

# Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks

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**Abstract** Although seed-dispersal networks are increasingly used to infer the functioning of ecosystems, few studies have investigated the link between the properties of these networks and the ecosystem function of seed dispersal by animals. We investigate how frugivore communities and seed dispersal change with habitat disturbance and test whether relationships between morphological traits and functional roles of seed dispersers change in response to human-induced forest edges. We recorded interaction frequencies between fleshy fruited plants and frugivorous bird species in tropical montane forests in the Bolivian Andes and recorded functional bird traits (body mass, gape width and wing tip length) associated with quantitative (seed-removal rate) and qualitative (seed-deposition pattern) components of seed-dispersal effectiveness. We found that the abundance and richness of frugivorous birds were

higher at forest edges. More fruits were removed and dispersed seeds were less clustered at edges than in the interior. Additionally, functional and interaction diversity were higher at edges than in the interior, but functional and interaction evenness did not differ. Interaction strength of bird species increased with body mass, gape width and wing tip length in the forest interior, but was not related to bird morphologies at forest edges. Our study suggests that increases in functional and interaction diversity and an even distribution of interaction strength across bird morphologies lead to enhanced quantity and tentatively enhanced quality of seed dispersal. It also suggests that the effects of species traits on ecosystem functions can vary along small-scale gradients of human disturbance.

**Keywords** Ecosystem functioning · Functional diversity · Morphological traits · Montane forest · Plant–frugivore interactions

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## Introduction

Seed dispersal is an important ecosystem function that contributes to the generation and maintenance of plant diversity in tropical ecosystems (Wang and Smith 2002). Up to 90 % of woody plant species in the tropics produce fleshy fruits that are dispersed by a wide spectrum of frugivorous birds and mammals (Howe and Smallwood 1982; Jordano 2000; Karubian et al. 2012) that establish the spatial template for subsequent processes in plant populations (Jordano et al. 2011). The main benefits of seed dispersal by animals to plant fitness are: (1) escape from mortality (i.e. an enhanced seedling survival away from parent trees); (2) directed seed dispersal to suitable sites (i.e. an enhanced probability of germination and establishment of new individuals); and (3) colonization (i.e. an enhanced seed deposition at unoccupied sites) (Howe and Smallwood 1982; Schupp et al. 2010). Seed dispersal by frugivores is therefore a key process for the functioning of tropical plant communities in space and time (Wang and Smith 2002) and the disruption of seed dispersal can have severe consequences for plant communities (Vanthomme et al. 2010).

Mutualistic interactions, such as animal-mediated seed dispersal, can be analysed from a community perspective with network analyses (Bascompte and Jordano 2007). Weighted networks are built from data of the frequencies of interaction events between pairs of species and are particularly suitable for description of the structure of interaction networks (Bascompte and Jordano 2007; Vázquez et al. 2009), for instance along spatial and temporal gradients (Díaz-Castelazo et al. 2010; Menke et al. 2012; Perea et al. 2012). The structure of mutualistic networks is described with metrics associated with the diversity of interactions and the importance of particular species within networks. The frequency of interaction events between pairs of species has been associated with the abundance of species (Bascompte and Jordano 2007; Vázquez et al. 2009), food resource fluctuations (Vázquez et al. 2007; Carlo and Yang 2011) and also morphological traits of interacting species (Stang et al. 2007; Santamaría and Rodríguez-Gironés 2007). Nevertheless, the relationship between network properties at network and species level and the ecosystem function provided by the interacting species remains vague in most network analyses (Carlo and Yang 2011).

One possibility to extend studies of mutualistic networks towards a functional perspective is provided by exploring the relationship between functional traits of interacting species and network properties. According to the concept of functional diversity (FD) (Tilman 2001), species can be described as an assemblage of traits that determine the functional roles of species as well as their interactions with other species (McGill et al. 2006; Mouchet et al. 2010). Previous studies have found that trait matching (i.e. complementarity

of traits in interacting species) is a key factor for explaining interaction strength and specialization of species in pollination networks (Stang et al. 2007; Junker et al. 2013). Furthermore, functional traits are relevant to identification of keystone species with particular importance in ecological communities (Chapin et al. 1997) and in networks of interacting species (McGill et al. 2006; Schleuning et al. 2014). Functional traits have been shown to respond to gradients of human disturbance, such as habitat fragmentation (Cadotte et al. 2011; Hagen et al. 2012), and because networks represent the interactions within ecological communities changes in FD may have a feedback on the structure of mutualistic networks along disturbance gradients.

Recent studies have started to explore how properties of mutualistic networks change along habitat gradients (Schleuning et al. 2011; Menke et al. 2012; Plein et al. 2013). Nevertheless, knowledge of the impacts of human-modified habitats on species interactions is still limited (Hagen et al. 2012). For instance, the creation of human-induced forest edges can have positive effects on avian seed dispersal, driven by the production of large crop sizes in fleshy fruit plant species (Alberti and Morellato 2010) and corresponding increases in the abundance and richness of frugivorous bird species at forest edges (Menke et al. 2012). On the other hand, forest edges can lead to local extirpations of species (Sodhi et al. 2004; Melo et al. 2007) and to reduced seed-dispersal distances (Herrera et al. 2011). The sensitivity of species to disturbance depends, among other factors, on species traits (Henle et al. 2004). While large-bodied birds have been recognized to be key species in tropical communities, they are particularly vulnerable to human disturbance, especially hunting, and to habitat fragmentation, due to their large home-range requirements (Haskell et al. 2002; Markl et al. 2012). Thus, human-induced forest edges may affect keystone species with distinct functional roles in a community, influencing the structure of ecological communities and mutualistic networks.

