LETTER

Seed-dispersal interactions in fragmented landscapes – a metanetwork approach

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Abstract

Mutualistic interactions repeatedly preserved across fragmented landscapes can scale-up to form a spatial metanetwork describing the distribution of interactions across patches. We explored the structure of a bird seed-dispersal (BSD) metanetwork in 16 Neotropical forest fragments to test whether a distinct subset of BSD-interactions may mediate landscape functional connectivity. The metanetwork is interaction-rich, modular and poorly connected, showing high beta-diversity and turnover of species and interactions. Interactions involving large-sized species were lost in fragments < 10 000 ha, indicating a strong filtering by habitat fragmentation on the functional diversity of BSD-interactions. Persistent interactions were performed by small-seeded, fast growing plant species and by generalist, small-bodied bird species able to cross the fragmented landscape. This reduced subset of interactions forms the metanetwork components persisting to defaunation and fragmentation, and may generate long-term deficits of carbon storage while delaying forest regeneration at the landscape level.

Keywords

Atlantic Forest, avian seed-dispersal interactions, beta-diversity of interactions, defaunation, ecological functions, habitat fragmentation, interaction centrality, meta-community, mobile links, tropical conservation.

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INTRODUCTION

Worldwide habitat fragmentation and defaunation challenge the maintenance of species and their ecological functions (Fahrig 2003; Hagen *et al.* 2012; Dirzo *et al.* 2014) with cascading consequences for ecosystem services (Bello *et al.* 2015; Haddad *et al.* 2015). Yet, the remnant patches can surprisingly hold a significant fraction of biodiversity (Morante-Filho *et al.* 2016; Sfair *et al.* 2016; Beca *et al.* 2017). However, the long-term persistence of viable populations requires connectivity among patches (Hanski 1998; Leibold *et al.* 2004), which may crucially depend on the maintenance of functional ecological interactions. A critical step in the analysis of fragments' connectivity is to understand the consequences of interaction loss and interaction persistence for metacommunity dynamics (Valiente-Banuet *et al.* 2014), seeking for general approaches independent of spatially explicit models or specific details of movements of organisms (Leibold *et al.* 2004). However, research on how habitat fragmentation determines the loss of functional interactions lacks empirical studies at large spatial scales. We ignore to what extent remnant interactions may compensate the functional loss ensuing extinct interactions (Valiente-Banuet *et al.* 2014; McConkey & O'Farrill 2016).

Frugivores maintain seed-dispersal from local to large spatial scales, contributing to *in situ* regeneration, and rescuing plants from severe dispersal limitation in fragmented landscapes (Nathan & Muller-Landau 2000; Sekercioglu *et al.* 2007). Bird seed-dispersal (BSD) interactions shared among habitat remnants are those that persist after fragmentation, as well as to defaunation, another important driver of tropical forests disturbance (Galetti *et al.* 2013). Persistent interactions reflect the same ecological function occurring 'redundantly' (i.e. exactly the same species partners interacting; Tononi *et al.* 1999) at the landscape level. Therefore shared BSD-interactions may represent the potential for the remnant sites to remain functionally similar and integrated in contemporary time, contributing to cohesiveness in a metacommunity scenario (Leibold *et al.* 2004). Moreover, they represent the baseline boundary for potential effective movement of seeds across the landscape, and the birds involved may act as mobile links among forest patches, i.e. the potential for an identical seed-dispersal service by exactly the same specific frugivore species to persist across fragments (Lundberg & Moberg 2003; Kremen *et al.* 2007; Gonzalez-Varo *et al.* 2017). However, actual information from field data about the movement of either frugivores or plants is extremely limited, especially at the community level and over large spatial scales (but see Pizo 2007, Lees & Peres 2009; Pizo

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& dos Santos 2011; Neuschulz *et al.* 2013; Velez *et al.* 2015; Cornelius *et al.* 2017). Large-bodied frugivore species, expected to provide more effective medium- to long-distance seed-dispersal (Jordano *et al.* 2007) are the first to vanish when defaunation takes place (Galetti *et al.* 2013). Besides, species from disturbed habitats tend to have smaller body mass and generalist behaviour, allowing them to feed on, or to be dispersed by, a wider range of interacting partners (McKey 1975; Tabarelli *et al.* 2012; Morante-Filho *et al.* 2016). Thus we might expect that only a subset of the plant–frugivore interactions would persist in small forest remnants and contribute to contemporary seed-dispersal in highly fragmented landscapes.

Each fragment holds local assemblages of interacting species, forming distinct networks. Network theory helps to understand the distribution of interactions across fragments and to identify their shared ecological functions (Hagen *et al.* 2012; Bascompte & Jordano 2014; Howe 2016). A fraction of species interactions may be shared across a metanetwork (Hagen *et al.* 2012) of fragments (Fig. 1). Two or more local networks may thus keep functionally connected whenever they share an interaction, i.e. a redundant dispersal function at the landscape level (Hagen *et al.* 2012; Poisot *et al.* 2014; Schleuning *et al.* 2015). From a graph-theoretical perspective (Urban & Keitt 2001), such a metanetwork graph is connected if there exists a direct or indirect path between each pair of nodes. We will use 'connectivity' to imply the potential for shared ecological interactions. Thus, the links among fragments in Fig. 1, based on species and interactions co-occurrence, can be thought as proxies for ecologically similar functions performed by specific, pairwise plant–frugivore interactions, with potential to affect contemporary seed-dispersal events.

