Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics

Running title: Intercontinental comparison of networks

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Abstract

Aim: Biogeographical comparisons of interaction networks help elucidate differences in ecological communities and ecosystem functioning at large scales. Neotropical ecosystems have higher diversity and different composition of frugivores and fleshy-fruited plants than Afrotropical systems, but a lack of inter-continental comparisons limits understanding of (i) whether plant-frugivore networks are structured similarly, and (ii) whether the same species traits define animals' roles across continents.

Location: Afrotropics and Neotropics

Time period: Current

Taxon: Fleshy-fruited plants and frugivorous vertebrates

Methods: We compiled a dataset comprising 17 Afrotropical and 48 Neotropical weighted seed-dispersal networks quantifying frugivory interactions between 1,091 fleshy-fruited plant and 665 animal species, comprising in total 8,251 interaction links between plants and animals. In addition, we compiled information on animals' body mass and degree of frugivory. We compared four standard network-level metrics related to interaction diversity and specialization, accounting for differences related to sampling effort and network location. Furthermore, we tested whether animal traits (body mass, degree of frugivory) differed between continents, whether these traits were related to species' network roles, and whether these relationships varied between continents.

Results: We found significant structural differences in networks between continents. Overall, Neotropical networks were less nested and more specialized than Afrotropical networks. At species level, a higher body mass and degree of frugivory were associated with an increasing diversity of plant partners. Specialization of frugivores increased with the degree of frugivory, but only in the Neotropics.

Main conclusions: Our findings show that Afrotropical networks have a greater overlap in plant partners among vertebrate frugivores than the more diverse networks in the Neotropics that are characterized by a greater niche partitioning. Hence, the loss of frugivore species could have stronger impacts on ecosystem functioning in the more specialized Neotropical compared to the more generalized Afrotropical communities.

Keywords: Afrotropics, birds, ecological networks, frugivory, macroecology, mammals, mutualism, Neotropics, seed dispersal.

Introduction

Species interactions are organized in complex ecological networks that influence the structure of ecological communities and are important for ecosystem functioning (Bascompte et al., 2003; Schleuning et al., 2015). The structural organization of species interaction networks can contribute to community stability and increase the ability of communities to recover from perturbations (Bascompte & Jordano, 2014). Given the importance of ecological networks for ecosystem functioning (Schleuning et al., 2015), there has been a growing interest in comparative macroecological studies of species interaction networks across large spatial scales (e.g., Schleuning et al., 2012; Sebastián-González et al., 2015; Dalsgaard et al., 2017). Macroecological analyses that take advantage of the large-scale variation in ecological, evolutionary and historical conditions can reveal how biogeographic legacies have shaped the structure of ecological networks (Kissling & Schleuning, 2015; Traveset et al., 2016).

About 90% of plant species participate in plant-frugivore networks in tropical ecosystems around the world (Jordano, 2000), and mutualistic seed-dispersal interactions between plants and animals provide a vital contribution to plant recruitment and forest regeneration (Neuschulz et al., 2016). Tropical plant-frugivore networks comprise diverse communities of plant and animal species (Fleming et al., 1987; Kissling et al., 2009) and are generally characterized by a low degree of specialization of plants and animals on specific interaction partners (Schleuning et al., 2012; Dalsgaard et. al., 2017). Many species of tropical frugivores strongly depend on fruit in their diet (Kissling et al., 2009) and usually feed on a large variety of different fruit resource species (Dalsgaard et al., 2017). Such frugivores with a high degree of frugivory usually fulfill essential structural roles in plant-frugivore networks and are important for the structural robustness of ecological communities (Mello et al., 2014; Ruggera et al. 2016). In addition, morphological traits, such as body size, can be associated with species' roles within networks

(Dehling et al., 2016), but relatively little is known about the generality of the relationship between species' traits and network roles across large scales (but see Sebastián-González, 2017).

Within the tropics, species diversity and taxonomic composition of plants and animals vary substantially, due to differences in evolutionary and historical legacies among biogeographic regions (Jansson & Davies, 2008; Carlucci et al., 2017). For example, the Afrotropics and Neotropics differ in their evolutionary history, due to major extinction events in the Afrotropics and greater diversification of angiosperms in the Neotropics (Carlucci et al., 2017). Consequently, Neotropical ecosystems comprise a higher diversity of fleshy-fruited plants (Terborgh et al., 2016) and avian frugivores than Afrotropical systems (Fleming et al., 1987; Kissling et al., 2009). Moreover, it has been suggested that more animal species in the Neotropics have specialized on fruit diet compared to the Afrotropics (Snow, 1981; Fleming et al., 1987). Higher plant diversity and degree of frugivory in the Neotropics suggest that Neotropical frugivores will, on average, interact with more plant partners than their African counterparts, which could lead to differences in overall network structure. For example, it has been shown that tropical networks that are dominated by animal species with a high degree of frugivory have a low degree of specialization and modularity (Schleuning et al., 2012, 2014). Previous macroecological studies of mutualistic networks have further shown that an increase in species richness tends to be associated with an increase in modularity and nestedness (Martín-Gonzalez et al., 2015; Sebastián-González et al., 2015). So far, macroecological studies of network structure, especially along latitudinal gradients (e.g., Schleuning et al., 2012, Sebastián-González et al., 2015), have revealed inconsistent results, e.g. due to analytical and conceptual differences among studies (Dalsgaard et al., 2017). Another explanation for the inconsistent patterns in these studies could be that latitudinal trends in network structure are altered by structural differences of networks among biogeographic regions.

To date, no study has tested how the differences between Afrotropical and Neotropical ecosystems influence the structure of plant-frugivore networks both at network and species level. Here, we address this knowledge gap and ask the following questions: (1) How does the structure of seed-dispersal networks differ between Afrotropical and Neotropical communities? We propose two alternative hypotheses: (a) The diverse Neotropical networks, comprising many animals with a high degree of frugivory, are more nested and less specialized than networks in the Afrotropics (Schleuning et al., 2012). Alternatively, (b) the higher plant and frugivore diversity of Neotropical networks enhances niche partitioning (Sebastián-González et al., 2015) and, thus, leads to lower nestedness and higher specialization in Neotropical compared to Afrotropical networks. (2) How do species' network roles differ between the Afrotropics and Neotropics, and how are these species' roles related to species' traits in both regions? We expect that Neotropical frugivores will, on average, interact with more partners than Afrotropical frugivores. We generally expect that large-bodied species with a high degree of frugivory will interact with more plant partners than small-bodied species that only occasionally feed on fruits.

Methods

Seed-dispersal networks

We used data from 65 networks of plant-frugivore interactions, including 17 Afrotropical and 48 Neotropical networks (Fig. 1). This bias reflects the prevalence of seed-dispersal studies in the Neotropics, while other tropical regions are understudied (Escribano-Ávila et al. in press). Most datasets were collected in forested habitats (12 Afrotropical, 45 Neotropical networks), but also covered savannah habitats, especially in the Afrotropics. All datasets included weighted interaction data, specifying the absolute frequencies of interactions between plants and animals. The networks did not include data on interaction efficiencies, but the frequency of interactions has been proposed to be a good proxy for the importance of animals for plants and vice versa (Vázquez et al., 2005). For each network, we collected detailed information on the sampling method to account for these differences in the analyses. Datasets differed in sampling approaches, based on the type of animal group on which the study was focused (usually, birds, mammals, or both), in how interaction data were collected (plant or animal-focused), and in the total sampling hours (see Tab. S2, Supporting Information). Most of the Neotropical networks comprised solely bird frugivore interactions (36 out of 48 networks), whereas nine networks comprised both mammals and birds, and three only mammals. African networks included four bird-exclusive networks, while the other 13 networks were formed by birds and mammals. 29 Neotropical networks were plant-based (fruit-removal observations), four were animal-based (fecal samples), and 15 included both methods. Sixteen Afrotropical networks used plant-based observations, while only one study used animal-based data. Neotropical networks generally had more sampling hours (median: 300 total sampling hours) compared to African networks (median: 125 total sampling hours; for details see Tab. S2, Supporting Information). In order to account for potential biases due to sampling differences, we account for sampling focus, method and hours in network-level analyses (see below).

In addition to sampling differences, we compiled information to account for network-specific differences in study location and human impact. For each network, we recorded absolute latitude, altitude, level of current human disturbance (i.e., anthropogenic edge, fragmentation, degradation, and defaunation), invasion (by introduced species), and species richness (total number of plant and animal species recorded in the network, see Tab. S2, Supporting Information). Human disturbance and invasion levels at the time of data collection were estimated on an ordinal scale of 1 to 4 by the data providers, with 1 corresponding to the lowest disturbance and 4 to the highest (see Tab. S1 for details, Supporting Information). Estimates of the different drivers of human disturbance were averaged for the analysis, yielding a single disturbance score ranging between 1 and 4 for each network.