Here, we explore the consequences of human-induced forest edges in tropical montane forests on the FD of frugivorous birds and on the structure of seed-dispersal networks. We focus on seed dispersal by frugivorous birds because birds represent the most important group of animal seed dispersers in tropical mountain forests (Herzog et al. 2005). We investigate how frugivore communities and seed dispersal change between forest interior and forest edge and test whether the relationships between traits and functional roles of species in the network differ between the two habitat types. We examine both seed removal by frugivorous birds (quantity component) and the pattern of seed deposition (quality component) of seed-dispersal effectiveness (Schupp et al. 1993, 2010). Specifically, we asked: (1) is the FD of frugivorous bird communities related to the Shannon interaction diversity and evenness of plant-frugivore networks in the two habitat types? We hypothesized

that interaction diversity of plant-frugivore networks will increase at forest edges, due to a high resource availability that attracts a morphologically and functionally diverse frugivore community. Moreover, we expect that an increase in FD of the frugivore community will lead to an enhanced quantity (seed removal rate) and quality (seed deposition pattern) of seed dispersal at forest edges. (2) Do morphological traits of frugivorous bird species influence species' interaction strength and is this relationship changing in response to habitat disturbance? Because large frugivore species are more sensitive to habitat disturbance than small species, they may be more important in the undisturbed forest interior (Menke et al. 2012). We therefore expect that the interaction strength of large-bodied frugivore species is larger in the forest interior than at forest edges.

## Materials and methods

### Study area

We carried out this study in a tropical mountain forest in the Bolivian Andes nearby the town of Chulumani (1,700–2,500 m a.s.l., 16°24'37.10"S, 67°31'37.08"W). Mountain forests in the area have been deforested and fragmented due to high levels of selective logging and deliberate fires for the expansion of coca (*Erythroxylum coca*) fields. Nowadays, two large forest remnants remain: one is a private ecological reserve under the administration of the local community (Apa-apa forest 10°20'50.60"S 67°30'48.46"W) and the other is an unprotected remnant (Cala-cala forest 16°24'39.12"S 76°34'0.91"W). Both forest remnants have an extension of approximately 3,000 ha (Gallegos et al. 2014). In the study area, the climate is seasonal, with a short dry season from May to September and a wet season from November to April when most trees bear fruit. The mean annual precipitation is about 2,300 mm and the mean annual temperature is 16.8 °C, according to Schawe et al. (2010). Thus far, 259 woody plant species belonging to 58 families have been recorded (Lippok et al. 2013). The most common species for this altitudinal gradient are *Clusia lechleri*, *Clusia sphaerocarpa*, *Clusia trochiformis* (Clusiaceae Lindley), *Myrsine coriacea* (Myrsinaceae R. Brown), *Clethra scabra* (Clethraceae Klotzsch), *Weinmannia pinata* (Cunoniaceae R. Brown) and *Hyeronima* cf. *laxiflora* (Euphorbiaceae A.L. de Jussieu). The forest has a mean canopy height of 15–20 m and three vertical strata (Navarro and Maldonado 2002).

### Study design

From June 2010 to February 2012, we recorded plant-frugivore interactions at eight study sites with a standardized

sampling design, encompassing a total of 768 h of observations. In each of the two forest remnants, we selected four sites separated from each other by at least 2,000 m. At every site, we established two 20 × 100-m<sup>2</sup> plots parallel to the forest margin (i.e. the border between the forest remnant and the deforested matrix): one at the forest edge, 10 m from the forest margin; and another in the forest interior, 160 m from the forest margin. In each plot, we recorded all bird species that fed on fleshy fruits during four observation sessions conducted during two dry seasons (2010–2011) and two wet seasons (2011–2012). The day before each observation session, surveys of plants bearing fleshy fruit were conducted in the two plots. All trees bearing fruits were marked and we established a single or several observation points per plot, from which the fruiting trees were visible. If fruiting trees were widely spaced and several observation points were required, we changed observation points approximately every 30 min. The visibility of fruiting trees from the respective observation points was similarly high in all study plots. We allocated sampling time according to fruit availability within plots with multiple fruiting trees, ensuring a representative sampling across the entire fruiting plant community.

### Plant-frugivore interactions and avian traits

In order to record frugivorous birds feeding on fleshy fruited plant species, two observers equipped with Nikon Monarch 10 × 42 DCF binoculars (Nikon, Tokyo) simultaneously observed frugivore activity at the forest edge and in the forest interior from 06:00 a.m. to 12:00 p.m. To exclude an observer bias, each observer observed once the edge and once the interior plot during 2 consecutive days of observation. Each observation session lasted for 24 h (12 h of observation by each observer) on 2 consecutive days at each study site. All frugivorous birds visiting a focal tree in the plot were recorded and identified to species level according to Schulenberg et al. (2007); unidentified bird individuals were discarded from the analysis. For every visit, we recorded foraging behaviour and counted the number of fruits removed by birds either by swallowing or carrying away from the parent tree; these two types of interactions were considered seed-dispersal events. If frugivorous birds visited trees in conspecific flocks, the foraging behaviour was recorded for a single, randomly chosen individual and was assumed to be representative for the entire feeding flock. In these cases, the number of fruits removed by the chosen individual was multiplied by the number of individuals in the feeding flock. The response variables derived from the observations were: (1) bird species richness, defined as the total number of species that dispersed fruit in each plot and observation session; (2) bird abundance (number of individuals), defined as the total

number of seed-dispersing individuals counted across all fruiting trees in each plot and observation session; and (3) seed removal (number of removed fruits) as a measure of seed-dispersal quantity defined as the total number of fruits removed from fruiting trees across all bird species during each observation session and plot. Prior to statistical analysis, the response variables were  $\log_{10}(n + 1)$  transformed to approximate normality.