We can assess the importance of specific interactions in the metanetwork in numerous ways, including estimating their centrality and assessing its correlates with species traits. BSD-interactions occurring in two or more forest fragments would form the central interactions, i.e. those most shared among fragments and conferring redundancy of ecological functions across the metanetwork. Central nodes promote network cohesiveness (Freeman 1979) and community stability (Jordan 2009), with a large number of their links connecting different parts of the network structure (González *et al.* 2010). Besides, recent studies have analysed the beta-component of interaction diversity and turnover of interactions across local networks (Poisot *et al.* 2012, 2014; Trøjelsgaard *et al.* 2015; CaraDonna *et al.* 2017). One can further identify which species traits are associated to higher centrality and more likely contributing to the persistence of a given interaction across many fragments.

Here we aim to understand the structure of a metanetwork of bird seed-dispersal (BSD) interactions in a tropical region, identify central interactions persisting across forest fragments, and test whether those interactions are random or distinct subsets of those in pristine areas. We gathered data of BSD-interactions in 16 forest fragments of the Atlantic Forest, a hotspot of biodiversity (Joly *et al.* 2014; Bello *et al.* 2017) that harbours a highly fragmented, matrix-laboured and yet relatively patch-connected landscape (Ribeiro *et al.* 2009) with high species beta-diversity (Morante-Filho *et al.* 2016; Sfair *et al.* 2016; Farah *et al.* 2017). Specifically, we aim to (1) estimate the potential for connectivity through shared interactions (i.e. metanetwork connectance), assessing whether fragments form distinct groups (i.e. metanetwork modularity), and how distinct the local assemblages of BSD-interactions are across fragments (i.e. beta-diversity, turnover and rewiring of interactions), (2) identify which interactions are most common among forest fragments and their role in the metanetwork structure (i.e. interaction centrality), and finally (3) determine the ecological correlates of species traits (body mass, seed diameter and bird movement) involved in central interactions potentially contributing to integrate a highly
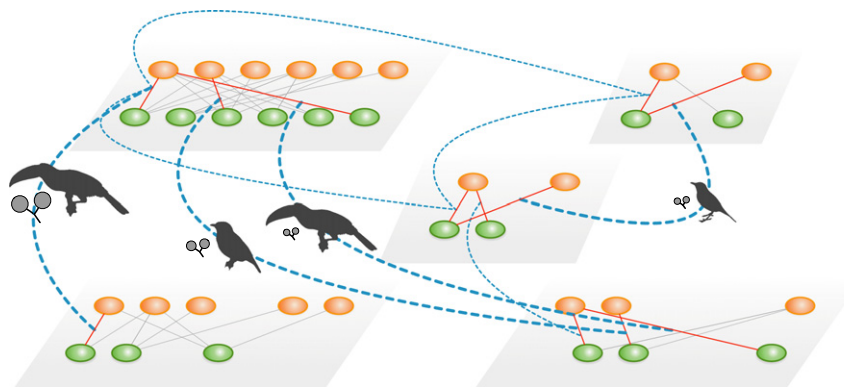

Figure 1 A spatial metanetwork of bird seed-dispersal interactions. Grey areas represent distinct forest fragments of distinct size and isolation that can be potentially connected in contemporary time through the activity and the functional outcomes of plant-bird seed-dispersal interactions. Each forest fragment includes a local network according to the local assemblages of bird species (orange nodes), plant species (green nodes) and their interactions (grey lines within networks). Blue, dashed, links indicate pairwise interactions that repeatedly appear in at least two local networks (red links in local assemblages), thus potentially acting as mobile links across the landscape. Silhouettes indicate distinct pairwise interactions that may involve, e.g. birds and fruits of different size. Those redundant interactions at the landscape level scale-up to form a metanetwork of forest fragments connected by the interactions they share. Shared interactions occurring in a larger number of fragments and connecting higher number of fragments, i.e. having higher centrality, are important to maintain network cohesiveness and stability. Those central interactions can potentially function as mobile links among forest fragments. Traits of both plant and bird species involved, such as body mass and seed diameter, are likely to determine which interactions perform the most central roles bounding the metanetwork.

fragmented landscape. We expect a modular metanetwork with high beta-diversity of interactions. Central interactions are expected to show distinct ecological traits of the interacting bird and plant partners, including small body mass and small seed size more likely to move in the fragmented landscape, and to persist in more disturbed habitats (Neuschulz *et al.* 2013; Morante-Filho *et al.* 2015).

MATERIAL AND METHODS

Data set

We compiled 16 studies of BSD-interactions in fragments of the SE Brazilian Atlantic Forest (see Table S1 and Fig. S1), a diverse and threatened tropical biome drastically reduced to *c.* 12% of its original cover (Ribeiro *et al.* 2009; Joly *et al.* 2014). The remaining landscape constitutes a complex mosaic formed mainly by small fragments (< 50 ha, *c.* 80% of the remaining area) and clusters of close neighbouring fragments (< 200 m apart) (Ribeiro *et al.* 2009). The surrounding matrix includes crop plantations, pastures, urban areas, non-sampled fragments of variable size and isolated trees that function as stepping-stones reducing forest isolation and favouring animal movement (Martensen *et al.* 2008; Uezu *et al.* 2008; Ribeiro *et al.* 2009; Boscolo & Metzger 2011). The studied fragments vary from 0.66 to 42 000 ha, in a gradient of disturbance from semi-pristine protected areas to secondary forests and restored plantations [mean distance between fragments: 309 km (min 26 km; max 1193 km)]. Our data set includes all studies designed to collect bird-eating-fruit interactions at the community level and over most of the annual seasonality in forest remnants of the Atlantic Forest. Therefore they did not necessarily record effective seed-dispersal; we carefully checked every data set and removed any interaction not characterising seed-dispersal events. We updated species names with taxise package (Chamberlain & Szocs 2013).