For each animal species in the networks, we gathered information on species traits relevant to their role as frugivores (body mass; the proportion of fruit in the diet as an estimate of the degree of frugivory measured in 10% steps from 0 to 100%) and taxonomy. For taxonomic information, we used the Clements taxonomic classification on Avibase for birds (Clements et al., 2016), and the IUCN Red List classification for mammals (IUCN, 2016). Overall, we compiled taxonomic information for 51 mammal species and 614 bird species and combined that to data on body mass and the degree of frugivory (Wilman et al., 2014). We complemented trait data, when necessary, with information from other literature sources (e.g., Dunning, 2007; Bello et al., 2017).

Network-level metrics

We analyzed interaction networks using the ‘bipartite’ package (Dormann et al., 2008) in R (R Core Team, 2016). Network-level metrics included weighted nestedness (wNODF), interaction evenness (EVE), quantitative modularity (Q), and complementary specialization (H_2'). Nestedness quantifies the degree to which species with few interactions are connected to highly connected species and has been proposed to be associated with network stability (Bascompte et al., 2003). Weighted NODF accounts for interaction frequencies between species. Weighted NODF was significantly correlated to binary NODF (Pearson's correlation r = 0.503, P

< 0.001, n = 65 networks in all cases) and weighted nestedness (Pearson's correlation r = 0.947, P < 0.001), both of which yielded similar trends in statistical comparisons (Table S2). Interaction evenness measures to what extent interactions are spread evenly across available partners, with high values indicating a more homogeneous distribution of interactions across species (Bersier et al., 2002). Modularity analysis detects the degree to which certain groups of animals interact more often with a specific group of plants (and vice versa), i.e., if species form tightly linked modules that are only weakly linked to species from other modules (Dormann & Strauss, 2014). Modularity values are computed by detecting to what extent the number of interactions between modules is lower than expected based on random interactions. We calculated modularity Q with the algorithm proposed by Beckett (2016) for weighted bipartite networks based on a single model run with 10^7 steps (Schleuning et al., 2014); repeated runs yielded identical Q values. Finally, H_2' measures the overall specialization within a network, i.e., whether species in a network tend to partition or share their interaction partners (Blüthgen et al., 2006). The metric is calculated by a comparison between observed and expected interaction frequencies, based on the species marginal totals, and it is less sensitive to differences in sampling effort than other metrics (Blüthgen et al., 2006). High values of H_2' and Q indicate a high degree of niche partitioning among species or modules, respectively, whereas low values indicate a high degree of niche overlap among species or modules.

We additionally calculated null-model-corrected metrics for weighted NODF, interaction evenness, modularity Q-values, and H_2', using 100 runs of the Patefield null-model (Patefield, 1981), which constrains the marginal totals of the network matrix from both sides. For each network, we calculated null-model corrected metrics (ΔwNODF, ΔEVE, ΔQ, and $\Delta H_2'$) as the difference between observed metrics and the mean value across the 100 null-model runs

(Dalsgaard et al., 2017). Observed and null-model corrected metrics were closely correlated for Q (r = 0.774, P < 0.001) and H_2' (r = 0.952, P < 0.001), but were only weakly related for weighted NODF (r = 0.150, P = 0.232) and interaction evenness (r = 0.189, P = 0.132), confirming that the latter two metrics strongly depend on the distribution of marginal totals (Blüthgen et al., 2008).

Species-level metrics

We quantified animal species roles within networks by four species-level metrics that correspond to the employed network-level metrics and are related to animal specialization on plants: normalized degree (ND), number of effective partners (EP), between-module connector values (c-values) and complementary specialization (d'). Normalized degree equals the number of links of a species divided by the total number of possible links, thereby accounting for differences in network size (i.e., the number of plant partners relative to all potential plant partners in the respective network). Effective partners is a weighted measure of niche breadth that accounts for the frequency of interactions and equals the number of partners a species would have if each link was equally common; it is, thus, a weighted version of species degree (Bersier et al., 2002). Between-module connector values (c-values) determine the importance of a species in connecting different modules by interactions with species that are part of other modules, thereby reducing modularity (e.g., Schleuning et al., 2014). If the interactions of a species are evenly distributed among modules, it has a c-value close to 1; if interactions are restricted to partners within a species' own module, the c-value is 0. Finally, complementary specialization (d') measures the degree of specialization of a species, by quantifying the niche exclusiveness of a species relative to a random distribution of interactions that is based on the marginal totals, analogous to the calculation of H_2' at the community level (Blüthgen et al., 2006).

Statistical analyses

We compared the structure of interaction networks (described by network metrics wNODF, EVE, *Q*, H_2') between the Afrotropics and Neotropics with linear models that account for network-specific differences in sampling and location. Covariates included sampling focus (plant, animal, or both), animal group (birds, mammals, or both), total sampling hours (log-transformed), absolute latitude, altitude, disturbance and invasion level, and total species richness (log-transformed). We defined a full model including main effects of all covariates plus a factor of biogeographic region (Afrotropical versus Neotropical) that was included in all models. We compared all model combinations nested within this full model, according to the small sample-size corrected version of the Akaike Information Criterion (AICc), by using the dredge function ('MuMIn' package in R, Barton 2016). We considered all models with a ΔAICc value < 2 (relative to the best model) to be equally supported and computed full model-averaged parameter estimates across the subset of best models (Burnham & Anderson, 2002). We ran the same statistical analyses for the four null-model corrected network metrics (ΔwNODF, ΔEVE, ΔQ, and $\Delta H_2'$).

To test how species' roles, and their relationship with species traits, differed between biogeographic regions, we fitted linear mixed-effects models for each species-level metric (ND, EP, *c*-values, *d'*, computed for all animal species within each network) with the 'lme4' package (Bates et al., 2015). To account for the facts that networks differed in size and other properties, that species could occur in more than a single network and might not be taxonomically evenly distributed across networks, all models included network identity and taxonomic identity (taxonomic levels nested in this order: class, order, family and genus) as crossed random effects on the model intercepts. As fixed effects, we included biogeographic region, body mass (log-transformed) and the degree of frugivory (proportion of fruit in diet: 0–100%, in 10% steps) plus the two-way interaction between region x body mass and region x fruit diet. Hence, the model tested whether the two species' traits were similarly or differently related to species-level metrics in the two biogeographic regions. As in the analyses at the network level, we compared all model combinations nested within this full model (including all main and interaction effects of the fixed effects), selected a subset of best models according to their AICc, and computed full model-averaged parameter estimates across the subset of best models. In addition to models of species' roles, we tested whether body mass and the degree of frugivory differed between biogeographic regions, i.e., whether body mass and/or degree of frugivory were, on average, larger in one of the biogeographic regions. We fitted a mixed-effects model with the respective species trait as response variable and biogeographic region as predictor variable, accounting for network and taxonomic identity in the random model components as described above.

Results

Afrotropical networks included a total of 253 vertebrate frugivore species (mean species number per network ± standard deviation = 29.0 ± 19.8) from 142 genera in 44 families, and 257 fleshy-fruited plant species (mean = 29.9 ± 22.1) from 145 genera in 59 families. In comparison, Neotropical networks included a total of 412 vertebrate frugivore species (mean = 37.8 ± 47.6) from 197 genera in 31 families, and 834 fleshy-fruited plant species (mean = 26.1 ± 28.7) from 242 genera in 90 families. In total, we recorded 8,251 links between plant and animal species across all networks, with 2,273 links recorded in the Afrotropics (mean 133.7 ± 120.4) and 5,978 links in the Neotropics (mean 124.5 ± 147.2). Across the 665 animal species, body mass ranged from 6.2 to 3,940,000 g (median = 31 g) and the proportion of fruit in the diet ranged from 0 to 100% (median = 40%).

Network-level metrics

When accounting for differences in sampling and locality (i.e., sampling focus, animal group, sampling hours, absolute latitude, altitude, disturbance and invasion level, and species richness), Afrotropical networks were significantly more nested than Neotropical networks (Fig. 2a; Tab. 1). In addition, Afrotropical networks showed lower interaction evenness than Neotropical networks (Fig. 2b; Tab. 1) and were significantly less specialized than Neotropical networks (Fig. 2c; Tab. 1). There was no significant difference between biogeographic regions in network modularity (Fig. 2d; Tab. 1). Analyses based on null-model corrected metrics yielded similar trends for network specialization and modularity, whereas trends tended to be opposite to the analysis of uncorrected metrics for nestedness and interaction evenness (Tab. S2, Supporting Information).

Sampling strategy also influenced network-level metrics (Tab. 1). Networks sampled with an only-plant or only-animal sampling focus registered lower nestedness and higher complementary specialization than networks with a combined animal and plant focus. Networks including mammals as the only sampled animal group had higher nestedness and lower complementary specialization than networks including either only birds or both mammals and birds. Furthermore, modularity and complementary specialization increased with increasing sampling hours (Tab. 1). Interaction evenness increased and complementary specialization decreased with increasing species richness, while modularity increased with altitude and increasing disturbance levels (Tab. 1).