We obtained morphological traits related to seed dispersal for all frugivorous birds recorded in the study. For each frugivorous species, we recorded data for three functional traits: body mass, which is related to dispersal distance and the number of fruits consumed (Wotton and Kelly 2012); length of wing tip, which relates to the mobility of seed dispersers and thus seed-dispersal distance (Böhning-Gaese et al. 2006); and gape width, which determines morphological limitations to swallow and disperse large fruits (Wheelwright 1993). Morphological information for each bird species is provided in Table S1. Body mass was derived from Dunning (2007). For the two other traits, we measured museum skins of two adult male and two adult female individuals. Values were averaged for the four skins. For the length of wing tip, we used Kipp's distance, defined as the distance between the tip of the first secondary feather and the tip of the longest primary feather (Eck et al. 2011). Gape width was approximated as the external distance between the two commissural points of the upper and lower bill as reference points following Wheelwright (1985). Prior to statistical analysis, morphological traits were  $\log_{10}$  transformed and standardized to zero mean and unit variance. Pearson's correlation tests among traits were conducted to test their collinearity. We found a weak positive correlation between wing tip length and gape width ( $r = 0.44$ ,  $P = 0.001$ ), and strong positive correlations between wing tip length and body mass ( $r = 0.75$ ,  $P < 0.001$ ), and gape width and body mass ( $r = 0.82$ ,  $P < 0.001$ ).

#### Fruit availability and spatial distribution of seeds

We estimated the amount of fruit resources (i.e. ripe and unripe fruits) in each plot and observation session to measure the overall fruit availability per plot (hereafter 'crop size'). We estimated the crop size of individual trees by counting the number of all fruits on at least five branches to obtain the average number of fruits per branch and multiplied this with the total number of branches with fruits in the tree. All fruiting plant species recorded in the plots were collected and coded. Plant species richness was defined as the number of fleshy fruited plant species recorded per plot and observation session. Species identification was made with reference to herbarium collections and identified samples were deposited in the Herbario Nacional de Bolivia.

To measure the seed-deposition pattern as a measure of seed-dispersal quality (Schupp et al. 2010), we installed eight seed traps per plot, located along transects of 20-m length parallel to the forest margin. Seed traps were constructed with a cotton-acrylic mesh sewed around a metal ring of 0.50-m diameter, placed at 0.80-m height (area  $\approx 0.20 \text{ m}^2$ ). Seeds in traps were censused and collected four times over 2 years: once at the end of each dry season (October 2010 and September 2011) and once at the end of each wet season (April 2011 and March 2012). We made a reference collection using fruits harvested directly from fruiting plant species present in the study area to identify seeds to morphotype or species level. Overall, we collected 13,013 seeds of 65 morphotypes. Forty of these morphotypes could be identified to species level, and 25 of the morphotypes identified to species level corresponded to species with frugivore observations. Seeds of these 25 plant species ( $n = 6,678$  seeds) were used in further analyses (Table S2). We calculated the number of dispersed fruits per trap and plant species by dividing the number of seeds recorded per trap by the species-specific number of seeds per fruit, accounting for variability in seed numbers among plant species. We then summed the estimated number of fruits for each plant species in each seed trap across the four seasons. The spatial distribution of captured seeds (standardized to fruit units) was calculated using a dispersion index (Clapham 1936), as a measure of seed-dispersal quality for each plant species in each habitat type. The species-specific dispersion index ( $D$ ) was defined as the ratio of variance  $\sigma^2$  in fruit number across all seeds traps in the respective habitat type to the mean fruit number  $\mu$  in the respective habitat type.

$$D = \frac{\sigma^2}{\mu}$$

A dispersion index close to zero indicates that seeds were deposited more regularly than random among seed traps. An index equal to one indicates random deposition of seeds. Regular and random patterns indicate non-directed seed dispersal and a rather even distribution of seeds in space, for instance due to complementary seed dispersal by different types of seed dispersers (Jordano et al. 2007). An index larger than one corresponds to overdispersion, indicating the existence of seed clusters and suggests directed seed dispersal (Wenny and Levey 1998). Prior to statistical analysis, the crop size and the dispersion index were  $\log_{10}$  transformed to approximate normality.

#### Network structure analysis

To obtain quantitative interaction matrices of avian seed removal, we constructed one network for each habitat type and forest remnant (two networks for forest edge and two

networks for forest interior). We calculated interaction frequency as the number of visits of each frugivore species on each tree species (the number of visits per species is provided in Table S3). Using the number of fruits removed, instead of the number of avian visits, resulted in qualitatively identical network metrics. We pooled data from the four plots per habitat type and forest remnant, because the number of observations per plot was too small to construct network matrices for every individual plot. This approach was meaningful because plant communities were similar in composition and diversity between forest remnants, whereas differences between habitat types were strong [for details about the plant community see (Lippok et al. 2013)].

