Effects of precipitation extremes on nestedness and modularity of tropical seed dispersal networks

Hernani de Oliveira[1], Bernal Rodriguez-Herrera[2], Maria Kuzmina[3], Stephen Rossiter[4], and Elizabeth Clare[1]

[1]Queen Mary University of London
[2]Affiliation not available
[3]University of Guelph Biodiversity Institute of Ontario
[4]Queen Mary, University of London

October 20, 2020

Abstract

El Niño is a major driver of fluctuations in tropical precipitation and fruiting production, with cascading effects on frugivores. As places get wetter, mutualistic networks tend to become more modular and less nested. In order to test the impact of severe floods and droughts caused by the El Niño cycle of 2015-2016 on nestedness and modularity of mutualistic networks, we determined the links between frugivorous bats and the plants in their diets by DNA barcoding bat faeces and used null models for our network comparisons. Despite the contrasting effects of droughts and floods in the dry forest and rainforest, respectively, we observed similar changes in network structure for both forests. We found higher values of modularity, but lower of nestedness for most networks comparisons. Over all we found higher nestedness in the dry forest than the rainforest and minimal difference between wet and dry season in the dry forest. A lower nestedness might reduce the number of species supported by the habitat as well as increase species competition. Although the increase in modularity might reduce the number of coexisting species in the environment, higher network compartmentalization leads to greater stability, slower spread of disturbance and smaller chances of having trophic cascades. Therefore, changes in network structure promoted by El Niño are likely to have dual effects on networks with some effects leading to greater stability while others to increasing competition.

Introduction

El Niño is one of the main drivers of precipitation fluctuations globally and is responsible for increasing seasonality in the tropics (Wright, Carrasco, Calderon, & Paton, 1999; Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Malhi & Wright, 2004). Such responses, however, differ widely among regions (Holmgren et al. 2001); for example, in parts of Central America, El Niño causes floods in the rainforests of the Caribbean coast, but droughts in the Pacific dry forests (Waylen, Caviedes, Poveda, Mesa, & Quesada, 1998). These contrasting effects are critically important as rainfall is a principal factor influencing plant phenology and thus primary productivity. The frequency of strong El Niño/Southern Oscillation (ENSO events) is also expected to increase with climate change (Cai et al. 2014). Indeed, the cycle of 2015-2016 is one of the strongest on record (Jacox et al. 2016). Although responses can be complex (Gunarathne & Perera, 2014; Butt et al. 2015), changes in weather due to El Niño, including both droughts and floods, have been directly linked to fluctuations in fruit production (Wright et al. 1999) with cascading effects for wild animal and plant populations (Wright et al. 1999; Harrison, 2000; Butt et al. 2015). Such impacts of El Niño might be especially important in the humid tropics, where nectarivorous and frugivorous vertebrates perform much of the pollination and seed dispersal; however, these consequences have been little-studied and remain poorly understood (Wright et al. 1999; Fredriksson & Wich, 2006; Wolfe, Ralph, & Elizondo, 2015).

The construction of ecological networks is a useful analytical approach for studying interactions among taxa across ecosystems (Ings et al. 2009). Studies of diverse taxa have suggested that mututalistic networks, those containing plants and frugivorous or nectarivorous animals, commonly show similar properties. In particular, mutualistic networks appear to be highly nested, where interactions involving specialist taxa represent a subset of those involving generalists, and also highly modular, with multiple weakly linked clusters of densely connected taxa (Bascompte, Jordano, Melián, & Olesen, 2003; Olesen, Bascompte, Dupont, & Jordano, 2007; Fortuna et al. 2010; Donatti et al. 2011; Krasnov et al. 2012). Such nestedness and modularlity both increase network stability, and resilience (robustness) to the loss of species from ecosystems, while minimizing perturbations (Memmott, Waser, & Price, 2004; Fortuna et al. 2010; Thébault & Fontaine, 2010). Nestedness is also thought to reduce interspecific competition, thereby allowing more species to coexist (Bastolla et al. 2009).

Here we focus on mutualistic interactions between frugivorous bats and plants in Costa Rica as a model system to assess the impact of ENSO events in different habitats. Bats number over 1,300 species worldwide, of which ~20% feed on nectar or fruit (Kunz, Braun de Torrez, Bauer, Lobova, & Fleming, 2011; Rojas, Vale, Ferrero, & Navarro, 2012; Fenton & Simmons, 2015). In the neotropics, phyllostomid bats are widespread and critically important pollinators and seed dispersers, and, together with frugivorous birds, account for over 80% of the seed dispersal activity (Galindo-González, Guevara, & Sosa, 2000). Previous work suggests bat-plant mutualistic networks in the neotropics are highly connected, nested and robust to plant extinctions, but with low modularity (Mello et al. 2011). Such network structures imply considerable behavioral flexibility that might confer resilience to changes in the environment, yet it is not known how extreme climatic events may affect the structure and robustness of these networks. During the El Niño event of 2015, rainfall levels during the rainy season in the wet forest of Costa Rica exceeded those of the previous 47 years, whereas the opposite trend was observed in the coastal dry forest, where rainfall levels were lower in the rainy season than those of the previous 31 years. Thus, both types of forest experienced extreme climatic conditions associated with El Niño (Seneviratne et al. 2012).

To determine how opposite extremes in rainfall (unusually wet and dry conditions) induced by El Niño influence mutualistic interactions among plants and frugivorous bats, we analyzed and compared networks of mutualistic interactions across the wet and dry seasons in both wet forest and dry forest in Costa Rica. We contrast this to the network of interactions during the wet season of the dry forest during a normal year. Because building networks is extremely labour-intinsive (Evans, Kitson, Lunt, Straw, & Pocock, 2016), which limites replication, null models are common in network ecology and have became one of the main statistical methods to assess the significance of observed network metrics (Delmas et al. 2019). We used null models to estimate the magnitude of the change of the observed network metrics in relation to randomized matrices.