Species-level metrics

Interaction data from the Afrotropics involved in total 34 mammal (24 genera, nine families, six orders) and 219 bird species (118 genera, 35 families, 10 orders), whereas we recorded interactions of 17 mammal (11 genera, three families, three orders) and 395 bird species (186 genera, 28 families, eight orders) in the Neotropics. In the Afrotropics, animal species had a significantly lower degree of frugivory than in the Neotropics (Fig. 3a). In contrast, animal body mass was not significantly different between the two biogeographic regions, although the largest seed dispersers were present in the Afrotropics (Fig. 3b).

By accounting for network identity and animal taxonomy, species' roles within the networks varied as a function of species' traits and biogeographic region. Normalized degree was significantly higher in the Afrotropics than in the Neotropics, especially for species with a high degree of frugivory (Fig. 4a; Tab. 2). The number of effective plant partners, which accounts for differences in interaction frequencies among partners, did not differ significantly between biogeographic regions and increased in both biogeographic regions with body mass and an increasing degree of frugivory (Fig, 4b; Tab. 2). *C*-values increased with an increasing degree of frugivory, but only in the Afrotropics (Fig. 4c; Tab 2). Complementary specialization (*d'*) and degree of frugivory were positively associated in the Neotropics, but were weakly negatively related in the Afrotropics (Fig. 4d; Tab. 2). There were no significant interactions between body mass and biogeographic region for any of the species-level metrics (Tab. 2).

Discussion

Afrotropical and Neotropical networks differed in their topological structure, probably due to the biogeographic differences in the diversity and composition of fleshy-fruited plants and animal frugivores between the two regions (Fleming et al., 1987; Jansson & Davies, 2008; Kissling et al., 2009). Our results at the network level lend support to our second hypothesis that Neotropical networks are less nested and more specialized than Afrotropical networks. This finding is supported by analyses at species level where we detected that a higher degree of frugivory was associated with an increasing diversity of explored food resources and a lower selectivity in food choices in the Afrotropics, whereas niche partitioning was greater among frugivores in Neotropical networks.

Afrotropical and Neotropical networks differed in network structure while controlling for potentially confounding factors such as the sampling focus, the studied animal group and the locally recorded species richness. Higher nestedness and lower interaction evenness and complementary specialization in Afrotropical than in Neotropical networks were, thus, independent of these differences in sampling. Analyses of null-model corrected metrics revealed that the differences in specialization were due to differences in species' selectivity between the two regions, as corroborated by the high correlation between observed and null-model corrected values of complementary specialization. This confirms previous studies that have shown that complementary specialization is a sensitive indicator for structural differences among networks at large spatial scales (Blüthgen et al., 2007; Schleuning et al., 2012). In contrast, inter-continental differences in nestedness and interaction evenness were due to differences in the distribution of species' marginal totals, which is consistent with previous comparative analyses of different types of network metrics (Blüthgen et al., 2008). Biogeographical patterns in these network metrics were, thus, likely driven by differences in the abundance distributions of plants and animals on the two continents. Since Neotropical ecosystems generally comprise a higher diversity of frugivores and fleshy-fruited plants than Afrotropical systems (Jansson & Davies, 2008; Kissling et al., 2009), a lower dominance and larger proportion of subdominant and rare plant and animal species is expected for Neotropical systems, consistent with the reported decrease in nestedness and increase in interaction evenness in the Neotropics. Our findings were apparently different from those of previous macroecological studies of seed-dispersal networks. In macroecological studies along latitudinal gradients, nestedness generally increased (Sebastian-Gonzalez et al., 2014) and network specialization decreased (Schleuning et al., 2012; Dalsgaard et al., 2017) in diverse tropical systems. Differently from these studies, we here focus on a comparison between biogeographic regions in tropical and subtropical ecosystems, and variation in latitude was unrelated to network structure (Table 1). Nevertheless, local species richness in the networks, which is related to the completeness of sampling and the size of the local species pool, was consistently negatively related to complementary specialization (Table 1, Table S3), which corresponds to patterns that have been reported previously (Schleuning et al., 2012).

We postulate that differences in network structure between Afrotropical and Neotropical networks are mostly due to differences in how Afrotropical and Neotropical frugivores partition the available fruit resources. Afrotropical ecosystems generally harbor a comparatively low diversity of fleshy-fruited plants (Terborgh et al., 2016), which constrains fruit choice of Afrotropical frugivores. Moreover, keystone fruit resources, such as the ubiquitous fig species in the Afrotropics (Kissling et al., 2007), favor animal aggregation and apparently result in a high degree of nestedness and niche overlap in these networks. In contrast, the higher diversity of fruit resources in the Neotropics facilitates niche partitioning among Neotropical frugivores (Fleming et al., 1987) and could act as a mechanism that reinforces the high diversity of plants in Neotropical compared to Afrotropical forests (Terborgh et al., 2016). Another explanation for the difference between continents could be that the frugivorous megafauna, such as primates or large ungulates, have a generalized diet (Campos-Arceiz & Blake, 2011; Chancellor et al., 2017). The extinction of frugivorous megafauna from the Neotropical continent about 10,000 years before present (Guimarães et al. 2008), which were likely diet generalists as well, could also be associated with lower nestedness and higher specialization in Neotropical than Afrotropical systems. Interestingly, our findings for seed-dispersal networks are consistent with a cross-continental study on avian plant-pollinator networks that found a higher degree of specialization in Neotropical than in Paleotropical plant-bird networks (Zanata et al., 2017). The high diversity of angiosperms in Neotropical ecosystems (Carlucci et al., 2017) may, thus, generally foster the potential for niche differentiation among mutualists in the Neotropics.

Greater functional redundancy among frugivores in the Afrotropics could foster the structural robustness of these networks as a greater functional redundancy is associated with a higher degree of ecosystem resilience (Walker 1995). Neotropical communities may, in contrast, be more vulnerable to the loss of animal frugivores that fulfill rather complementary roles in these networks (Vidal et al., 2014). Several recent studies have demonstrated that the loss of frugivores from Neotropical communities leads to changes in gene flow, plant recruitment and carbon storage (e.g., Carvalho et al., 2016; Peres et al., 2016). Peres et al. (2016) used field data to model the loss of dispersal functions from overhunting of large frugivores in the Brazilian Amazon and predicted losses of above-ground biomass of up to 30% in some locations. Carvalho et al. (2016) documented that defaunation of large frugivores can lead to microevolutionary changes in a Brazilian Atlantic forest palm (*Euterpe edulis*) through the loss of dispersal functions from large seed dispersers, which can even result in a decrease in seed size in defaunated habitats (Galetti et al., 2013). Functional consequences of species loss have been shown to be particularly severe if generalized species are lost, since they help to stabilize seed-dispersal functions against the loss of specialists (Rumeu et al. 2017), or if specialist seed dispersers cannot be replaced by generalists (Guaraldo et al., 2013). Species loss could be buffered by other species that switch their preference to compensate for lost interactions. A high flexibility of frugivores to temporal variation in fruit availability has been described for Neotropical seed-dispersal networks (Blendinger et al., 2016). However, this flexibility is limited by morphological constraints, as large frugivores are generally more flexible and are able to disperse larger seeds than small frugivores; thus, small frugivores are unlikely to functionally compensate for the loss of large seed dispersers (Bender et al., 2017). Similarly, altered interaction patterns in response to competition could be to the detriment of plants with specialized interactions (Fricke et al. 2017), which is more likely to happen in systems with high diversity, such as Neotropical ecosystems.

Although the higher degree of nestedness in Afrotropical networks could make them more robust against the loss of species, previous studies have demonstrated that the loss of frugivores in Africa can affect plant recruitment by disrupting mutualistic interactions between plants and their seed dispersers (Cordeiro & Howe, 2003). Poulsen et al. (2013) found that even partial defaunation in Afrotropical forests can lower dispersal distances of mammal-dispersed trees, and Correia et al. (2016) highlighted the importance of large mammal dispersers for restoration of seed-dispersal functions in Africa. Nevertheless, comparative studies of African frugivore communities in disturbed forest habitats found a rather high robustness of bird-mediated seed dispersal to human impact (Farwig et al., 2006; Neuschulz et al., 2011). These findings suggest a rather high degree of functional redundancy among bird dispersers, whereas the loss of mammal frugivores, such as primates or elephants, is likely to have severe ecological consequences, especially for large-seeded plants that depend on this megafauna (Campos-Arceiz & Blake, 2011; Correia et al., 2016).