At the network level, we computed a set of metrics to describe network structure. We used Shannon diversity of interactions to measure the overall diversity of interactions between species (Dormann et al. 2009) and interaction evenness to estimate the uniformity of the distribution of interactions between species in the network (Tylianakis et al. 2007). At the species level, we calculated interaction strength of bird species [i.e. species strength sensu Bascompte and Jordano (2007)]. Interaction strength was given by the relative frequency of a frugivore species on a particular plant species (number of visits of frugivore species  $j$  to plant species  $i$  divided by the number of visits of all frugivore species to plant species  $i$ ) and was summed across all plant species to determine the overall impact of a frugivore species (Schleuning et al. 2011). Thus, interaction strength reflects the quantitative importance of a particular frugivore species for the entire plant community. To investigate if bird species with single observations (singletons) influenced the analysis of interaction strength (Bascompte et al. 2006), we computed this index with and without singletons. As results were similar in both approaches, we did not remove singletons. Prior to statistical analysis, interaction strength was log10 transformed to approximate normality. All network analyses were carried out with R 2.15.1 (R Development Core Team 2009) and the bipartite package (Dormann et al. 2009).

### Functional diversity

To compare the FD of morphological bird traits (i.e. body mass, wing tip length and gape width) between habitat types, we first compiled a community matrix; the frequencies of frugivore species in each habitat type and forest remnant were given by the overall interaction frequencies for each bird species. The trait matrix for frugivorous birds was given by the mean trait values for each bird species. We used a distance-based framework to calculate multidimensional FD indices, computed on the basis of the community and trait matrix (Mouchet et al. 2010). We calculated the functional richness (FRic) that measures the size

of the convex hull around the functional trait space in a community, and functional evenness (FEve) that estimates the uniformity of the distribution of species abundances in functional trait space (Mason et al. 2005; Villéger et al. 2008). Prior to the analysis, the community and trait matrix were square root and log10 transformed, respectively. The analyses were carried out with R 2.15.1 (R Development Core Team 2009) and the FD package (Laliberté and Legendre 2010).

### Statistical analysis

We analysed the effects of habitat type (forest edge vs. forest interior), plant species richness and crop size on: (1) bird species richness; (2) bird abundance, and (3) fruit removal with linear mixed-effects models (LMMs) assuming Gaussian error distributions (Baayen et al. 2008; Bolker et al. 2009). As random effects, we included study site and observation session to control for random variation among study sites and observation sessions. Similarly, we used LMMs to assess effects of habitat type and crop size on the plant species-specific seed-dispersion index. In order to control for random variation among plant species, we included plant species as random effect in this model. Furthermore, we analysed main and interaction effects of bird traits (i.e. body mass, wing tip length and gape width) and habitat type on the interaction strength of bird species in the four networks. We included bird species as random factors in order to control for random variation among bird species. For analyses of interaction strengths of bird species, we compared models with all combinations of predictor variables (i.e. bird traits, habitat type and their two-way interaction terms) according to the Akaike's information criterion with a correction for small samples sizes (AICc). All statistical analyses were carried out with R 2.15.1 (R Development Core Team 2009).

## Results

### Frugivore community and seed dispersal

Frugivore and plant community metrics as well as seed removal were affected by habitat type. Plant species richness and crop size were significantly higher at forest edges than in the forest interior ( $P < 0.01$  in both cases, for details see Fig. S1). Effects of habitat type on frugivore communities and seed removal were maintained after accounting for variability in crop size and plant species richness between the two habitat types. Bird species richness and abundance of frugivores were higher at forest edges than in the forest interior (Table 1; Fig. 1). Fruit removal, expressed as the number of consumed fruits, was also higher at the edge

**Table 1** Results from linear mixed-effects models of the effects of habitat type, crop size and plant species richness on bird species richness, bird abundance, seed removal, and the seed-dispersion index

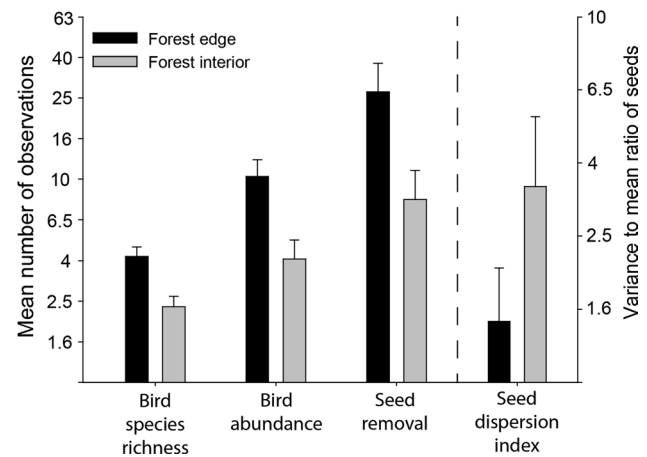
	Estimate	SE	<i>t</i>	<i>P</i>
<b>Bird species richness (<i>n</i> = 64)</b>				
Intercept	0.57	0.05	9.55	<0.01
Habitat (interior)	−0.15	0.06	−2.50	0.01
Crop size	0.07	0.03	2.17	0.03
Plant species richness	0.06	0.03	1.96	0.05
<b>Bird abundance (<i>n</i> = 64)</b>				
Intercept	0.94	0.12	7.81	<0.01
Habitat (interior)	−0.27	0.11	−2.41	0.01
Crop size	0.09	0.06	1.43	0.15
Plant species richness	0.10	0.06	1.61	0.11
<b>Seed removal (<i>n</i> = 64)</b>				
Intercept	1.38	0.18	7.32	0.00
Habitat (interior)	−0.42	0.19	−2.16	0.03
Crop size	0.24	0.11	2.18	0.03
Plant species richness	−0.05	0.11	−0.48	0.62
<b>Seed-dispersion index (<i>n</i> = 38)</b>				
Intercept	0.16	0.14	1.12	0.26
Habitat (interior)	0.29	0.15	1.89	0.06
Crop size	0.03	0.12	0.02	0.97

Forest remnants and observation sessions were included as random effects in the models, and plant species in the model of the seed-dispersion index. Significant values ( $P < 0.05$ ) are highlighted in *italic*. Crop size and plant species richness were scaled to zero mean and unit variance

than in the interior (Table 1; Fig. 1). Dispersed seeds were less clustered at the forest edge than in the forest interior where they were highly clustered (Fig. 1). However, differences between habitat types were only marginally significant (Table 1).

