak width and wing pointedness on museum specimens following Eck *et al.* (2011) (a list of specimens is provided in Dehling *et al.*, 2014). We measured beak length as the distance from the commissural point of the upper and lower beak to the tip of the closed beak and beak width as the external distance between the two commissural points, which is functionally equivalent to gape width (Wheelwright, 1985). We measured the pointedness of a bird's wing as Kipp's index, which is Kipp's distance (the distance from the tip of the first secondary to the wing tip measured on the folded wing) divided by wing length. We compiled data on bird body mass from Dunning (2007) and from specimen labels. We measured

all morphological plant traits in the field. For each plant recorded in our plots and in the networks, we recorded fruit length and fruit diameter, plant height and crop size (the number of fruits on the plant, estimated for trees with very large crops). We used tree height as a proxy for the height at which fruits were offered. For epiphytes we recorded the height at which they grew. In the analyses, we used the species means of all morphological bird and plant traits. The product of mean crop size and mean fruit mass was used to estimate total fruit crop mass. Body mass and crop mass were log-transformed to improve normality, and all traits were standardized to zero mean and unit variance.

Fourth-corner analysis of plant–bird networks

To investigate the relationships between the functional traits of interacting bird and plant species, we extended the application of the fourth-corner analysis (Legendre *et al.*, 1997; Dray & Legendre, 2008) to the analysis of network data. Fourth-corner analysis is used to investigate the relationship between species traits and environmental variables by relating a matrix of environmental conditions of the sites (R; sites × environmental conditions) to a matrix of species traits (Q; species × traits) via a matrix of species occurrences at the different sites (L; species × site) (Dray & Legendre, 2008). In this study, we modified the approach and used the species interaction matrix (unit: interaction strength, the proportion of visits of a frugivore species to each plant species; Jordano, 1987) from Wayqecha and San Pedro as the matrix L (birds × plants) in order to compare a matrix of plant traits (matrix R, plant species × plant traits) with a matrix of bird traits (matrix Q; bird species × bird traits). We tested the relationships between the following corresponding bird and plant traits: beak length and beak width versus fruit length and fruit diameter, Kipp's index versus plant height, and body mass versus crop mass. For significance testing, we used a combination of permutation methods 2 (entire rows of the interaction matrix are permuted) and 4 (entire columns of the interaction matrix are permuted; Dray & Legendre, 2008) and took the larger of the two *P*-values as suggested by Ter Braak *et al.* (2012). To test if sample size influenced the results of our study, we randomly drew a fixed proportion of interactions from our networks (0.1 to 0.9 in steps of 0.1) and repeated the analyses 1000 times for each subsampled proportion of observations.

Functional diversity and individual traits along the gradient

We calculated the functional diversity of bird and plant assemblages as functional richness (FRic) which measures the volume of a convex hull around all species of an assemblage projected in a multidimensional trait space (Villéger *et al.*, 2008). Species are projected into trait space based on the Euclidean distances between them as calculated from the morphological traits using Principal Coordinates Analysis (PCoA). We used the four functional bird traits (beak length, beak width, Kipp's index, body mass) to calculate the FRic of bird assemblages and the four

corresponding functional plant traits (fruit length, fruit diameter, plant height, crop mass) to calculate the FRic of plant assemblages. We standardized FRic to range between 0 and 1 by dividing observed FRic values by the total FRic value calculated from all species in the regional species pool. To test whether patterns of functional richness were associated with differences in the filling of the functional trait space, we also calculated functional evenness (FEve), which measures the regularity of distances between species in trait space along a minimum spanning tree (Villéger *et al.*, 2008). FEve ranges between 0 and 1 with values close to 1 indicating very similar distances and values close to 0 indicating very irregular distances between species in the assemblage.

To test if patterns of FRic and FEve were driven by a small number of species with extreme trait combinations, we calculated nearest neighbour distances between species in the functional trait space for the seven assemblages along the gradient and then excluded all species that were more than three times the median of nearest neighbour distances away from any other species in the respective assemblage. We recalculated FRic and FEve for the assemblages along the gradient excluding these species with extreme trait combinations. We used linear regression models to test for trends of species richness, FRic and FEve (with and without the species with extreme trait combinations), along the elevational gradient. We also used linear regression models to test for the relationships between the species richness and FRic of the plant assemblages and the species richness and FRic of the bird assemblages. To assess whether patterns of functional trait diversity reflected those of phylogenetic diversity, we approximated phylogenetic diversities by the numbers of families and genera of frugivorous birds and fleshy-fruited plants and tested their relationships along the elevational gradient. A calculation of the phylogenetic diversity based on phylogenetic data was not possible, because phylogenetic data were not available for all plant species in the dataset.

To test whether patterns of functional richness were driven by strong trends in single traits or rather by a change in the number of realized trait combinations, we analysed the relationships between individual functional traits and elevation with fourth-corner analysis (Legendre *et al.*, 1997; Dray & Legendre, 2008). To visualize trends for FRic along the elevational gradient, we plotted the first two PCoA axes for the assemblages at 500, 1500 and 3000 m. To visualize the trends for individual traits, we then used the function ordisurf in the R package vegan (Oksanen *et al.*, 2012) which fits a smooth surface for each trait into the plots using generalized additive models (Oksanen *et al.*, 2012).