Metanetwork structure

We built the metanetwork by pooling the 16 within-fragment communities in a single binary A_{mn} adjacency matrix in which m is the number of studied fragments (rows), and n is the number of pairwise BSD-interactions (columns); the mn elements represent the presence/absence of interaction $i_{1...n}$ in fragment $j_{1...m}$. Interactions were determined by the unique pairwise combination of each bird and plant species recorded interacting in the study sites. Then, we characterised the metanetwork structure by estimating: (1) number of bird species, plant species and their interactions, (2) connectance, C: the ratio of the number of BSD-interactions recorded in each fragment relative to the number of all potential BSD-interactions (Dunne *et al.* 2002), (3) modularity, M: to test whether interactions present in each fragment form distinct groups (i.e. modules) or aggregate according to a gradient of disturbance in which interactions present in smaller, impoverished fragments would be a subset of larger, more pristine fragments. We used the DIRTLPAwb+ algorithm recently proposed for maximising modularity (Beckett 2016) that identifies groups

of nodes (here, BSD-interactions) that interact more strongly within than among modules (Girvan & Newman 2002), (4) interaction centrality: to identify which interactions show greater redundancy and potential for metanetwork connectivity we used an unipartite projection of the A_{mn} matrix in which n BSD-interactions are nodes and each pair of nodes is connected if the two interactions co-occur in at least one fragment. With this projection we estimated:

1 Degree, k – the number of fragments in which a given interaction occurs, implying the combined co-occurrence of its partner plant and bird species.
2 Betweenness centrality (hereafter, betweenness), B_C – the proportion of the shortest paths linking any pair of nodes in a network (Freeman 1979; González *et al.* 2010); here interpreted as the most parsimonious way to go from one fragment to another through the co-occurrence of BSD-interactions. Given that we have no data on effective movements across fragments in the study area, we use $B_C > 0$ as a proxy to identify BSD-interactions most likely to contribute to enhance contemporary functional connectivity at the landscape scale. Besides, nodes with $B_C > 0$ are theoretically important for network cohesiveness because they link different network parts that would be otherwise poorly connected, or even isolated (Urban & Keitt 2001; Jordan 2009).

We further investigated the role of individual species in the metanetwork structure, independently of the interactions they perform, by substituting the nth vector element in the A_{mn} matrix by either the plant or bird species, and re-run the network metrics for plant and bird species, separately. Finally, we investigated whether interactions with higher centrality involved central bird or plant species using Pearson's correlation test with permutation. We tested the statistical significance of connectance and modularity against a set of null models (Table S3 for details) including an equiprobable null model distributing equally the interactions among fragments, a fixed-fixed model that maintains constant the interaction frequency and the total interactions per fragment while changing network structure [a *Quasiswap* variant, (Miklós & Podani 2004; Oksanen *et al.* 2017)], and two other variants preserving only the total interactions per fragment.

Beta-diversity of species and interactions

We followed Baselga (2010) and Poisot *et al.* (2012, 2017) to investigate the contribution of different mechanisms to explain the variation in species and interaction composition among the Atlantic Forest fragments, using the A_{mn} matrix. Accordingly, we calculated (1) the total beta-diversity estimated from the Sørensen dissimilarity index and (2) its turnover component, using the Simpson dissimilarity index. Both indexes were estimated at the pairwise- and multiple-sites scales using the betapart package (Baselga *et al.* 2013). To test whether beta-diversity would be a primary consequence of geographical distance we performed Pearson's correlation tests among the pairwise geographical distances between fragments (Haversine distance [km]), and the pairwise Sørensen and Simpson dissimilarities of species and interactions between fragments, with their significance tested by randomisation. Then, we employed

Poisot *et al.* (2012, 2017) approach for estimating interaction rewiring across multiple-sites with high species turnover. It assumes that rewiring happens when the same pairwise species co-occur in different fragments but interact in only a subset of those. Thus, we calculated the difference between realised interactions within-fragments and the overall potential interactions at the metanetwork-regional level (β_{OS}'); values close to 0 indicate the presence of most potential interactions, whereas values close to 1 suggest the loss of most potential interactions at the local-fragment level. We further used analyses of variance to test for differences in β_{OS}' caused by fragment area.

Species traits and interaction centrality

We used bird species' body mass (g), plant seed diameter (mm) and bird's movement (as the capacity to move in the fragmented landscape) as determinants of plant-frugivore interaction outcomes (Jordano 2014) that may influence interactions persistence (see Suppl. Mat.). Metanetwork metrics were estimated in the bipartite package (Dormann *et al.* 2009). All analyses were run in R v. 3.3.3 (R Development Core Team 2014).