#### Seed-dispersal networks and FD

We recorded 539 interactions between 40 plant species (36 at the forest edge vs. 20 in the forest interior) and 47 bird species (41 at the forest edge vs. 23 in the forest interior). The percentage of interactions recorded at the forest edge (71 % of observations,  $n = 383$ ) was two times higher than in the forest interior (29 %,  $n = 156$ ). Habitat type affected aspects of both network structure and FD. The structure of seed-dispersal networks in terms of Shannon interaction diversity was always higher at the forest edge than in the forest interior (Figs. 2, 3a), whereas interaction evenness was similar in both habitats (Fig. 3c). FD followed the same pattern, in which FRic was higher at the forest edge compared to the forest interior (Fig. 3b), and FEve was similar in both habitats (Fig. 3d). Interaction evenness was greater than functional evenness. Differences between



**Fig. 1** Effects of habitat type (forest edge vs. forest interior) on bird species richness, bird abundance, seed removal ( $n = 32$  in each habitat type), and seed-dispersion index ( $n = 22$  plant species in edge and 16 species in interior habitat). Means + 1 SE are given. The dispersion index (right axis) represents the average variance to mean ratio of the number of estimated fruits captured per seed trap for each plant species and habitat type; SEs correspond to the variability among plant species within the respective habitat type. Values equal to one indicate random distribution of seeds and values larger than one correspond to a clumped distribution

habitat types could not be formally tested because of too few replicate networks.

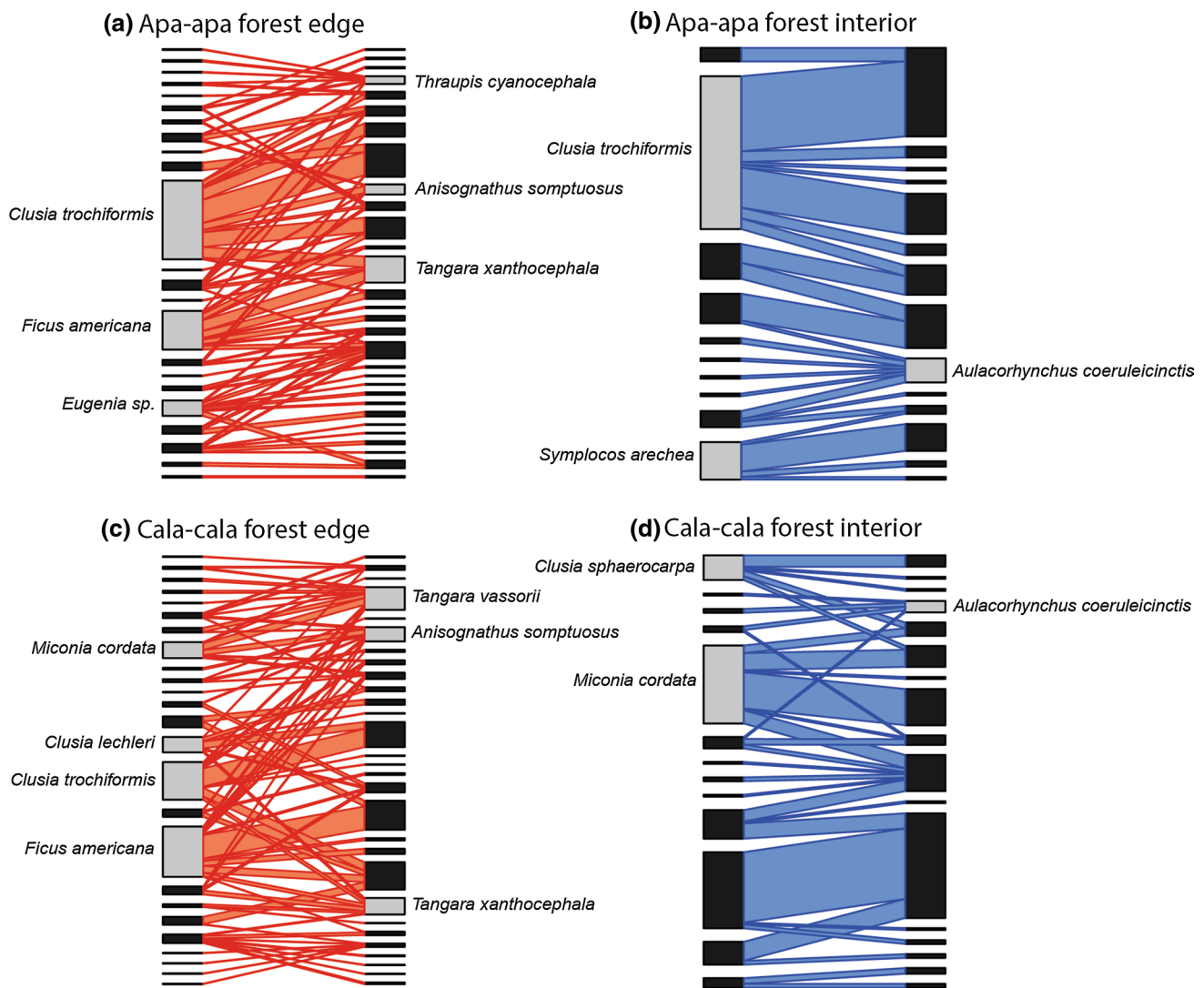
#### Effects of bird traits on interaction strength