Species-level analyses indicate generally lower specialization in Afrotropical than in Neotropical networks, consistent with our findings at the network level. Across regions, the number of effective plant partners increased with the degree of frugivory, which is consistent with previous findings (Schleuning et al. 2014; Fricke et al., 2017). The increase in normalized degree and between-module connector values with the degree of frugivory was only evident in the Afrotropics, suggesting that highly frugivorous Afrotropical species use a large proportion of the available resources. This applies, for instance, to avian lineages with a high dependence on fruits in their diet, such as the African barbets (Lybiidae) or bulbuls (Pycnonotidae; Schleuning et al., 2014). The generalized foraging of these taxa results in overlapping resource use with other frugivores, especially at tropical latitudes (Dalsgaard et al., 2017). In the Neotropics, we found no association between the degree of frugivory and normalized degree or between-module connector values. This suggests that species with a mostly frugivorous diet have relatively more fruit resources to choose from in the Neotropics and show less resource overlap with other co-occurring species (Fleming et al., 1987). We found indeed that Neotropical species with a high degree of frugivory overlapped less in resource choice than species with less fruits in their diet. This suggests that the evolution of frugivory in the Neotropics trends towards specialization on specific fruit resources, which could have been reinforced by plant trait convergence in diverse mutualistic networks—that is, convergence of plant species on different fruit-trait syndromes could reinforce and strengthen niche partitioning (Guimarães et al., 2011; Escribano-Ávila et al. in press). This finding is also consistent with a high degree of trait matching between avian frugivores and their preferred foraging plants in the Neotropics (Bender et al., 2018). Although plants and frugivores in the Afrotropics show similar patterns of trait matching, (Vollstädt et al., 2017), the higher resource diversity in the Neotropics should lead to higher resource specialization and niche partitioning in Neotropical frugivores.

Our findings show that frugivores in the Afrotropics, on average, fulfill more generalized functional roles than their Neotropical counterparts as they disperse a larger proportion of the available resources. Generalization of Afrotropical frugivores may functionally compensate for the lower diversity of animal frugivores compared to the Neotropics. Interestingly, this trend towards a greater generalization in Afrotropical frugivores with a high fruit dependence was unrelated to body mass and, thus, is not a result of the generalized diet of large mammals only (Campos-Arceiz & Blake, 2011; Chancellor et al., 2017), but more fruit-dependent animals in the Afrotropics appear to be more generalized in their fruit resource use regardless of body size. Our findings corroborate earlier studies that have also shown that the degree of frugivory is generally a more important functional trait than body mass in seed dispersal networks (Mello et al., 2014; Sebastián-González, 2017). The degree of frugivory could, therefore, be used as a quick and useful proxy for the identification of keystone frugivores in tropical ecosystems, although such keystone species could differ in their functional roles depending on the specific ecological and regional context. For example, in less diverse networks, such as in most Afrotropical systems, generalized frugivores may play a critical role in contributing to network robustness and functionality, whereas in more diverse networks, such as in many Neotropical systems, specialized frugivores are critical role for maintaining seed-dispersal services to the entire plant community.

Our findings indicate important structural differences between Afrotropical and Neotropical seed-dispersal networks. We argue that these differences are a consequence of biogeographic differences in the diversification of frugivores and fleshy-fruited plants as well as in the persistence of frugivorous megafauna in the two regions. Regional differences were most pronounced for animal species with a high degree of frugivory that overlapped more in the use of fruit resources in the Afrotropics, but were more specialized on specific resource species in the Neotropics. These differences might have important consequences for ecosystem functioning in both regions. In the Afrotropics, generalist frugivores are particularly crucial for maintaining seed-dispersal functions at plant community level. In the Neotropics, the extirpation of animal species with a high degree of frugivory is more likely to trigger the loss of seed-dispersal functions in plant communities unless functional flexibility of frugivores allows for the compensation of lost interactions.

Data accessibility

Data on network metrics, location and sampling of the 65 networks are provided in Supplementary Tables S4 and S5.

Biosketch and author contributions

This meta-analysis was initiated by a team of researchers at the Frugivores and Seed Dispersal Symposium and Workshop in South Africa in 2015. Interaction and trait data were jointly provided by all authors. PJD and LN prepared the database, PJD analyzed the data with input from MS, PJD and MS drafted the manuscript, all authors commented on the manuscript.

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Table 1. Linear model estimates and standard errors for network-level metrics, including weighted nestedness (wNODF), interaction evenness, modularity (*Q* values) and complementary specialization (H_2'). For this analysis, 48 seed-dispersal interaction networks from the Neotropics were compared to 17 networks from the Afrotropics. Shown are estimates derived from model averaging over the subset of best models with ΔAICc < 2; estimates of 0 indicate that the respective predictor was not included in the subset of best models. Sampling focus was tested as a factorial predictor at three levels: "animals only," "plants only," and "both animals and plants". Animal group was tested as a factorial predictor at three levels: "birds," "mammals," and "both birds and mammals". Continuous predictors (absolute latitude, altitude, disturbance, invasion, species richness [log-transformed], and sampling hours [log-transformed]) were z-transformed.

	Weighted nestedness		Interaction evenness		Modularity *Q*		Specialization H_2'	
	No. of best models = 3		No. of best models = 3		No. of best models = 3		No. of best models = 2	
	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error
Afro- vs Neotropics	**-14.4 *****	**4.27**	**0.058 ***	**0.002**	**0.057**	**0.039**	**0.104 ***	**0.049**
Absolute latitude	0	-	0	-	0.011	0.015	0	-
Altitude	0	-	0	-	0.013	0.015	0	-
Disturbance	0	-	0.002	0.006	0	-	0	-
Invasion	0	-	0	-	0	-	0	-
log Species richness	-1.51	1.98	0.054 ***	0.011	0	-	-0.077 ***	0.021
log Sampling hours	-2.62	2.03	-0.002	0.007	0.041 **	0.015	0.063 **	0.020
Sampling focus (animals)	-24.6 **	9.32	0	-	0	-	0.239 *	0.106
Sampling focus (plants)	-11.2 **	3.89	0	-	0	-	0.103 *	0.049
Animal group (birds)	5.05	3.73	0	-	-0.057	0.036	-0.073	0.047
Animal group (mammals)	40.0 **	12.3	0	-	-0.197 *	0.076	-0.439 **	0.138

*, p < 0.05; **, p < 0.01; ***, p < 0.001.

Table 2. Estimates and standard errors of linear mixed effects models for species-level metrics (normalized degree, effective partners, between-module connector value [*c*-value], and complementary specialization [*d'*]) of animal species in seed-dispersal networks of the Afrotropics and Neotropics. Analyses are based on 411 animal species from 48 networks in the Neotropics and 254 animal species from 17 networks in the Afrotropics. Shown are estimates derived by model averaging over the subset of best models with ΔAICc < 2; estimates of 0 indicate that the respective predictor was not included in the subset of best models. Fixed effects were the degree of frugivory (i.e., the proportion of fruit in the diet), body mass (g) [log-transformed], and biogeographic region (Afrotropics vs. Neotropics). Random effects were animal taxonomy (class, order, family, and genus) and network identity. Estimates are comparable within each model because degree of frugivory and body mass were z-transformed.

	Normalized degree		Effective partners		*c*-value		Specialization *d'*	
	No. of best models = 2		No. of best models = 2		No. of best models = 2		No. of best models = 3	
	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error
Afro- vs Neotropics	-0.085 **	0.031	-0.028	0.050	-0.046	0.034	0.068 *	0.033
Degree of frugivory	0.060 ***	0.011	0.062 *	0.025	0.065 ***	0.015	-0.017	0.013
log (Body mass)	0.003	0.006	0.045 ***	0.013	0.005	0.009	0.003	0.008
Frugivory x Afro-Neo	-0.051 ***	0.012	-0.029	0.028	-0.048 **	0.017	0.033 *	0.015
Body mass x Afro-Neo	0	-	0	-	0	-	0.003	0.010

*, p < 0.05; **, p < 0.01; ***, p < 0.001.