For all statistical analyses, we used R version 3.0 (R Development Core Team, 2013) and the packages ade4 (Dray & Dufour, 2007), FD (Laliberté & Legendre, 2010) and vegan (Oksanen *et al.*, 2012).

RESULTS

The accumulation curves showed that the networks were well sampled, with the numbers of frugivore species and interacting species pairs approaching the expected values in both networks

Table 1 Fourth-corner correlations between functional traits of interacting species of frugivorous birds and fleshy-fruited plants in plant–bird interaction networks at two sites in the Manú Biosphere Reserve, Peru. Correlations are based on the interaction strength (relative interaction frequencies) between species. Significant correlations are in bold. The relationship beak length–fruit diameter is not shown because it was very similar to the relationship beak length–fruit length. $n = 1344$ (Wayqecha) and 4988 (San Pedro) plant–frugivore interaction events.

Site	Corresponding traits	r	P
Wayqecha (3000 m)	Beak length–fruit length	**0.69**	**0.001**
	Beak width–fruit diameter	**0.59**	**0.003**
	Body mass–crop mass	**0.41**	**0.002**
	Kipp's index–plant height	0.16	0.246
San Pedro (1500 m)	Beak length–fruit length	**0.41**	**0.002**
	Beak width–fruit diameter	**0.52**	**< 0.001**
	Body mass–crop mass	**0.32**	**0.015**
	Kipp's index–plant height	**0.39**	**< 0.001**

(Appendix S1 in Supporting Information). There were significant positive correlations between nearly all corresponding traits of interacting species in the interaction networks (Table 1), showing that matching of bird and plant traits resulted in higher interaction frequencies. The strongest relationships were between beak size (beak length, beak width) and fruit size (fruit length, fruit width; $0.41 \leq r \leq 0.69$; Table 1). The relationship between Kipp's index and plant height was only significant in the network at 1500 m (Table 1). Simulations with random subsamples of the observed interactions yielded similar relationships between traits (Appendix S2). Even when including only about half the number of observed interactions in the analysis, the 95% confidence intervals of simulated P-values were below the 0.05 level for all significant trait relationships (Appendix S2).

Species richness of birds decreased significantly with increasing elevation ($r^2 = 0.98$, $t = 14.53$, $P < 0.001$), whereas the decrease of plant species richness with increasing elevation was not significant ($r^2 = 0.39$, $t = -1.79$, $P = 0.134$). By contrast, functional richness (FRic) of both birds and plants declined exponentially with increasing elevation (birds, $r^2 = 0.95$, $t = -10.17$, $P < 0.001$, Fig. 1a; plants, $r^2 = 0.93$, $t = -8.13$, $P < 0.001$, Fig. 1b). Functional evenness (FEve) showed only a weak relationship with elevation (Fig. 1c, d). Although bird FEve declined marginally significantly with elevation ($r^2 = 0.54$, $t = -2.45$, $P = 0.06$; Fig. 1c), the slope was close to zero, and the change of bird FEve (a decrease of 0.1 units or 14.0%) was very small compared with the 92.3% decrease in bird FRic between the assemblages at 500 and 3500 m (Fig. 1a, c). Analyses of FRic and FEve excluding species with extreme trait combinations gave results that were virtually identical to those obtained for the analyses that included all species (Appendices S3 & S4). Consistent with our expectation, plant FRic was a much better predictor of bird species richness and bird FRic along the elevational gradient than plant species richness (Table 2). In line with this
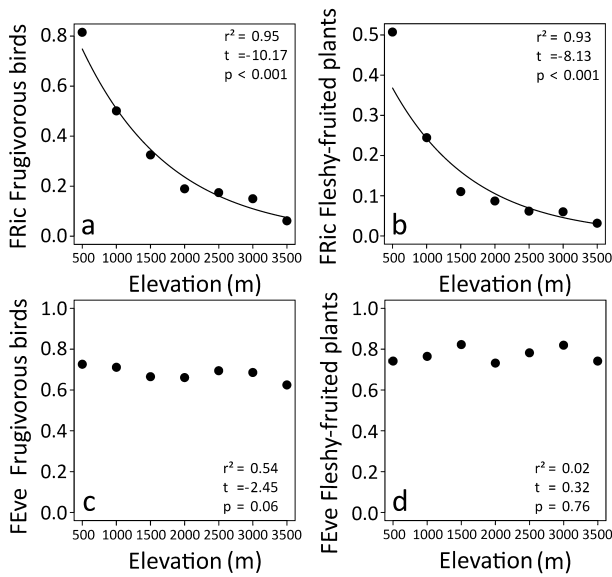
Figure 1 Relationship of functional richness (FRic) of (a) frugivorous birds and (b) fleshy-fruited plants, and functional evenness (FEve) of (c) frugivorous birds and (d) fleshy-fruited plants with elevation in the Manú Biosphere Reserve, Peru ($n = 7$ elevational belts between 500 and 3500 m a.s.l). Exponential declines in (a) and (b) were fitted with log(FRic)–elevation.