We found positive relationships between morphological traits and interaction strength of bird species, but only in the forest interior (Fig. 4). Body mass (Fig. 4a), gape width (Fig. 4b) and wing tip length (Fig. 4c) were positively associated with interaction strength in the networks recorded in the forest interior (Table 2). In contrast, at the forest edge there were no significant relationships of bird traits with interaction strength. The three models including main and interaction effects of the respective bird trait and habitat type were equally supported in model comparisons ( $\Delta AICc < 1.6$ ). Other competing models that included more than a single bird trait were less supported ( $\Delta AICc > 2$  in all cases).

## Discussion

### Frugivore community and seed-dispersal functions

Human-induced forest edges had favourable effects on the abundance and richness of the frugivorous bird community. Thus far, our results are among the first to show that quantitative components of seed-dispersal effectiveness were



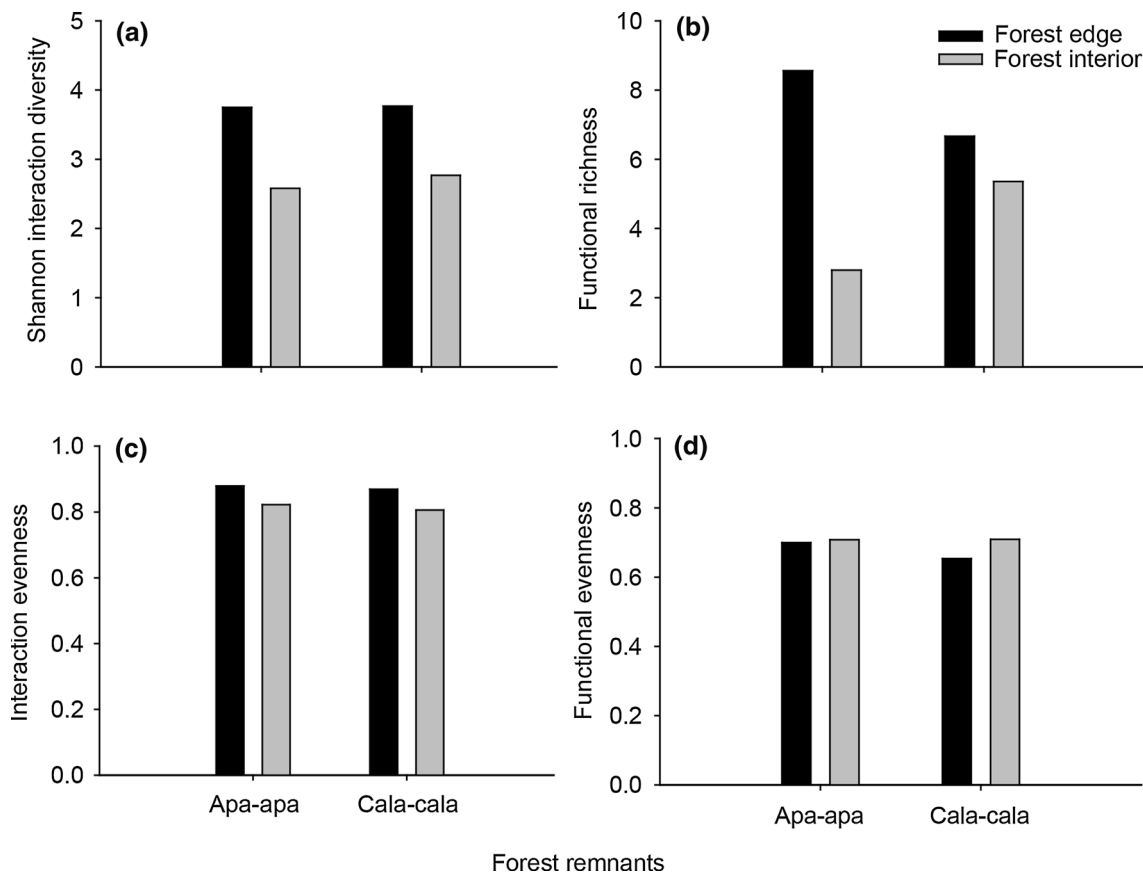
**Fig. 2** Quantitative seed-dispersal networks at forest edges (**a, c**) and in the forest interior (**b, d**) in two mountain forests in the Bolivian Andes (Apa-apa vs. Cala-cala). Plant species are indicated by *boxes* in the *left column*, bird species by *boxes* in the *right column*. *Box*

*height* corresponds to the proportion of interactions contributed by each species to the network and *width of links* is proportional to the number of observed interaction events per link. *Grey boxes* represent key species in the network

consistently enhanced at forest edges. Furthermore, forest edges showed a trend towards a less-clustered seed dispersal in comparison to the forest interior, which may favour seed dispersal to multiple micro-sites enhancing seed-dispersal quality. However, other qualitative components of seed dispersal, such as the quality of seed treatment by frugivores, could differ between forest edges and forest interior and have not been tested in this study.