RESULTS

Metanetwork structure

The BSD metanetwork includes 335 plant species interacting with 170 bird species across 16 forest fragments of the Atlantic Forest (Fig. 2a). Combined, they comprised a total of 2587 BSD-interactions mostly exclusive to a single fragment (82.26%), forming a highly modular ($M = 0.74$, $P < 0.001$) and poorly connected ($C = 0.07$) metanetwork. Each fragment formed a distinct module (i.e. 16 modules, Fig. 2a) functionally connected by a subset of core interactions (Fig. 2b). If the core interactions vanish, the metanetwork structure is lost and fragments become functionally isolated (Fig. 2c). Furthermore, modularity was lower when only bird or plant species were considered (Table S3, Fig. S3).

We identified high levels of beta-diversity among fragments considering the composition and turnover of species, genera and interactions (Table 1, S4 and S5). The pairwise dissimilarity in composition and turnover of species and interactions among fragments were significantly and positively correlated with the pairwise geographical distance (Table S6). Most potential interactions at the landscape level were realised at the local-fragment level (β_{OS}' ranging from 0.043 to 0.326), whereas β_{OS}' values were not related to fragment area ($F_{1,14} = 0.109$, $P = 0.746$, $R^2 = -0.063$; Fig. S4).

Central interactions

A low number of BSD-interactions occurred in at least two fragments [459 (17.74%); $k \geq 2$; Fig. 2b] including just 200 bird-plant partner combinations connecting different parts of the metanetwork ($B_C > 0$; Table S7). In contrast, most BSD-interactions (2128, 82.26%) occurred in a single fragment ($k = 1$, $B_C = 0$; Fig. 2c). Beta-diversity and turnover of central

interactions ($B_C > 0$) increased with distance among fragments ($r_b = 0.44$, $t = 7.76$, $P < 0.001$; $r_t = 0.36$, $t = 6.25$, $P < 0.001$). Highly central interactions were usually performed by highly central bird ($r_k = 0.218$, $r_{Bc} = 0.119$, $P < 0.001$) or plant species ($r_k = 0.394$, $r_{Bc} = 0.227$, $P < 0.001$) yet the variation was very high (Fig. S5). For example the great kiskadee *Pitangus sulphuratus* was recorded in all studied fragments ($k = 16$, $B_C = 0.061$, Table S8) but performed only six out of the 200 interactions (2%) connecting the metanetwork (Table S7). In contrast, none of the plant species were present in all fragments; *Schinus terenbenthifolius* (Anacardiaceae) was the plant with highest number of occurrences ($k = 8$, $B_C = 0.061$; Table S9), also involved in the highest central interaction (*Schinus terebinthifolius* and *Thraupis sayaca*, $k = 7$, $B_C = 0.054$) and in other 37 (18.41%) interactions connecting the metanetwork (Table S7).

Species traits

From the pool of interactions with complete information on body mass and seed size (1298 interactions), most interactions in the metanetwork (1087; 83.74%) included small-bodied bird species (< 100 g) associated to small-seeded plant species (< 12 mm) (Fig. 3). However, the types of BSD-interactions across the gradient of fragment area (0.66 – 42 000 ha; Table S1) were very different depending on the combinations of partner species sizes. Interactions involving both small-bodied bird and small-seeded plant species appeared in the whole gradient of fragment sizes (Fig. 3). In contrast, interactions involving large-bodied bird and large-seeded plant species were restricted to the largest fragments (i.e. none of these interactions occurred in fragments < 10 000 ha). These interactions were exclusively recorded in two out of the three more pristine fragments (PE Intervales and PE Ilha do Cardoso), which also have the largest areas (Fig. 3). Among them (10 interactions in total), only the interaction between the large-seeded *Virola bicuhyba* (Myristicaceae; mean seed diameter = 16 mm] and the large-bodied *Ramphastos dicolorus* (Ramphastidae; mean body mass = 331 g) was a metanetwork connector ($B_C = 0.005$, Table S7). Less than 20% of the interactions involving species of contrasting sizes (e.g. large-bodied bird and small-seeded plant species) were recorded in fragments < 1000 ha, suggesting that fragment area may impose strong limitations to the appearance of seed-dispersal interactions involving any large-sized partner.