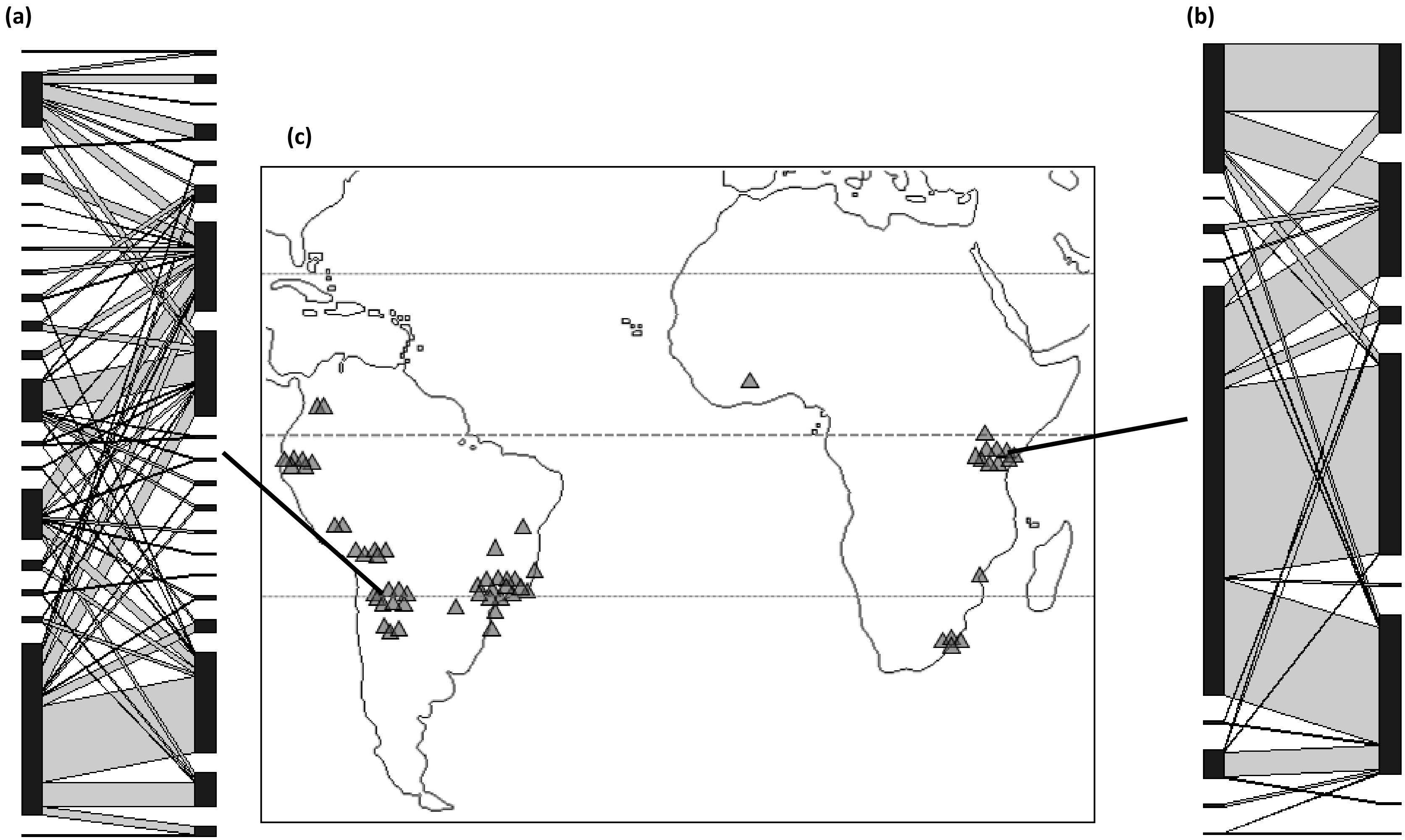

Figure 1. Bipartite graphs of example networks from the (a) Neotropics and (b) Afrotropics. Black boxes denote plant species (left) and animal frugivores (right). Widths of boxes (black) and connecting lines (grey) denote the relative number of observed interactions. Bold lines indicate the approximate location of the corresponding study site for each network. The Neotropical network has been collected in Argentina (Network ID = w37), the Afrotropical network in Tanzania (Network ID = w59). (c) Spatial distribution of seed dispersal networks in the Neotropics and Afrotropics. Data were from 48 Neotropical networks and 17 Afrotropical networks. Dashed lines indicate the equator and the northern and southern limits of the tropics at 23.4°.

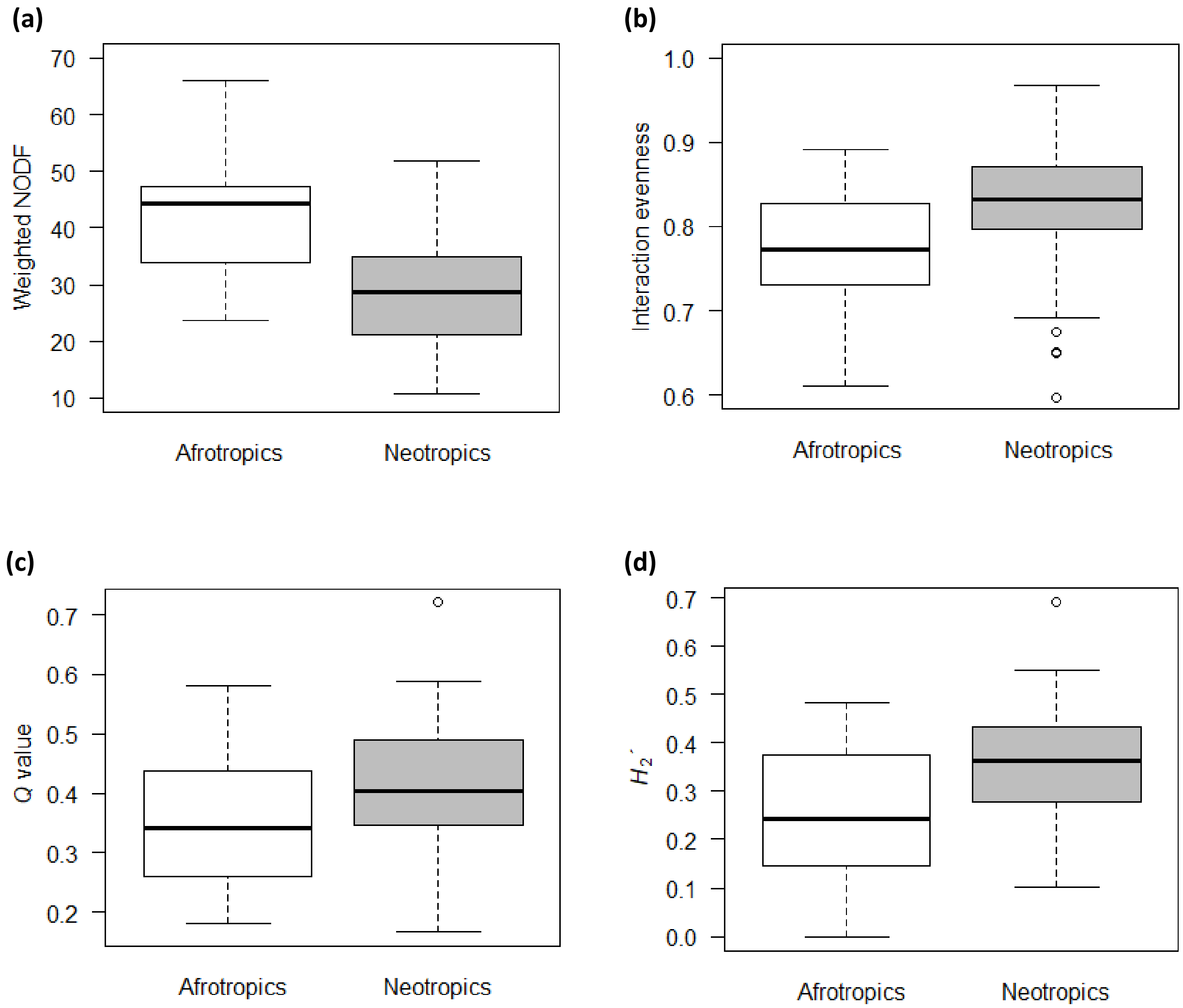

Figure 2. Differences in network-level metrics between Afrotropics and Neotropics, including (a) weighted nestedness (wNODF), (b) interaction evenness, (c) modularity (*Q* value), and (d) complementary specialization (H_2'). Here 17 seed-dispersal networks from the Afrotropics were compared to 48 networks from the Neotropics. Shown are partial residuals plus model intercepts from the respective linear model (see Table 1 for statistical differences). Lines across boxes are medians, boxes denote 25th and 75th percentiles, whiskers indicate the data range, and circles denote outliers.

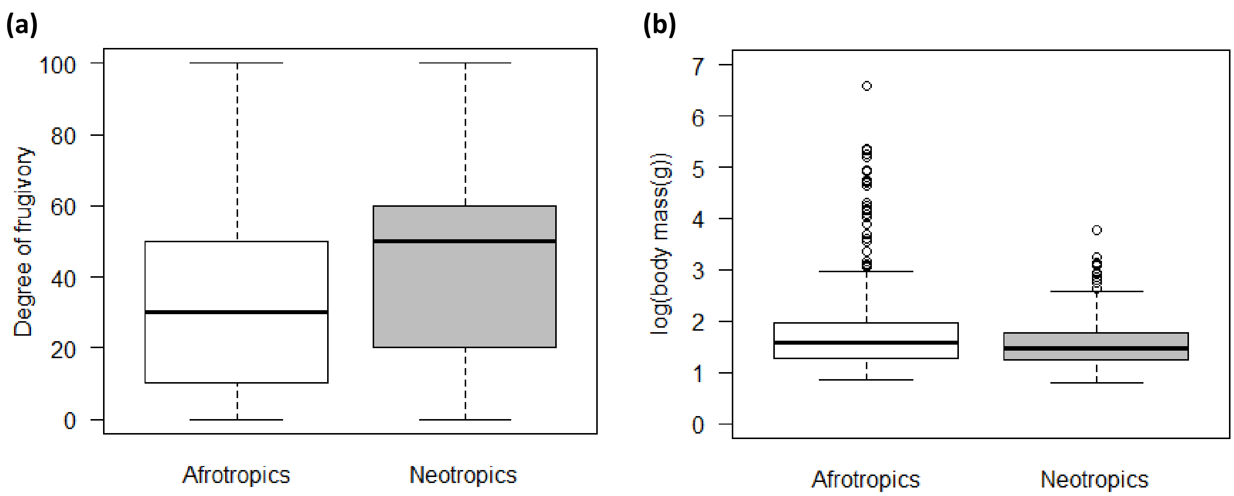

Figure 3. Differences in animal species traits between Afrotropics and Neotropics. Shown are differences in the (a) degree of frugivory (i.e., the proportion of fruit in diet, recorded in 10% steps) and (b) body mass (log-transformed) between biogeographic regions. Analyses are based on 17 seed-dispersal networks from the Afrotropics and 48 networks from the Neotropics. Afrotropical networks included a total of 254 animal species from 197 genera in 31 families, Neotropical networks included a total of 411 animal species from 142 genera in 44 families. Estimates (±SE) from linear-mixed effects models accounting for taxonomic differences among animal species (taxonomic levels: class, order, family, and genus): degree of frugivory, 13.10 (±2.69); body mass, 0.005 (±0.022).