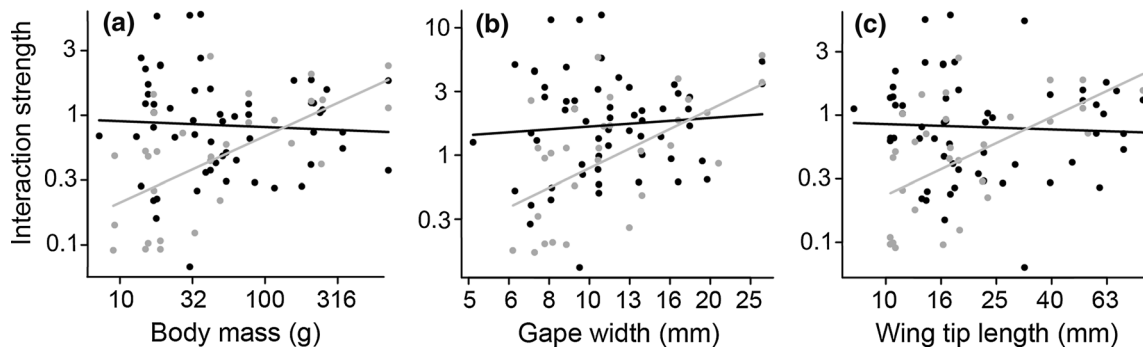
For our system, an increase in the quantity of seeds dispersed at forest edges can be partly explained by the attraction of birds to forest margins with abundant fruit resources (Howe and Smallwood 1982; Alberti and Morellato 2010). Almost all bird species observed in the networks were forest species (Schulenberg et al. 2007) that only occasionally

forage outside the forest and may be attracted to edge habitats because of their high resource availability. Similarly, previous studies of frugivore communities in Kenyan rain forest found high bird species richness and abundance at forest edges with many fruit resources, mostly driven by an increase of forest-visiting bird species (Menke et al. 2012). Our results are consistent with other studies showing that frugivorous animals track fruit resources, both in space and in time (de Castro et al. 2012; Plein et al. 2013). It is likely that bird species are attracted by magnet plant species with large and conspicuous fruit crops (Eshiamwata et al. 2006), such as *Ficus* spp., *Miconia* spp. and *Clusia* spp. at forest edges. Since habitat significantly affected variation in seed removal after accounting for differences in crop sizes and



**Fig. 3** Differences in network structure and functional diversity between habitats (forest edge vs. forest interior) and forest remnants (Apa-apa vs. Cala-cala). The structure of the seed-dispersal networks

is represented by **a** Shannon interaction diversity and **c** interaction evenness, and the functional diversity by **b** functional richness and **d** functional evenness



**Fig. 4** Partial residual plots of the relationships between avian interaction strength and bird species traits accounting for random variation among bird species. Relationships are given for **a** body mass, **b** gape

width and **c** wing tip length ( $n = 39$  bird species for each functional trait). *Black symbols and black lines* correspond to species at the forest edge, *grey symbols and black lines* to species in the forest interior

plant species richness, additional factors such as a higher visibility of fruit crops at forest edges could also contribute to the attraction of frugivorous birds to forest edges (Galetti et al. 2003). Differences in the nutritional quality, e.g. in sugar contents, between fruits presented in the forest interior and at forest edges could be another factor attracting

frugivores to edge habitats. Thus, both fruit quantity and quality may be important for explaining edge effects on plant-frugivore interactions and their effects should be disentangled in future studies.

Previous studies on seed-dispersal networks at forest edges considered only visitation rates (Menke et al. 2012;



**Table 2** Results from linear mixed-effects models of main and interaction effects of bird traits and habitat type on interactions strength

	Estimate	SE	<i>t</i>	<i>P</i>
<b>Bird body mass</b>				
Intercept	−0.52	0.08	−5.88	<0.01
Body mass	−0.02	0.09	−0.24	0.80
Habitat (interior)	−0.24	0.11	−2.11	<i>0.03</i>
Body mass × interior	0.28	0.11	2.45	<i>0.01</i>
<b>Bird gape width</b>				
Intercept	−0.52	0.08	−5.91	<0.01
Gape width	0.03	0.09	0.38	0.69
Habitat (interior)	−0.26	0.11	−2.26	<i>0.02</i>
Gape width × interior	0.20	0.11	1.81	0.07
<b>Bird wing tip length</b>				
Intercept	−0.52	0.08	−5.94	<0.01
Wing tip length	−0.01	0.08	−0.22	0.82
Habitat (interior)	−0.21	0.11	−1.81	0.07
Wing tip length × interior	0.29	0.12	2.36	<i>0.02</i>

Given are models for bird body mass, gape width and wing tip length (Kipp's distance)

Bird species identity was included as a random effect in all models. Significant values ( $P < 0.05$ ) are highlighted in *italic*. Species traits were scaled to zero mean and unit variance

Plein et al. 2013), ignoring the amount of removed fruits (quantitative component of seed dispersal) and the subsequent spatial distribution of dispersed seeds (qualitative component of seed dispersal). We found that seed deposition at forest edges was less clustered than in the forest interior. The more even seed deposition pattern at forest edges may primarily result from: (1) high abundance and diversity of frugivorous birds, potentially leading to complementary effects of frugivore species on seed dispersal (Morales et al. 2013); and (2) changes in avian movement patterns in response to changes in vegetation structure (Herrera et al. 2011; Breitbach et al. 2012). Highly clustered seed deposition in the forest interior could also be associated with a high number of null dispersal events beneath fruiting trees in the forest interior (see Breitbach et al. 2012). Similarly, the leptokurtic distribution of the animal-mediated seed shadows in continuous forest could contribute to clustered seed shadows (Lenz et al. 2011). However, clustered seed-deposition patterns in the forest interior could also be related to directed seed dispersal, potentially to particularly suitable micro-habitats for plant recruitment (Wenny and Levey 1998). Different deposition patterns of seeds between forest edges and the forest interior may have large impacts on the abundance and richness of seedlings recruited at forest edges (Melo et al. 2007), and the ultimate consequences of changes in seed deposition patterns for seedling recruitment deserve more attention in future work. For the disturbed Andean forests,

we expect that enhanced seed dispersal at forest edges aids natural forest regeneration at edges and in adjacent deforested areas. Two important frugivore species in the networks (*Mionectes striaticollis* and *Thraupis cyanocephala*) were observed to occasionally move towards deforested areas and thus likely contribute to seed dispersal and natural regeneration of anthropogenically deforested habitats outside the forest.