Table 2 Linear regression models testing the relationships between the species richness and functional richness of fleshy-fruited plants and the species richness and functional richness of frugivorous birds along an elevational gradient in the Manú Biosphere Reserve, Peru. Significant correlations are in bold. $n = 7$ elevational belts between 500 and 3500 m a.s.l.

	Plant species richness			Plant functional richness		
	r^2	t	P	r^2	t	P
Bird species richness	0.34	1.60	0.169	**0.70**	**3.45**	**0.018**
Bird functional richness	**0.58**	**2.64**	**0.046**	**0.96**	**11.48**	**< 0.001**

Table 3 Fourth-corner correlations between the functional traits of frugivorous bird species ($n = 219$) and fleshy-fruited plant species ($n = 401$) with elevation along the Manú elevational gradient ($n = 7$ elevational belts between 500 and 3500 m a.s.l.) Significant correlations are in bold.

		Elevation	
		r	P
Birds	Beak length	−0.08	0.101
	Beak width	**−0.09**	**0.035**
	Body mass	−0.06	0.140
	Kipp's index	−0.07	0.115
Plants	Fruit length	**−0.17**	**0.041**
	Fruit diameter	−0.16	0.055
	Crop mass	−0.03	0.401
	Plant height	**−0.19**	**0.004**

finding, the relationships between family numbers ($r^2 = 0.34$, $P = 0.17$) and between genus numbers ($r^2 = 0.32$, $P = 0.19$) of frugivorous birds and fleshy-fruited plants along the elevational gradient were much weaker than the relationship between FRic values.

In contrast to the strong relationship between elevation and FRic, the correlations between elevation and singular species traits in the fourth-corner analysis were generally weak (Table 3), although there was a significant decrease of beak width, fruit length and plant height and a marginally significant decrease of fruit diameter with increasing elevation. In the visualization of species traits in the functional trait space, trends for beak length and beak width were similar and fairly orthogonal to the trend for Kipp's index (Fig. 2). Accordingly, in the plant functional trait space, the trends for fruit length and fruit diameter were similar and orthogonal to the trend for plant height (Fig. 2).

DISCUSSION

On the scale of individual interactions, the correlations between corresponding functional traits of interacting frugivorous bird and fleshy-fruited plant species indicate a close matching of functional bird and plant traits. On the regional scale, there was a close positive relationship between the functional diversities of frugivorous birds and fleshy-fruited plants, indicating a strong matching of bird and plant traits on the macroecological scale as well. On the other hand, species numbers of birds and plants were not significantly correlated. The strong relationship between the functional diversities of birds and plants, despite the low correlation of their species numbers, implies that functional diversities are better suited to investigate mutual dependences between interacting species than correlations of species numbers.