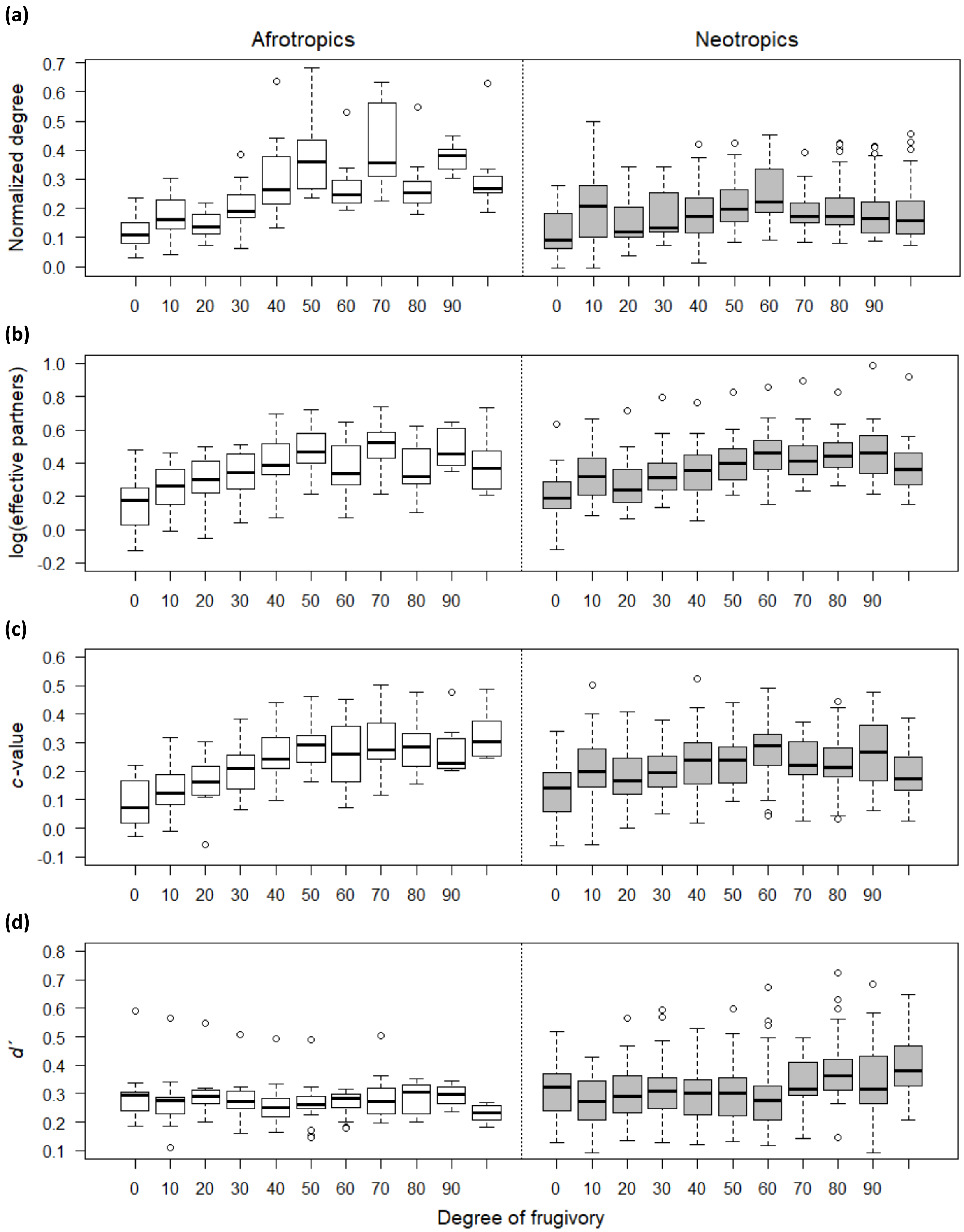

Figure 4. Relationships between species-level metrics and the degree of frugivory in Afrotropics and Neotropics. Shown are the predicted values according to model estimates from the respective linear mixed-effects models for (a) normalized degree, (b) effective partners (log-transformed), (c) *c*-value, and (d) *d´* (see Table 2 for details). Box plots denote variation among networks in the Afrotropics and Neotropics, i.e., for visualization the fitted values of the species-level metrics were averaged for each level of frugivory within each network.

Supporting Information

Table S1. Scoring scheme of disturbance and invasion levels for the 65 networks. Four disturbance drivers (anthropogenic edge, fragmentation, degradation, defaunation) were assessed on an ordinal scale from 1 to 4. Mean disturbance was calculated as the mean score of these four disturbance drivers. Invasion was assessed similarly accounting for invasion by either plants or animals and was treated as a separate predictor variable in statistical analyses.

Anthropogenic edge	**Fragmentation**
1: >1,000 m from habitat border	1: habitat size >10,000 ha
2: <1,000 m from habitat border	2: habitat size 1,000-10,000 ha
3: <100 m from habitat border	3: habitat size 100-1,000 ha
4: <10 m from habitat border	4: habitat size <100 ha
Degradation	**Defaunation**
1: no logging, exploitation etc. during last 50 yrs	1: no spp. locally extinct during last 50 yrs
2: <10% of habitat impacted or converted	2: only a few spp. locally extinct
3: >10% of habitat impacted or converted	3: >10% of spp. locally extinct
4: >50% of habitat impacted or converted	4: >25% of spp. locally extinct
Invasion	
1: only native spp.	
2: only a few alien spp.	
3: >10% of interactions by aliens	
4: >25% of interactions by aliens	

Table S2. Linear model estimates and standard errors for null-model corrected network-level metrics, including weighted NODF, interaction evenness, modularity (*Q* values) and complementary specialization (H_2'). For this analysis, 48 seed-dispersal interaction networks from the Neotropics were compared to 17 networks from the Afrotropics. Shown are estimates derived from model averaging over the subset of best models with ΔAICc < 2; estimates of 0 indicate that the respective predictor was not included in the subset of best models. Sampling focus was tested as a factorial predictor at three levels: "animals only," "plants only," and "both animals and plants". Animal group was tested as a factorial predictor at three levels: "birds," "mammals," and "both birds and mammals". Continuous predictors (absolute latitude, altitude, disturbance, invasion, species richness [log-transformed], and sampling hours [log-transformed]) were z-transformed.

	Δ weighted NODF		Δ interaction evenness		Δ modularity *Q*		Δ specialization H_2'	
	No. of best models = 7		No. of best models = 1		No. of best models = 2		No. of best models = 2	
	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error
Afro- vs Neotropics	**4.43**	**3.03**	**-0.002**	**0.008**	**0.027**	**0.029**	**0.086**	**0.052**
Absolute latitude	1.01	1.38	0	-	-0.004	0.010	0	-
Altitude	-0.104	0.493	-0.002	0.004	0	-	0	-
Disturbance	0	-	-0.003	0.004	0	-	00	-
Invasion	-0.167	0.652	0	-	0	-	0.005	0.013
log Species richness	0.515	1.08	0	-	-0.028*	0.013	-0.065 **	0.022
log Sampling hours	-2.93*	1.30	-0.006	0.004	0.047***	0.014	0.061 **	0.020
Sampling focus (animals)	0	-	0	-	-0.107*	0.048	0.271 *	0.112
Sampling focus (plants)	0	-	0	-	0.018	0.032	0.119 *	0.047
Animal group (birds)	0	-	0	-	0	-	-0.070	0.045
Animal group (mammals)	0	-	0	-	0	-	-0.447 **	0.146

*, p < 0.05; **, p < 0.01; ***, p < 0.001.

Table S3. Linear model estimates and standard errors for binary NODF and weighted nestedness. For this analysis, 48 seed-dispersal interaction networks from the Neotropics were compared to 17 networks from the Afrotropics. Shown are estimates derived from model averaging over the subset of best models with ΔAICc < 2; estimates of 0 indicate that the respective predictor was not included in the subset of best models. Sampling focus was tested as a factorial predictor at three levels: "animals only," "plants only," and "both animals and plants". Animal group was tested as a factorial predictor at three levels: "birds," "mammals," and "both birds and mammals". Continuous predictors (absolute latitude, altitude, disturbance, invasion, species richness [log-transformed], and sampling hours [log-transformed]) were z-transformed.