#### Seed-dispersal networks and FD

Interaction diversity and FRic of seed-dispersal networks were similar in the two forest remnants, but differed between habitat types. We found high levels of FRic at forest edges, associated with a high number of interactions recorded in edge networks. Changes in FRic corresponded to the high diversity of plant species at forest edges and the positive relationship between plant and bird species richness at forest edges. The high structural and FD of networks at forest edges also suggests that these seed-dispersal networks are more robust against disruption than those in the forest interior (Menke et al. 2012), potentially increasing and stabilizing seed-dispersal functions in edge habitats (Tylianakis et al. 2010).

Interaction evenness (the uniformity of the frequencies of interaction events in the network) was, in general, higher than FEve (the uniformity of species frequencies in the functional trait space). Given that both metrics were based on interaction frequencies and were equally scaled, this suggests that patterns in interaction networks were more even than one would expect from the distribution of functional traits in the frugivorous bird community. This suggests that there was a high flexibility in the selection of fruit resources by avian frugivores exceeding the evenness of functional bird traits in the community (Plein et al. 2013). This flexibility in resource use was reflected by an overlap in seed dispersers for plant species with similar fruit morphology, such as *Clusia* spp. and *Miconia* spp. (for details see Table S2). Interestingly, functional and interaction evenness were similar in both habitat types, despite substantial differences in FRic and interaction diversity. This suggests that in both habitats bird species were similarly distributed in the functional trait space and that interaction evenness was robust against variation in species abundances and interaction frequencies. By contrast, Tylianakis et al. (2007) found large differences in the interaction evenness of host-parasitoid food webs between near-natural and highly modified habitats. Different to patterns in parasitoid food webs, many frugivore species have similar phenotypes and are, at least to some extent, redundant in their functional roles in a community, suggesting a rather high stability of ecosystem functioning (Hector et al. 2001).

## Effects of morphological traits on interaction strength

We found evidence that morphological traits related to seed-dispersal functions, i.e. body mass, gape width and wing tip length, influence the interaction strength of frugivore species in the forest interior. The contribution of large-bodied bird species to seed dispersal across all plant species was pivotal in the forest interior, whereas at the forest edges contributions to seed dispersal were more evenly distributed among bird species. For instance, in the forest interior, large-bodied and wide-gaped birds (e.g. *Aulacorhynchus coeruleicinctis*) were important seed dispersers for plant species with both small and large fruits. By contrast, at forest edges small tanager species, such as *Anisognathus somptuosus*, *Tangara xanthocephala*, *Thraupis cyanocephala* and *Tangara vassorii*, increased in relative importance and were as important as the large-bodied species. This is in line with previous work showing that small-bodied species increase in importance at anthropogenic forest edges (Menke et al. 2012). At forest edges in the tropical Andes, plant species of the genus *Miconia* (Melastomataceae) are widespread because many *Miconia* species are pioneers and grow in deforested areas or at forest edges (Gentry 1982). In our study system, we found nine *Miconia* species at forest edges but only three *Miconia* species in the forest interior. Large crop sizes of the small *Miconia* fruits may be one reason for the particular importance of small frugivorous birds at forest edges.

The even contribution of bird species with different morphologies to seed dispersal at forest edges may contribute to enhanced quantity and, tentatively, quality of seed dispersal. Because morphologically distinct bird species are characterized by differences in movement behaviour, home ranges and habitat preferences, this variability in functional roles might increase the functional complementarity among seed-dispersing species (Jordano et al. 2007; Morales et al. 2013). By contrast, the large contributions of morphologically similar bird species in the forest interior may reduce functional complementarity and may lead to more clustered seed dispersal. However, the importance of large-bodied species in the forest interior also reflects the unique role of these species for both quantitative and qualitative seed-dispersal components in tropical forests (Wotton and Kelly 2012; Galetti et al. 2013). The crucial importance of these species may make these networks prone to functional collapse in the future because large-bodied species are particularly susceptible to human disturbance (Markl et al. 2012; Galetti et al. 2013). By contrast, the functional redundancy across different bird morphologies may stabilize seed-dispersal networks at forest edges against environmental fluctuations.

## Conclusion

Our findings show that quantitative and, to some extent, qualitative components of seed-dispersal effectiveness were enhanced at human-induced edges in tropical mountain forests. Enhanced seed-dispersal functions were reflected by higher functional and interaction diversity in seed-dispersal networks, but not by changes in their functional and interaction evenness. Most importantly, effects of human disturbance also altered the relationship between functional traits and functional importance of frugivore species in the seed-dispersal networks and led to a more even contribution of different bird morphologies to seed dispersal at forest edges. Hence, the effects of functional traits on biotic interactions and associated ecosystem functions are likely to vary along small-scale gradients of human disturbance also for other types of ecosystem functions.

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