Functional relationships in interaction networks

Fourth-corner analysis was a powerful method to identify the close functional relationships between corresponding bird and plant traits. The method was very sensitive for trait relationships in the interaction networks and yielded very similar relationships even if we used as few as 50% of the observed interactions. We recommend it for the identification of traits for large-scale analyses of functional relationships between species groups. The matching of ecomorphological traits of frugivorous bird and fleshy-fruited plant species in the interaction networks is remarkable because the relationships between bird and plant traits were not expected to be exclusive since birds with large beaks could also eat small fruits and birds with rounded wings could also forage in the canopy. Nevertheless, birds appear to consume fruits of plant species that closely match their traits,
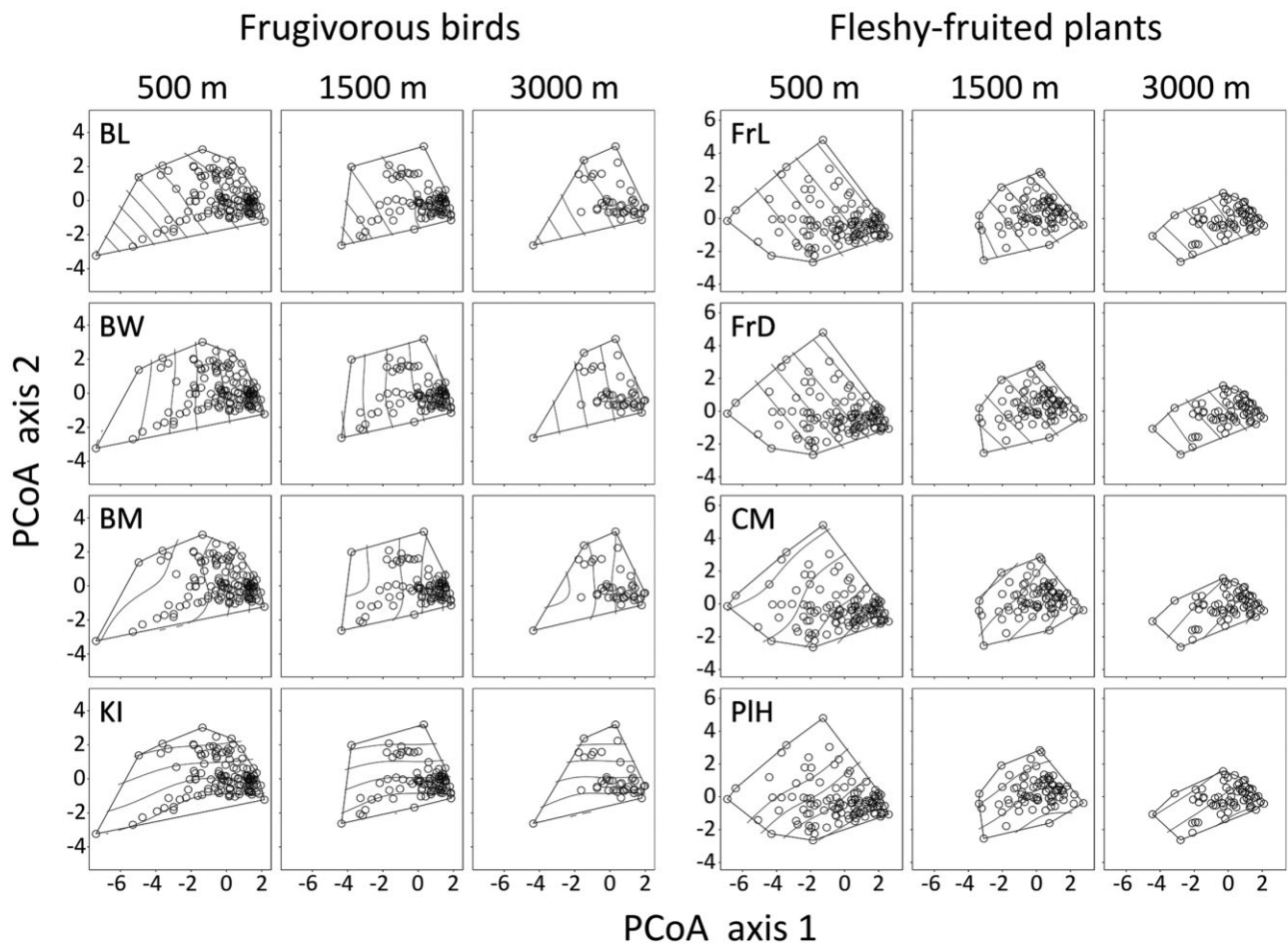
Figure 2 Visualization of the functional trait spaces of frugivorous birds (left) and fleshy-fruited plants (right) exemplified for three assemblages along the elevational gradient and trends for individual traits. The first two Principal Coordinates Analysis (PcoA) axes are shown which explain 90.8 and 91.2% of the variance in bird and plant functional richness (FRic), respectively. The four rows show the trends of individual traits in the trait spaces (BL, beak length; BW, beak width; BM, body mass; KI, Kipp's index; FrL, fruit length; FrD, fruit diameter; CM, crop mass; PlH, plant height). Lines in the trait spaces represent standard deviations of trait values fitted into the trait spaces as smooth surfaces using generalized additive models.

probably because they can exploit these fruit resources more efficiently than other bird species (Fleming, 1979). This suggests that co-evolved interactions in plant–animal mutualisms result in higher trait complementarity in interacting partners, and trait convergence in species of the same trophic level, as expected from theoretical models of network evolution (Guimarães *et al.*, 2011).

Two common dispersal strategies of plants are to produce either many small fruits that contain mostly sugar and are usually consumed by a large number of usually small frugivore species, or few large fruits that contain more lipids and protein and are mostly consumed by relatively large (and large-gaped) frugivore species (Howe, 1993). The strong correlations between beak and fruit size, as well as between body mass and crop mass, support this dichotomy and probably reflect differences in food specialization of birds and dispersal strategies of plants. The relationship between plant height and Kipp's index was significant in the San Pedro (1500 m), but not in the Wayqecha

(3000 m) network. In tropical forests there are several layers of vegetation, from understorey plants to trees that emerge above the canopy (Richards, 1996), and most bird species in tropical forests are adapted to certain foraging heights (Munn, 1985; Schleuning *et al.*, 2011). With increasing elevation, plant height declined significantly in Manú and, as a result, differences in bird foraging heights were probably less pronounced, breaking up the partitioning into stratum-specific foraging guilds towards higher elevations.

Functional relationships along the elevational gradient

The positive relationship between the functional diversities of frugivorous birds and fleshy-fruited plants along the elevational gradient corroborated the close match of bird and plant functional traits on the scale of individual interactions and suggests a congruency in the diversities of functional roles in frugivorous

bird and fleshy-fruited plant assemblages. The close match of bird and plant traits along the elevational gradient is remarkable because there is very high turnover of bird and plant species, as well as of functional and phylogenetic assemblage structure, across elevations (Jankowski *et al.*, 2013; Dehling *et al.*, 2014). Consequently, interactions also change constantly along the gradient. Although the Wayqecha (3000 m) and San Pedro (1500 m) interaction networks have almost no species in common, the relationships between birds and plant traits were similar at the two elevations. This indicates that similar functional relationships between frugivorous birds and fleshy-fruited plants have emerged at both elevations, resulting in covariation of functional diversities of birds and plants along the elevational gradient.