We next investigated if these differences in frequency of interactions were associated to differences in frequency of small and large-bodied bird and small and large-seeded plant species. In fact, small-seeded plants are prevalent in our dataset (< 12 mm, 91.43%; 128 out of 140 species with seed size information available), whereas only 12 plant species are large-seeded (8.57%). Large-seeded species performed an even lower frequency of interactions (1.35%, 35 interactions) and only two of those connected the metanetwork structure ($B_C = 0.005$, Table S7). Likewise, most seed-dispersers were small-bodied species (137 species, 84.57%) and just a small fraction was large-bodied species (25 species, 15.43%). In this case though the proportion of interactions performed by large-bodied species was similar to the proportion of large-bodied
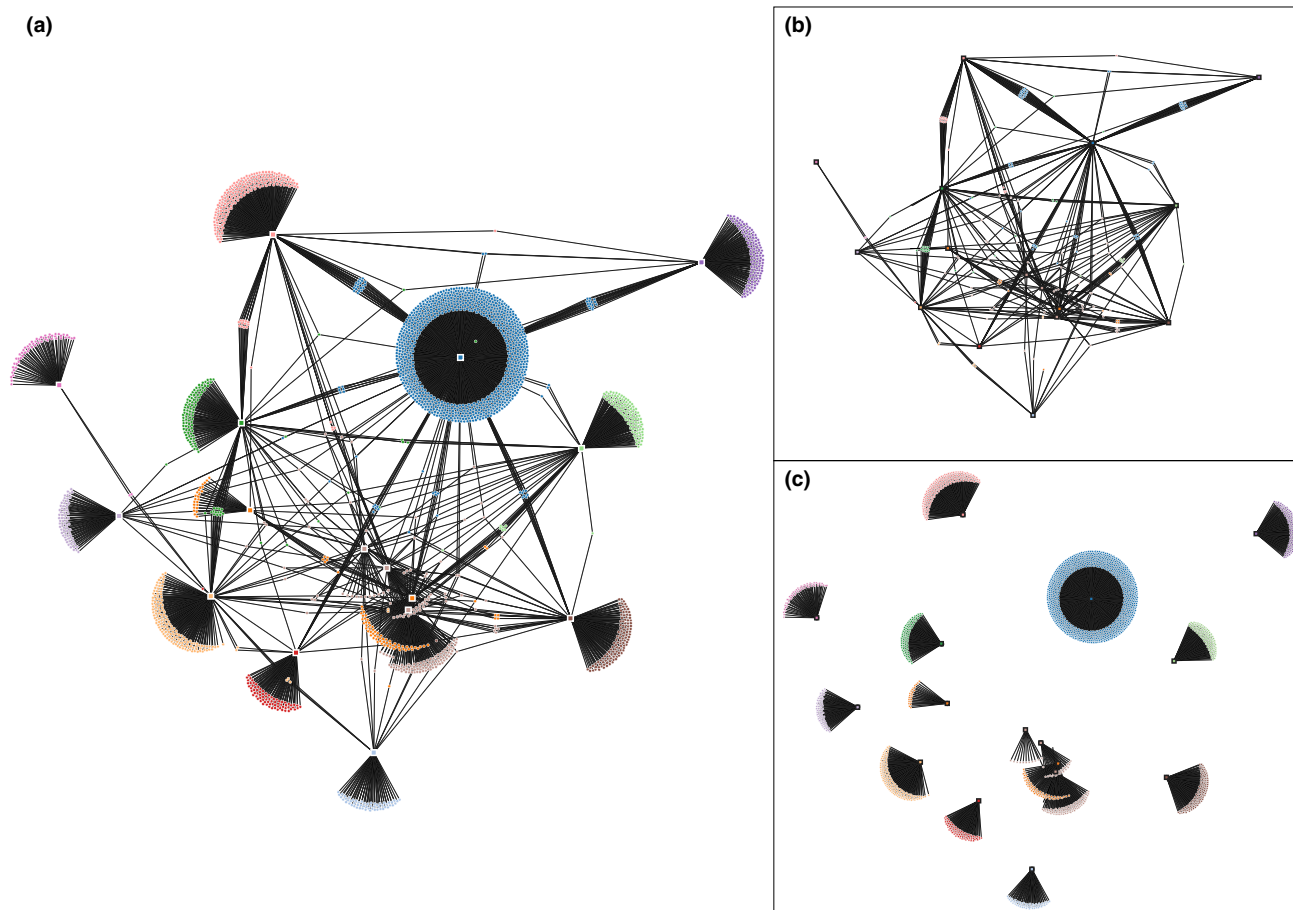
Figure 2 The metanetwork of Atlantic Forest fragments connected by shared pairwise interactions of frugivorous birds and fleshy-fruited plant species (a). The graph representation follows a force-directed drawing that organises nodes with greater centrality to more central positions (Bannister *et al.* 2013), displaying the fragments (squares) with different colours for each locality. Circles indicate pairwise bird seed-dispersal interactions. The interactions present in at least two fragments (betweenness score $B_C > 0$) lie on the links (isolated in panel b). (a) The structure of the metanetwork of the Atlantic Forest including all bird seed-dispersal interactions recorded in each of the 16 fragments and the interactions shared among fragments. (b) The structural backbone of the metanetwork in which only interactions with a significant role in connecting the different parts of the metanetwork structure are maintained (i.e. only interactions with betweenness $B_C > 0$, and that occur in at least two fragments, $k \geq 2$). (c) The opposite of panel b, representing the metanetwork structure when the 'connector' interactions are removed, resulting in completely isolated forest fragments. Figures built with Network3D package (Gandrud 2015), in R. An interactive version of panel (a) is available at http://pedroj.github.io/AF_metanetwork/.

Table 1 Results from the beta-diversity and turnover of bird seed-dispersal interactions among the 16 forest fragments of the Atlantic Forest. Both indexes were calculated for plants, birds and the interactions among them, at the genus and species level. *N*, number of taxa or interactions in each level.

	N	β-diversity (Sørensen)	β-turnover (Simpson)
Genus level			
Plants	113	0.899	0.846
Birds	96	0.842	0.757
Interactions	921	0.943	0.925
Species level			
Plants	335	0.956	0.907
Birds	170	0.878	0.795
Interactions	2328	0.987	0.972

species in the frugivore assemblage (296 interactions, 11.44% of all interactions). Relatively few interactions connected the metanetwork ($B_C > 0$, Table S7), 440 interactions performed by small-bodied species and 14 interactions performed by large-bodied species.