	Binary NODF		Weighted nestedness	
	No. of best models = 5		No. of best models = 4	
	Estimate	Std. error	Estimate	Std. error
Afro- vs Neotropics	**-19.7*****	**5.19**	**-0.076^{+}**	**0.054**
Absolute latitude	0.411	1.35	0	-
Altitude	-0.241	0.902	0	-
Disturbance	0	-	-0.006	0.013
Invasion	-0.403	1.16	0	-
log Species richness	-0.268	1.06	0	-
log Sampling hours	-5.17**	1.89	-0.010	0.016
Sampling focus (animals)	-32.9**	10.8	-0.150*	0.068
Sampling focus (plants)	-11.1*	4.97	-0.154***	0.044
Animal group (birds)	7.97	4.76	0	-
Animal group (mammals)	58.1***	13.1	0	-

$^{+}$, p < 0.1; *, p < 0.05; **, p < 0.01; ***, p < 0.001.

Table S4. Network-level metrics and metadata for 48 Neotropical and 17 Afrotropical networks used in the analysis. For each network, we provide a unique identifier (Network ID) and the biogeographic region and country plus the following network metrics: weighted NODF (wNODF), interaction evenness (EVE), modularity (*Q*), and complementary specialization (H_2'). We also provide the following metadata: latitude (Lat), longitude (Lon), altitude (Alt), mean disturbance (mDist), invasion (Inv), animal group (Anim Grp), total sampling hours (Sam Hr), sampling focus (Sam Foc), and total species richness (Sp Rich).

Network ID	Region	Country	wNODF	EVE	*Q*	*H2'*	Lat	Lon	Alt	mDist	Inv	Anim Grp	Sam Hr	Sam Foc	Sp Rich
w1	Neo	Peru	23.8	0.733	0.190	0.294	-13.1	-71.6	1500	1.25	1	birds	960	plant	113
w2	Neo	Peru	24.6	0.853	0.374	0.336	-13.2	-71.6	3000	1.5	1	birds	720	plant	77
w3	Neo	Bolivia	10.5	0.880	0.498	0.538	-16.3	-67.5	2100	2.5	2	birds	768	plant	53
w4	Neo	Bolivia	11.0	0.823	0.575	0.733	-16.3	-67.5	2100	2	2	birds	768	plant	24
w5	Neo	Bolivia	11.5	0.870	0.553	0.578	-16.4	-67.6	2000	2.5	2	birds	768	plant	54
w6	Neo	Bolivia	11.4	0.806	0.571	0.701	-16.4	-67.6	2000	2	2	birds	768	plant	30
w7	Neo	Ecuador	29.6	0.844	0.243	0.224	-4.10	-79.0	1000	1	1	birds	300	plant	77
w8	Neo	Ecuador	22.5	0.818	0.344	0.398	-4.00	-79.1	2000	1.25	1	birds	300	plant	59
w9	Neo	Ecuador	11.6	0.912	0.486	0.455	-4.10	-79.2	3000	1.25	1	birds	300	plant	33
w10	Neo	Ecuador	43.4	0.830	0.224	0.210	-4.08	-79.0	1000	3	2	birds	300	plant	98
w11	Neo	Ecuador	23.7	0.744	0.321	0.450	-4.00	-79.1	2000	3	2	birds	300	plant	61
w12	Neo	Ecuador	4.72	0.954	0.676	0.548	-4.10	-79.2	3000	3	2	birds	300	plant	39
w13	Neo	Colombia	20.0	0.877	0.415	0.424	4.74	-75.4	1800	1.25	1	both	600	plant	75
w14	Neo	Colombia	12.2	0.849	0.538	0.554	4.72	-75.6	2400	1.25	1	both	600	plant	71
w15	Neo	Brazil	20.7	0.675	0.410	0.404	-23.5	-45.1	220	3.75	2	birds	304	plant	44
w16	Neo	Brazil	28.2	0.867	0.376	0.342	-16.0	-48.0	1086	2	1	birds	569	plant	85
w17	Neo	Brazil	20.9	0.941	0.340	0.304	-22.6	-42.3	85	3.5	1	birds	150	plant	58
w18	Neo	Brazil	25.4	0.812	0.470	0.451	-19.8	-40.0	50	3	1	birds	527	plant	63
w19	Neo	Brazil	18.7	0.888	0.416	0.386	-23.5	-46.7	750	3.5	1	birds	64	plant	48
w20	Neo	Brazil	29.5	0.830	0.412	0.389	-28.5	-47.6	700	4	1	birds	242	plant	40
w21	Neo	Brazil	16.5	0.924	0.394	0.359	-22.8	-47.1	660	3	1	both	360	plant	64
w22	Neo	Brazil	21.0	0.941	0.368	0.231	-20.8	-42.9	650	2.5	1	birds	250	plant	54
w23	Neo	Brazil	3.91	0.993	0.300	0.066	-24.3	-48.4	900	1	1	birds	350	plant	267
w24	Neo	Brazil	22.2	0.841	0.389	0.341	-25.1	-47.9	150	1.25	1	birds	175	plant	65
w25	Neo	Brazil	35.3	0.823	0.317	0.233	-22.6	-46.4	800	3.75	2	birds	308	both	75

Table S4, continued.

Network ID	Region	Country	wNODF	EVE	*Q*	*H2'*	Lat	Lon	Alt	mDist	Inv	Anim Grp	Sam Hr	Sam Foc	Sp Rich
w26	Neo	Brazil	31.9	0.901	0.351	0.345	-22.4	-47.4	650	4	2	birds	60	plant	35
w27	Neo	Brazil	12.9	0.876	0.386	0.396	-22.2	-47.3	640	4	3	both	172	animal	73
w28	Neo	Brazil	9.93	0.854	0.519	0.481	-22.5	-47.2	550	4	2	both	702	both	37
w29	Neo	Brazil	17.1	0.875	0.414	0.401	-22.3	-47.3	610	4	2	both	766	both	71
w30	Neo	Brazil	16.8	0.870	0.587	0.569	-22.4	-47.1	570	4	2	both	685	both	51
w31	Neo	Argentina	33.8	0.791	0.279	0.316	-27.2	-65.6	455	1.5	2	birds	80	both	31
w32	Neo	Argentina	40.8	0.857	0.225	0.161	-27.3	-65.9	1120	1.25	2	birds	80	both	39
w33	Neo	Argentina	55.3	0.727	0.109	0.112	-27.0	-65.8	1584	1.25	1	birds	80	both	22
w34	Neo	Argentina	35.6	0.825	0.297	0.271	-24.7	-64.7	1020	1	1	birds	80	both	43
w35	Neo	Argentina	58.3	0.854	0.239	0.172	-24.8	-64.7	1309	1	1	birds	80	both	26
w36	Neo	Argentina	49.8	0.851	0.221	0.162	-24.1	-64.4	1870	1.75	1	birds	80	both	33
w37	Neo	Argentina	27.2	0.821	0.404	0.365	-23.7	-64.9	1099	1	1	birds	80	both	40
w38	Neo	Argentina	34.9	0.843	0.345	0.313	-23.0	-64.1	1480	1	1	birds	80	both	35
w39	Neo	Argentina	37.0	0.885	0.231	0.221	-22.3	-64.7	1635	1.5	1	birds	80	both	30
w40	Neo	Argentina	48.4	0.511	0.097	0.234	-26.8	-65.3	600	2.25	4	birds	200	plant	18
w41	Neo	Argentina	29.1	0.749	0.398	0.360	-26.8	-65.3	1100	1.5	1	both	703	both	65
w42	Neo	Argentina	29.7	0.830	0.422	0.341	-26.8	-65.3	850	1.75	2	both	211	both	47
w43	Neo	Argentina	40.4	0.569	0.105	0.209	-25.5	-65.0	900	2.25	2	mamm	91	animal	12
w44	Neo	Argentina	55.9	0.793	0.229	0.166	-24.0	-65.1	1100	1	2	mamm	262	animal	21
w45	Neo	Argentina	48.6	0.726	0.268	0.431	-25.7	-54.5	200	1.25	2	mamm	232	animal	19
w46	Neo	Brazil	20.2	0.838	0.222	0.210	-22.8	-43.7	30	4	3	birds	103	plant	42
w47	Neo	Brazil	19.5	0.568	0.471	0.826	-13.0	-41.3	950	2.25	1	birds	193	plant	19
w48	Neo	Brazil	19.4	0.897	0.400	0.396	-24.2	-48.0	500	1.75	2	birds	34120	plant	91
w49	Afro	Kenya	21.4	0.840	0.355	0.298	0.40	34.9	1600	1.75	2	both	924	plant	121
w50	Afro	Tanzania	17.5	0.888	0.549	0.506	-3.31	37.7	800	1.5	2	both	125	plant	64
w51	Afro	Tanzania	16.0	0.730	0.200	0.524	-3.31	37.2	800	3.5	4	both	125	plant	26
w52	Afro	Tanzania	35.3	0.852	0.407	0.362	-3.17	37.2	1600	1.5	2	both	125	plant	59
w53	Afro	Tanzania	21.9	0.870	0.534	0.502	-3.34	37.5	1600	3.5	4	both	125	plant	35

Table S4, continued.