The rather constant values of functional evenness (FEve) along the gradient showed that species were distributed in functional trait spaces in a similar way at all elevations. This indicates that the mechanisms that influence the structure of the species assemblages of frugivorous birds and fleshy-fruited plants are similar along the entire gradient (Dehling *et al.*, 2014). The analyses excluding species with extreme trait combinations yielded results that were very similar to the analyses that included all species (Appendices S3 & S4). The patterns of FRic for birds and plants were therefore not driven by a small number of species with extreme traits but rather by a continuous decline in functional roles throughout the bird and plant communities. Moreover, the weak changes of individual functional traits along the gradient show that the declines of FRic were not driven by the decrease of a single or few traits, but by a decreasing number of trait combinations (Fig. 2). This is also corroborated by the orthogonal (i.e. independent) trends for different combinations of bird and plant traits (Fig. 2).

The FRic of fleshy-fruited plants was a much better predictor of the species richness and FRic of frugivorous birds than the species richness of fleshy-fruited plants. In fact, the species richness patterns of birds and plants did not match very well along the gradient, adding to the conflicting results found by previous studies (Hawkins & Porter, 2003; Kissling *et al.*, 2008; Jetz *et al.*, 2009). The similarly weak relationships between the family and genus numbers of frugivorous birds and fleshy-fruited plants along the gradient suggest that phylogenetic diversity does not adequately reflect the functional relationships between species. These findings are in line with previous results for frugivorous birds from the same study system that show that patterns of functional and phylogenetic diversity along the elevational gradient differ, despite a significant phylogenetic signal in all morphological traits (Dehling *et al.*, 2014).

There are several explanations for incongruent species numbers of interacting species groups on large spatial scales. First, species do not usually form exclusive interaction pairs in which two species are totally dependent on each other. Consequently, the number of interaction partners varies considerably among species (Zamora, 2000) and in space (Schleuning *et al.*, 2012) which may lead to incongruence of species numbers between trophic levels on large spatial scales. Second, different levels of specialization on a resource within a guild may influ-

ence the number of species that can co-occur at a site (Fleming, 2005). For instance, several functionally similar species might co-occur because they have only a small dependence on a resource (or interaction partner) and only opportunistically participate in the interaction (Zamora, 2000), whereas specialized species that depend heavily on a resource are more likely to exclude functionally similar species. If patterns of specialization vary spatially (Schleuning *et al.*, 2012), relationships between the diversities of interacting groups of species may be context dependent and lead to a mismatch between the species numbers of interacting species groups on large spatial scales. Studies of functional diversity are more likely to correct for specialization-driven incongruence in species numbers because species that fulfil functional roles that are similar to those of other species contribute little to the functional diversity of the assemblage, whereas functionally unique species with distinct functional roles will contribute strongly to functional diversity.

CONCLUSIONS

We compared patterns of functional diversity of interdependent groups of species (here, a feeding guild and its resource) on different spatial scales. First, we introduced a method to analyse data from interaction networks to identify suitable traits for analyses of functional diversity. Second, we showed that functional relationships between birds and plants were consistent on the scale of individual interactions and on the regional, macroecological scale. This is in accordance with the assumption that the diversity of functional roles should match between interacting species groups (Janzen, 1980; Janzen 1985). Most importantly, our study implies that comparisons of functional diversity are better suited than comparisons of species richness patterns to reveal mechanisms behind species co-occurrence and richness patterns in multispecies assemblages. The incorporation of trait-based functional relationships between species might improve analyses and predictions of diversity patterns of multispecies assemblages in space and time.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Accumulation curves and estimated richness for the number of frugivorous bird species and the number of interacting species pairs for the plant–bird interaction networks.
Appendix S2 Influence of sample size on the correlation coefficients and *P*-values for the fourth-corner correlations between functional traits of frugivorous birds and fleshy-fruited plants.
Appendix S3 Relationships of functional richness and functional evenness with elevation excluding species with extreme trait combinations.
Appendix S4 Visualization of the functional trait spaces along the elevational gradient excluding species with extreme trait combinations.

BIOSKETCH

D. Matthias Dehling is interested in macroecology and biogeography, with a focus on diversity patterns and species interactions. This article forms part of his dissertation conducted at the Biodiversity and Climate Research Centre (BiK-F), Frankfurt.

Author contributions: D.M.D. and M.S. conceived the ideas; all authors discussed the study design; D.M.D. collected species interaction networks and plant data; D.M.D. and T.T. collected bird data; D.M.D. analysed the data; D.M.D. wrote the first draft of the manuscript; all authors contributed to the manuscript.