We found evidence for decreasing body mass and seed diameter of species and interactions with higher centrality, despite the high variance and heteroscedasticity of the data. Bird species engaging in interactions occurring in a larger number of sites and connecting different parts of the metanetwork (i.e. higher betweenness) tended to have smaller body mass (Table 2). Likewise, plant species performing central interactions showed a marginal trend to have smaller seed diameter (Table 2). Examples of those interactions (mean seed diameter or body mass in parentheses) involve *Schinus terebenthifolia* (3.5 mm) – *Thraupis sayaca* (32.5 g), *Trema micrantha* (1.7 mm) – *Dacnis cayana* (13.0 g), *Casearia sylvestris* (1.3 mm) – *Tachyphonus coronatus* (20.3 g) (Table S7). When species were analysed independently of the interactions they performed, plant centrality was negatively correlated with seed diameter, whereas body mass showed no significant
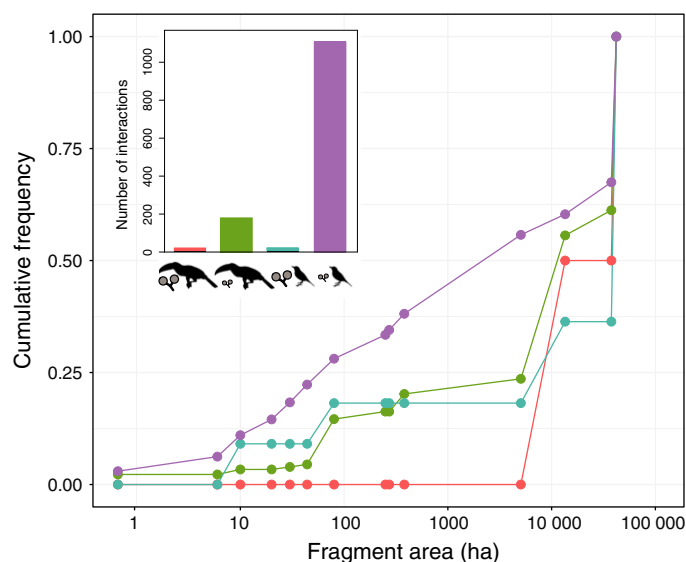
Figure 3 Frequencies of four functional groups of bird-fruit interactions in relation to fragment area. The inset shows the number of pairwise interactions recorded in the metanetwork involving: (1) large-bodied frugivore/large-seeded plant (red); (2) large-bodied frugivore/small-seeded plant (green); small-bodied frugivore/large-seeded plant (blue); and (4) small-bodied frugivore/small-seeded plant (purple). Lines show the cumulative proportion of interactions in each group occurring in fragments of increasing area, each dot indicating the probability of occurrence of an interaction in a given group in a fragment as large, or smaller, than the corresponding area. Functional groups were classified according to the pairwise combination of body mass (g) of the bird frugivore and seed diameter (mm) of the plant species involved in the interaction. The threshold for establishing large bird species was body mass > 100 g, and for large seeds we used seed diameter > 12 mm (Galetti *et al.* 2013).

correlation with bird centrality (Table 2, Table S8, S9). Finally, higher centrality of bird species, both at the species- and interaction-level, was significantly associated to their higher capacity to move in the fragmented landscape (see Suppl. Mat. for results, Fig. S6, S7). Larger bodied species were more sensitive to disturbance, whereas an intermediate body size seems to favour the capacity to cross the matrix and the dependence of forest habitats (Fig. S8).

DISCUSSION

We found that forest fragments facing strong anthropogenic pressure still hold highly unique assemblages of bird seed-dispersal interactions. This translates into high beta-diversity at the landscape level, resulting in a metanetwork structured into modules and sparsely connected by an impressively reduced number of interactions, representing *c.* 8% of the overall interactions. Our approach implicitly assumes that a high occurrence of specific interactions across fragments is a proxy to identify those that may maintain fragments functionally integrated. These shared interactions represent (1) redundant functions (i.e. exactly the same partner species involved) and (2) may imply a strong potential as mobile links (Kremen *et al.* 2007) contributing to functional connections across the fragmented landscape (Urban & Keitt 2001). Interactions with higher centrality, therefore with higher potential to integrate

Table 2 Results from the Spearman correlation tests between species traits (body mass and seed diameter) and network centrality estimated for each pairwise bird seed-dispersal interactions, and for each bird and plant species, composing the metanetwork of the Atlantic Forest. Species traits were tested individually against each centrality metric (degree and betweenness) according to the species involved in that interaction. Only complete pairwise interactions (i.e. with information of both birds' and plants' traits) were included in the analyses.

	Degree (k)		Betweenness (B_C)	
	ρ	*P*-value	ρ	*P*-value
Interactions				
Body mass (g)	−0.043	0.040	−0.042	0.042
Seed diameter (mm)	−0.051	0.065	−0.051	0.065
Species				
Body mass (g)	−0.013	0.548	0.023	0.262
Seed diameter (mm)	−0.165	< 0.001	−0.196	< 0.001

fragments, were performed by small-bodied bird species associated to small-seeded plant species characteristic of secondary forest growth (Blake *et al.* 1990). This mainly resulted from the constraints imposed by fragment area to the occurrence of large-sized species. The incidence of interactions involving large-sized species vanished in fragments < 10 000 ha, and < 20% of the interactions involving species of contrasting sizes (e.g. large-bodied bird and small-seeded plant species) were recorded in fragments < 1000 ha, indicating a strong filtering by habitat fragmentation acting over the functional diversity of BSD-interactions.