Network ID	Region	Country	wNODF	EVE	*Q*	*H2'*	Lat	Lon	Alt	mDist	Inv	Anim Grp	Sam Hr	Sam Foc	Sp Rich
w54	Afro	Tanzania	36.2	0.623	0.370	0.468	-3.25	37.3	1600	3	4	both	125	plant	29
w55	Afro	Tanzania	57.4	0.723	0.171	0.172	-3.18	37.2	1600	3.5	3	both	125	plant	21
w56	Afro	Tanzania	46.2	0.763	0.361	0.281	-3.14	37.2	2400	1.25	2	both	125	plant	40
w57	Afro	Tanzania	58.4	0.668	0.314	0.271	-3.19	37.5	2400	1.75	2	both	125	plant	23
w58	Afro	Tanzania	38.4	0.571	0.156	0.272	-3.10	37.3	3000	1.25	1	both	125	plant	30
w59	Afro	Tanzania	39.5	0.647	0.236	0.359	-3.16	37.4	3000	1.75	1	both	125	plant	17
w60	Afro	Mozambique	9.45	0.832	0.431	0.432	-20.0	34.4	30	1.25	2	both	140	animal	130
w61	Afro	South Africa	27.7	0.668	0.409	0.506	-30.7	30.3	500	2	2	birds	288	plant	42
w62	Afro	South Africa	20.9	0.845	0.402	0.381	-30.7	30.3	500	2	4	birds	486	plant	43
w63	Afro	South Africa	31.4	0.827	0.318	0.299	-30.3	30.6	500	2	1	birds	1854	plant	84
w64	Afro	South Africa	41.3	0.834	0.307	0.241	-29.0	31.8	15	3.5	1	birds	482	plant	25
w65	Afro	Ivory Coast	51.2	0.723	0.244	0.206	9.00	-3.60	275	3.5	2	both	425	plant	75

Table S5. Supplementary network-level metrics for 48 Neotropical and 17 Afrotropical networks used in the analysis. For each network, we provide a unique identifier (Network ID) and the biogeographic region and country plus the following network metrics: null-corrected weighted NODF (Δ wNODF), interaction evenness (Δ EVE), modularity (Δ *Q*), and complementary specialization (Δ H_2'); binary NODF (bNODF), and weighted nestedness (wNest).

Network ID	Region	Country	ΔwNODF	ΔEVE	ΔQ	ΔH2'	bNODF	wNest
w1	Neo	Peru	-26.5	-0.005	0.138	0.284	37.6	0.568
w2	Neo	Peru	-23.8	-0.031	0.268	0.325	36.6	0.553
w3	Neo	Bolivia	-18.8	-0.039	0.282	0.488	19.8	0.404
w4	Neo	Bolivia	-31.2	-0.067	0.379	0.683	19.4	0.586
w5	Neo	Bolivia	-21.6	-0.055	0.369	0.509	24.0	0.546
w6	Neo	Bolivia	-25.6	-0.083	0.372	0.556	18.6	0.430
w7	Neo	Ecuador	-23.9	0.012	0.145	0.074	42.6	0.598
w8	Neo	Ecuador	-23.8	-0.016	0.226	0.263	27.3	0.556
w9	Neo	Ecuador	-8.42	-0.020	0.175	0.314	19.2	0.420
w10	Neo	Ecuador	-10.6	0.006	0.139	0.156	58.2	0.765
w11	Neo	Ecuador	-23.0	-0.036	0.212	0.370	34.6	0.642
w12	Neo	Ecuador	-1.07	-0.032	0.280	0.373	15.1	0.231
w13	Neo	Colombia	-15.1	-0.025	0.239	0.374	33.2	0.589
w14	Neo	Colombia	-21.7	-0.064	0.360	0.470	22.3	0.423
w15	Neo	Brazil	-17.2	-0.128	0.285	0.245	52.3	0.289
w16	Neo	Brazil	-30.3	-0.024	0.313	0.213	44.4	0.425
w17	Neo	Brazil	-10.1	-0.017	0.158	0.178	45.3	0.195
w18	Neo	Brazil	-32.6	-0.037	0.403	0.335	42.7	0.609
w19	Neo	Brazil	-15.0	-0.018	0.223	0.325	35.1	0.473
w20	Neo	Brazil	-27.4	-0.041	0.315	0.337	51.1	0.437
w21	Neo	Brazil	-11.2	-0.029	0.192	0.240	35.5	0.515
w22	Neo	Brazil	-1.19	-0.001	0.078	0.214	39.1	0.689
w23	Neo	Brazil	-0.06	0.003	-0.017	0.039	20.8	0.558
w24	Neo	Brazil	-7.39	-0.025	0.224	0.311	43.0	0.673
w25	Neo	Brazil	-10.8	-0.002	0.215	0.216	56.2	0.801
w26	Neo	Brazil	-10.8	0.010	0.178	0.313	55.8	0.769
w27	Neo	Brazil	-6.32	-0.031	0.096	0.369	21.9	0.462
w28	Neo	Brazil	-11.4	-0.053	0.222	0.411	20.9	0.591
w29	Neo	Brazil	-15.0	-0.037	0.243	0.373	31.1	0.524
w30	Neo	Brazil	-19.9	-0.071	0.384	0.439	29.8	0.611
w31	Neo	Argentina	-17.8	-0.013	0.162	0.281	44.0	0.718
w32	Neo	Argentina	-11.7	-0.009	0.103	0.024	60.3	0.708
w33	Neo	Argentina	-6.44	0.020	0.040	0.058	72.1	0.837
w34	Neo	Argentina	-6.98	-0.021	0.151	0.132	51.2	0.751
w35	Neo	Argentina	-6.07	-0.025	0.135	0.019	75.7	0.688

Table S5, continued.

Network ID	Region	Country	ΔwNODF	ΔEVE	ΔQ	ΔH2'	bNODF	wNest
w36	Neo	Argentina	-0.94	-0.011	0.094	0.069	71.3	0.756
w37	Neo	Argentina	-15.5	-0.017	0.264	0.269	40.5	0.689
w38	Neo	Argentina	-14.8	-0.034	0.208	0.247	57.5	0.637
w39	Neo	Argentina	-11.7	0.009	0.097	0.073	61.8	0.650
w40	Neo	Argentina	-19.4	-0.007	0.074	0.071	62.5	0.755
w41	Neo	Argentina	-26.2	-0.031	0.235	0.195	37.9	0.739
w42	Neo	Argentina	-21.0	-0.040	0.302	0.215	44.9	0.625
w43	Neo	Argentina	-15.5	-0.058	0.035	0.080	60.3	0.467
w44	Neo	Argentina	-2.18	-0.020	0.147	0.094	77.5	0.620
w45	Neo	Argentina	-20.9	-0.035	0.223	0.359	73.1	0.673
w46	Neo	Brazil	-13.1	0.001	0.032	0.161	43.1	0.616
w47	Neo	Brazil	-41.1	-0.126	0.415	0.730	33.1	0.337
w48	Neo	Brazil	-20.9	-0.032	0.265	0.347	33.7	0.477
w49	Afro	Kenya	-21.4	-0.032	0.242	0.214	34.6	0.482
w50	Afro	Tanzania	-18.4	-0.050	0.392	0.410	33.7	0.502
w51	Afro	Tanzania	-36.4	0.042	0.142	0.430	22.5	0.673
w52	Afro	Tanzania	-21.9	-0.035	0.303	0.269	50.7	0.647
w53	Afro	Tanzania	-18.3	-0.054	0.364	0.481	50.9	0.449
w54	Afro	Tanzania	-34.4	-0.049	0.334	0.425	48.9	0.428
w55	Afro	Tanzania	-8.10	-0.010	0.115	0.097	74.9	0.827
w56	Afro	Tanzania	-18.8	-0.021	0.298	0.211	67.8	0.749
w57	Afro	Tanzania	-15.7	-0.012	0.274	0.226	72.7	0.807
w58	Afro	Tanzania	-28.9	-0.018	0.124	0.241	58.7	0.552
w59	Afro	Tanzania	-27.9	-0.031	0.197	0.220	63.4	0.573
w60	Afro	Mozambique	-11.5	-0.057	-0.014	0.385	21.3	0.546
w61	Afro	South Africa	-31.5	-0.059	0.338	0.425	44.5	0.668
w62	Afro	South Africa	-24.1	-0.043	0.266	0.361	38.0	0.416
w63	Afro	South Africa	-32.1	-0.010	0.282	0.181	47.7	0.589
w64	Afro	South Africa	12.9	-0.025	0.267	0.219	80.7	0.559
w65	Afro	Ivory Coast	-21.6	0.015	0.219	0.099	69.7	0.829