Editor: Christy McCain

1   Supporting Information for Dehling et al. Functional relationships beyond species richness

2   patterns: trait matching in plant-bird mutualisms across scales

3
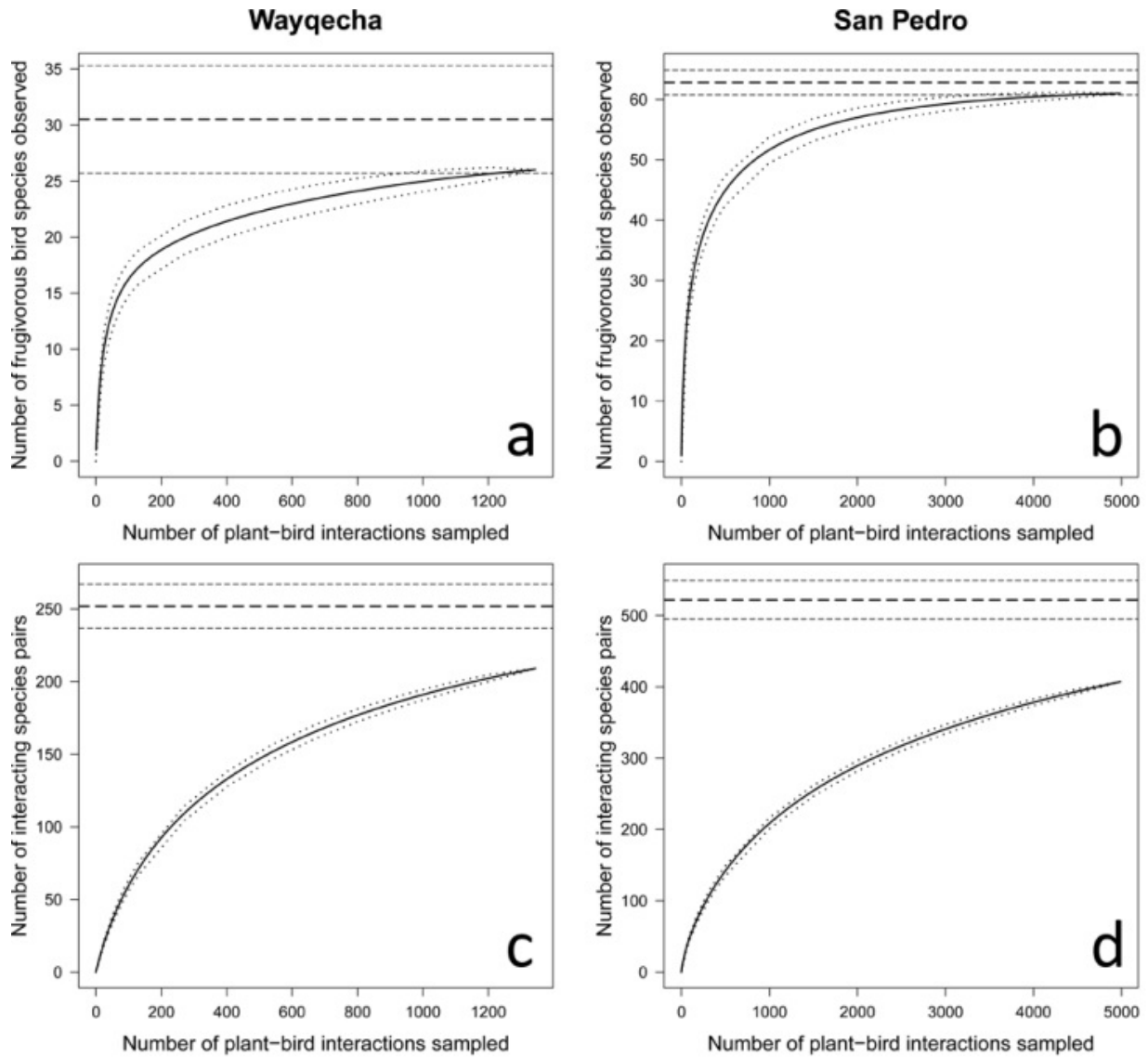
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5   Appendix S1: Accumulation curves and estimated richness for the number of frugivorous bird

6   species (a, b) and the number of interacting species pairs (c, d) for the plant-bird interaction

7   networks in Wayqecha (3000 m a.s.l.) and San Pedro (1500 m a.s.l.). Dotted lines around the

8   accumulation curves show standard errors, dashed lines show the expected total richness with

9   standard errors for the assemblages calculated with Chao's richness estimator in the R

10   package vegan (Oksanen *et al*., 2012).

11   Appendix S2: Influence of sample size on the correlation coefficients and p-values for the

12   correlations between functional traits of frugivorous birds and fleshy-fruited plants in

13   Wayqecha (3000 m a.s.l., above) and San Pedro (1500 m a.s.l., below). We randomly drew

14   1000 samples for each fixed proportion (subsamples of 0.1 to 0.9 in steps of 0.1) of observed

15   interactions (Wayqecha: 1344 observed interactions, San Pedro: 4988). For each draw, we ran

16   a fourth-corner analysis to assess the relationships between functional bird and plant traits.

17   Solid lines show mean values, dotted lines show standard deviations, and dashed lines show

18   the 95% confidence intervals for correlation coefficients and p-values of the fourth-corner

19   correlations calculated from the simulated observations. Observed values correspond to a