Limitations

Research on multilayer representations of networks like the one studied here, with local networks connected across multiple spatial scales, is at its infancy (Genrich *et al.* 2017; Pilosof *et al.* 2017). Our analyses represent an initial empirical attempt in this direction, dealing with an extremely diverse network of interactions. The high turnover of interactions found here may be related to the ample spatial scale considered and to the fact that, for logistic limitations, not all forest patches in the study area were sampled (Fig. S1). Besides, high interaction turnover is expected due to autocorrelated effects, and to the high beta-diversity of birds and plants seem in the Atlantic Forest (Morante-Filho *et al.* 2016; Sfair *et al.* 2016; Farah *et al.* 2017).

A second limitation relates to the assumption that plant and bird species occupying more fragments will be the most likely to contribute to cross-fragments integration through redundant functions, detected by the higher centrality interactions in the metanetwork. Sampling limitations in high-diversity networks (Jordano 2016) may have biased our results for finding such a high frequency of interactions unique to a single fragment. Yet our analysis of sampling effort (Fig. S2; Bello *et al.* 2017) suggests sampling appears robust for the detection of species and their potential interactions (Fig. S2). When interactions are unique to a single fragment, we expect them to have a reduced potential for among-fragment movement compared to interactions where both partner species occupy multiple fragments.

A highly diverse, defaunated and fragmented tropical metanetwork

The high modularity found for the Atlantic Forest metanetwork shows a regional pool of bird frugivore interactions split into fragments that hold distinct sets of species interactions. The resulting low connectance suggests low redundancy of seed-dispersal at the landscape level. In addition, when species are considered independently of the interactions they perform, modularity drops and connectance increases, indicating that the distribution of interactions in a metanetwork context does not necessarily reflect the distribution of the species involved. Thus, frugivorous bird species and bird-dispersed plant species are more redundant at the landscape level than the functional pairwise interactions they perform.

The metanetwork configuration may entail the isolation of species, and their interactions, within fragments. In the long term that may lead to gene flow depression among fragmented populations likely affecting species eco-evolutionary trajectories (Cote *et al.* 2017; Pérez-Méndez *et al.* 2017) that may respond differently to local-selective pressures (Thompson 2005). Yet, by decomposing the patterns of turnover in species richness turnover and species interaction turnover we showed that the former contributes unprecedented levels for the second. Therefore, understanding the distribution of interactions may provide insights not only about the persistence of species but also the persistence of communities in which interactions are organised in human-modified landscapes (Poisot *et al.* 2017).

Small fragments may effectively contribute to connectivity across large areas (Urban & Keitt 2001). The mosaic landscape of the Atlantic Forest, interspaced by forest remnants of variable sizes, mostly < 200 m apart, provides opportunity for the movement of generalist bird species (Uezu *et al.* 2005; Martensen *et al.* 2008; Uezu *et al.* 2008) that can fly up to 300 m between fragments (Awade *et al.* 2017; Cornelius *et al.* 2017). Therefore, small fragments may act as 'stepping-stones' favouring the movement of bird and plant partners contributing to propagate the distinct subset of interactions that functionally integrate fragments in the metanetwork context (Uezu *et al.* 2005; Sekercioglu *et al.* 2007; Neuschulz *et al.* 2013). Field observations from the Chaco-Serrano Woodland showed that the small-sized, generalist bird species *Pitangus sulphuratus* and *Turdus amaurocholinus* can fly among fragments distant 300 m and 200 m apart respectively (Velez *et al.* 2015). These same species showed high centrality in our metanetwork and high capacity to move in the fragmented landscape; they are examples of species performing interactions that may enhance landscape connectivity in contemporary time.

Nonetheless, rare events of seed-dispersal can also contribute to species movement and gene flow in fragmented landscapes (Nathan 2006; Jordano *et al.* 2007; Sekercioglu *et al.* 2007; Tella *et al.* 2016; García & Borda-de-Água 2017). Diet-generalist, small-sized bird species contribute effectively to the seed-rain of pristine-forest species in rare events of dispersal among tropical forest fragments (Carlo & Morales 2016). Several frugivorous birds recorded in our metanetwork are regional, altitudinal or long-distance migrants (e.g. *Turdus* spp.) known to move considerable distances (Chesser 1994; Capllonch *et al.* 2008) that may eventually result in seed-dispersal. For instance, radio-tracking recorded flying bouts for small *Tangara* and *Turdus* up to three and 5.8 km in a few hours (Sekercioglu *et al.* 2007). With distances between fragments in the Atlantic Forest varying from a few to several thousand metres, events of long-distance seed-dispersal are likely to be common depending on the matrix permeability and the bird flying capability. The 16 fragments studied here span a very large geographical scale and may result in an underestimated connectivity due to high species and interaction turnover. Yet our results emphasise the importance of small fragments as stepping-stones potentially connecting sites within fragmented landscapes, confirming previous connectivity models (e.g. Urban & Keitt 2001).