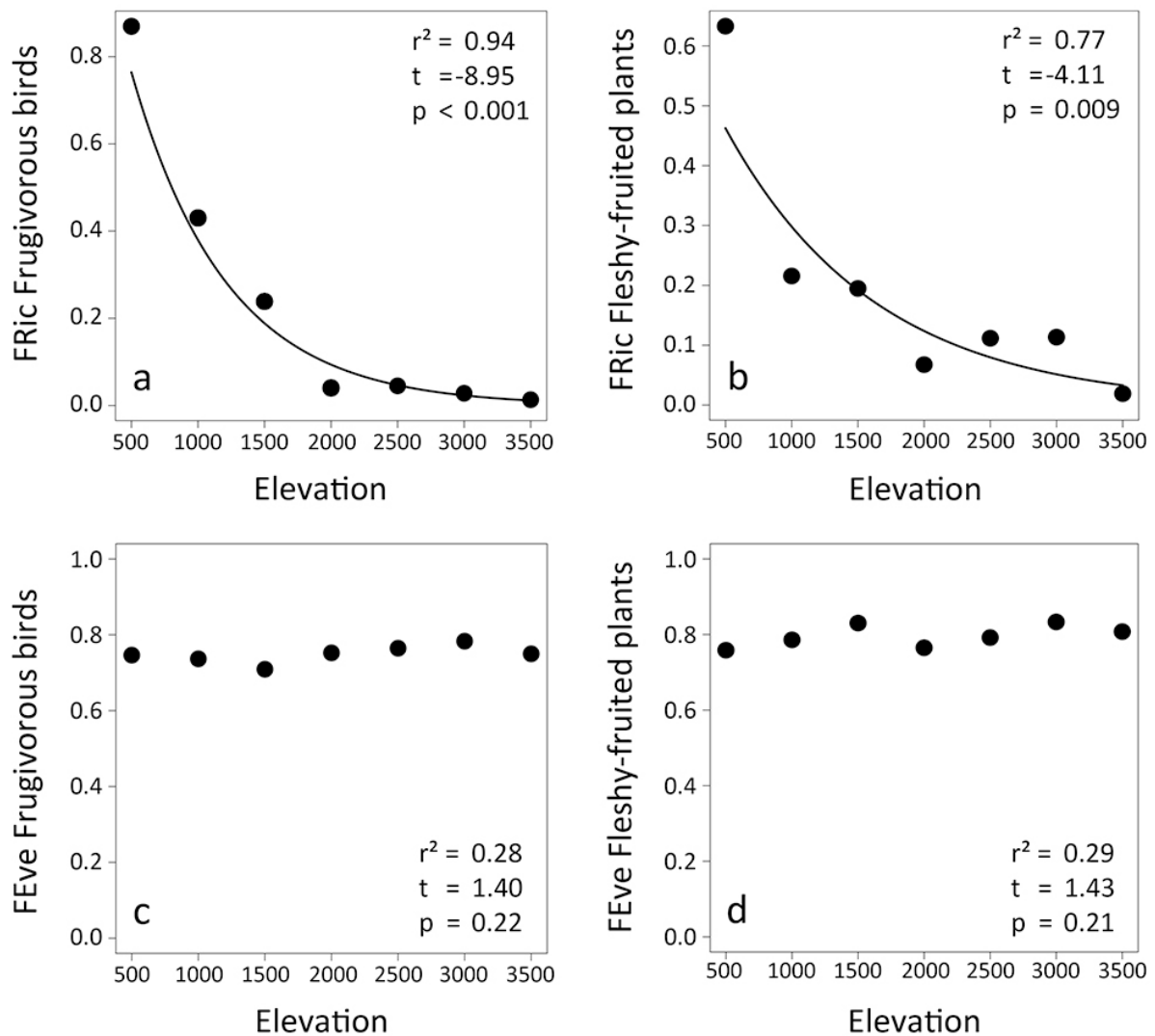20   proportion of 1.

21   Wayqecha:

22

23   San Pedro:

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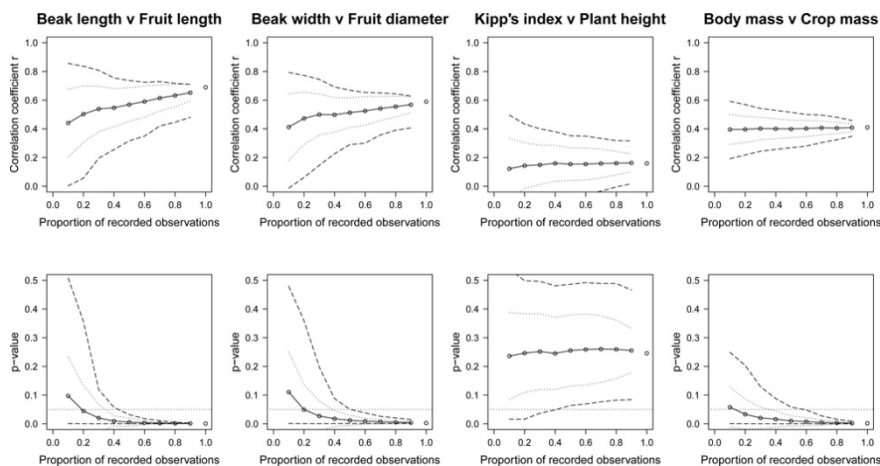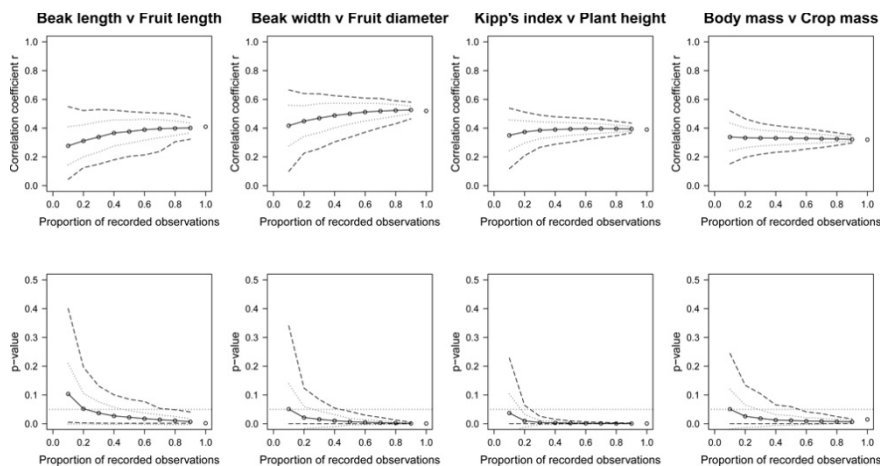
Appendix S3: Relationship of functional richness of a) frugivorous birds and b) fleshy-fruited plants, and functional evenness of c) frugivorous birds and d) fleshy-fruited plants with elevation in the Manú Biosphere Reserve, Peru excluding species with extreme trait combinations. Species more than three times the median values of nearest neighbour distances away from any other species in the respective original assemblages were excluded, leading to the exclusion of 7, 9, 11, 13, 10, 7 and 2, respectively, frugivorous bird species and 8, 2, 1, 3, 1, 1 and 4, respectively, fleshy-fruited plant species from the assemblages between 500 and 3500 m elevation. n = 7 elevational belts.
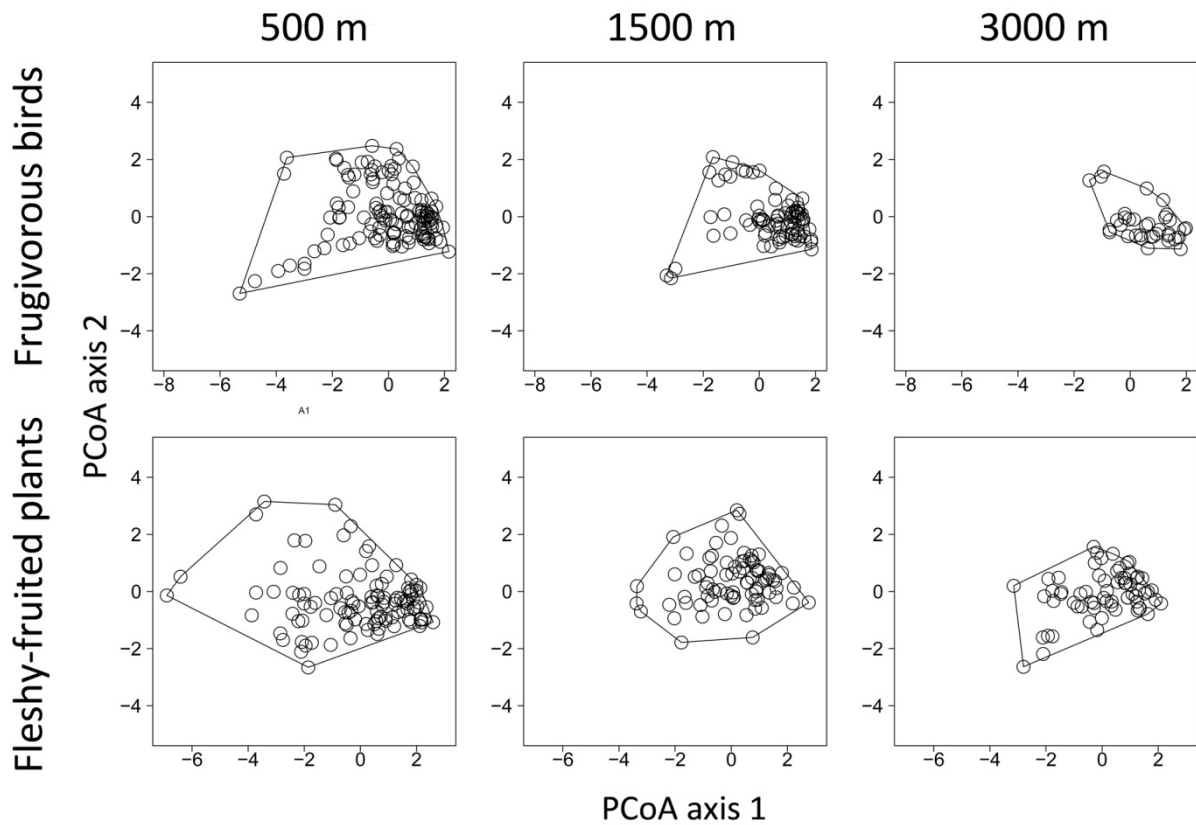
Appendix S4: Visualization of the functional trait space of frugivorous birds (above) and fleshy-fruited plants (below) exemplified for three assemblages along the elevational gradient excluding species with extreme trait combinations. The first two PCoA axes are shown which explain 90.7 and 91.8 percent of the variance in bird and plant FRic, respectively. Species more than three times the median values of nearest neighbour distances away from any other species in the respective original assemblages were excluded, leading to the exclusion of 7, 9, 11, 13, 10, 7 and 2, respectively, frugivorous bird species and 8, 2, 1, 3, 1, 1 and 4, respectively, fleshy-fruited plant species from the assemblages between 500 and 3500 m elevation.