Central taxa present in a fragment do not necessarily become partners in a central interaction at the landscape level despite we found that central species tend to perform central interactions. This effect, contributing to the high beta-diversity of interactions, may be attributable to constraints from forbidden links (Olesen *et al.* 2011) due to a mismatch between bird occurrence and plant phenology, or size-related constraints for the interaction to occur (Galetti *et al.* 2013). Thus, interaction rewiring may change the identity of species partners maintaining network structure within and among fragments (CaraDonna *et al.* 2017; Pilosof *et al.* 2017). Indeed, some potential interactions at the local-fragment level were not realised, especially in restored areas and despite relatively low values (Fig. S4), suggesting some degree of rewiring within-local networks. Yet rewiring was not related to a reduction in fragment area but may be a consequence of the loss of interaction partners due to defaunation (Galetti *et al.* 2013). The loss of species and mismatches between interaction partners may result in lower dispersal rates among distinct fragments, leading to structural reorganisation of local networks (Thompson & Gonzalez 2017). Those factors combined suggest an arena in which forest fragments with higher selective pressure become hotspots of eco-evolutionary changes on interactions, whereas less disturbed fragments could be seen as cold spots in which changes are slower, or evolution is characterised by stabilising selection (Thompson 2005; Galetti *et al.* 2013; Cote *et al.* 2017).

Functional downsizing of bird seed-dispersal interactions

Despite our results evidencing a trend for reduced body mass and seed size among the species involved in central interactions, we failed to capture strong evidences for interaction centrality co-varying with interaction traits. At most, the data reveal a decreasing centrality of taxa of larger size. Species traits were obtained at the species level, so the values attributed to each species are approximations of the average of intraspecific variation for a given trait in a given population. Therefore we could not capture all processes likely determining species associations, such as intraspecific variation on body mass due to reduced resource availability, or seed size variation due to environmental fluctuations (Violle *et al.* 2012). Besides, trait data were available for about 50% of the interactions, possibly underestimating the downsizing effect across fragments.

Yet, the downsized bird and plant species remaining in smaller area fragments seem to play the winners role in the

fragmented arena (Tabarelli *et al.* 2012), contributing to a higher incidence of smaller sized interactions in smaller area fragments. The prevalence of small–small interactions and the absence of interactions by large-bodied bird species throughout the range of fragment area translate into a distinct spatial organisation of bird–plant interactions, where any interaction involving large-bodied frugivorous birds and/or large-seeded plant species quickly vanishes when the fragment area is < 10 000 ha. Fragmentation thus conveys the pervasive extinction of a distinctly non-random set of plant–frugivore interactions, not just a 'simple' loss of individual species.

Advancing the field and implications for conservation

To further test the metanetwork hypothesis we need a holistic framework that integrates key factors influencing species interaction persistence and landscape connectivity. The challenge ahead involves a detailed scanning of the movement of interacting species at different spatial scales, including frugivore movement patterns and their potential to contribute contemporary dispersal of plant propagules (Nathan & Muller-Landau 2000; García & Borda-de-Água 2017), intraspecific response to environmental changes (Awade *et al.* 2017; Cornelius *et al.* 2017) and the type of matrix (Emer *et al.* 2013; Biz *et al.* 2017) in which the metanetwork is embedded. Combining new technologies such as radio tracking (Nathan 2006; Cornelius *et al.* 2017) and DNA barcoding (Carvalho *et al.* 2016; Gonzalez-Varo *et al.* 2017; Pérez-Méndez *et al.* 2017) associated to spatially explicit analyses (Dale & Fortin 2010) and novel null models incorporating species traits and seasonal dynamics (Dormann *et al.* 2017; Tylianakis & Morris 2017) would enhance our understanding of how ecological processes scale-up from the local-individual level to the metacommunity, regional-landscape level.

Fragments of the Atlantic Forest hold a unique heritage of species, and their interactions, remaining after centuries of overexploitation and habitat destruction. Therefore, if a single fragment disappears, even a small-sized one, unique interactions will also vanish (da Silva & Tabarelli 2000; Hagen *et al.* 2012; Tabarelli *et al.* 2012). Yet, we revealed that the dispersal of large-seeded plant species by large-bodied bird species requires large areas (> 10,000 ha). With more than 80% of the remaining Atlantic Forest fragments smaller than 50 ha, the conservation of specific functional groups of interactions is at risk and restricted to a few relict forest patches. Our results indicate that the preservation of the ecological functions conveyed in interactions between large-seeded plant and large-bodied bird species will not be preserved by the rewiring of the participant species in other forest remnants.

In the long run, the dominance of small-sized species in forest fragments associated to the local extinction of interactions performed by larger bodied frugivore species may select for smaller fruit and seed-sized plant species (Galetti *et al.* 2013; Carvalho *et al.* 2016). A negative functional effect of this selection towards small-seeded plant species is that they are generally associated to reduce carbon storage capacity, which may lead to a pervasive deficit in the carbon balance relative to semi-pristine forests (Bello *et al.* 2015). The documented changes in bird seed-dispersal interactions due to defaunation and habitat fragmentation may cause structural changes in the Atlantic Forest vegetation, imposing long delays for the recovering of forest tracts and for the functional integration of forest fragments within a cohesive metanetwork.

AUTHORSHIP

CE, PJ and MG conceived the study; MG, MAP, SM, AP and PJ gathered data; CE and PJ analysed the data; CE wrote a first version of the manuscript, with contributions by PJ, and both completed the final version with contributions by MG, MAP, PRG and AP.

DATA ACCESSIBILITY

Data are available at the Atlantic-Frugivory database (Bello *et al.* 2017), and the full dataset and R code are available in GitHub ([https://doi.org/github.com/carineemer/metanetwork]; https://doi.org/10.5281/zenodo.1115562).

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