A major challenge of constructing mutualistic networks is characterizing the links between plants and animals (Clare, 2014). Many vertebrate frugivores may feed on fruit pulp, egesting no identifiable material (e.g. seeds) for morphological examination. For these reasons, DNA barcoding, which can be applied to traces of DNA, has proven to be a powerful means of inferring ecological interactions (Clare, 2014; Evans et al. 2016; Roslin & Majaneva, 2016). Such molecular approaches have resolved previously unknown links in already well-studied food webs, revealing metrics such as connectance and nestedness to differ by orders of magnitude from earlier estimates derived from traditional approaches (Wirta et al. 2014). On the other hand, most studies using molecular tools to analyze animal diets have focused on predation (Jedlicka, Sharma, & Almeida, 2013; Brown et al. 2014; Clare et al. 2014; Kruger, Clare, Symondson, Keiss, & Petersons, 2014; Chanin et al. 2015) with fewer studies using DNA barcoding to understand plant-mammal mutualisms, though this is rapidly changing (Bradley et al. 2007; Quémére et al. 2013; Kartzinel et al. 2015; Galimberti et al. 2016; Clare et al. 2019).

Using a molecular approach, we measure the impact of seasonality and ENSO on mutualistic interactions of neotropical bats and plants. Earlier work indicates network structure is strongly influenced by precipitation (Trøjelsgaard & Olesen, 2013), including historical climate change (Dalsgaard et al. 2013). In general, higher

rainfall and seasonality are correlated with more modular networks (Dalsgaard et al. 2013; Trøjelsgaard & Olesen, 2013; Schleuning et al. 2014), and lower rainfall with greater nestedness (Rico-Gray, Díaz-Castelazo, Ramírez-Hernández, Guimarães, & Holland, 2012), consequences that are likely to result from changes in resource availability. We therefore hypothesize that networks will show higher modularity and lower nestedness in the wet forest than in the dry forest in comparison with the expected differences estimated from the null models. Similarly, within each forest type, we predicted that wetter seasons than normal would have higher modularity and lower nestedness than what would be expected from the null models while drier seasons than usual would have higher nestedness and lower modularity than null models. Additionally, we looked for changes in other network metrics to evaluate the magnitude of the changes in the structure of species interactions in relation with the null models and added comparisons for all network metrics of the wet season in the rainforest during the El Niño year with data from a normal wet season at the same site.

Materials and Methods

Study sites

Fieldwork was conducted at two forest sites in Costa Rica that show contrasting seasonality and precipitation: the Atlantic rainforest of La Selva Biological Station (10°25'19" N, 84deg00'54" W) and the Pacific dry forest at Sector Santa Rosa of Area de Conservacion Guanacaste (ACG) (10deg48'53" N, 85@36'54" W) in Costa Rica (Figure 1). La Selva Biological Station covers 1,611 ha of lowland wet tropical forest between 35 to 137 m on the Caribbean slope of the Cordillera Central mountain range. It has a mean annual temperature of 25@ C with a mean annual precipitation of 3,962 mm (Sigel, Sherry, & Young, 2006). Sector Santa Rosa (of ACG) covers >38,000 ha of tropical dry forest ranging from 0 m to 300 m, and is part of Área de Conservación Guanacaste (Asensio, Schaffner, & Aureli, 2015). Sector Santa Rosa (of ACG) has a mean annual temperature of 25@ C with a mean annual precipitation of 1,575 mm. Seasonality is more pronounced in the former site (range 2,809-6,164 mm) than the latter (range 880-3,030 mm, six-month dry season) (Gillespie, Grijalva, & Farris, 2009).

Bat sampling

We captured bats using four to six mist nets (6m – 12m) opened along trails and near watercourses in the study area from 18h – 22h. In addition, a canopy net and harp trap were used in 2009 but these had low capture rates and so were not used in 2015. Sampling took place in the dry season during January-February (Sector Santa Rosa of ACG) and Mar-Apr (La Selva) (2015), in the wet season May-Jul (Santa Rosa of ACG) (2009), and in the wet season July-August (Sector Santa Rosa of ACG) and September-October (La Selva) (2015). Sampling and bat identification during the normal year was conducted as described in Clare et al. (2019). Sampling effort using mist nets was equal to approximately 2,250 m^2.hours within each season during the El Niño year, and approximately the same during the normal year. We collected wing punches for another study and these also served to avoid recaptures. We measured the forearm length with callipers (0.1 mm precision) and identified species following Reid (1997), Timm & Laval (1998) and Laval & Rodriguez-Herrera (2002). Bats were held in cloth bags for a maximum of two hours for the collection of faecal samples. All samples were frozen after collection (-20° C).

DNA extraction, PCR and sequencing

For this study, we focused on nectar and fruit eating species, which produced faecal samples consisting of either seeds or digested fruit pulp. For the DNA extraction, PCR and sequencing of the samples we followed standard protocols for plants and all works was conducted by the Canadian Centre for DNA barcoding (CCDB) following these procedures (Ivanova, Kuzmina, & Fazekas, 2011). In brief, dried plant material from faeces (fruit pulp or seed) was placed in a sterile strip-tube with pre-aliquoted sterile stainless steel beads and the tissue was ground using a Tissue Lyser (Qiagen, USA). The ground material was incubated with 2x CTAB buffer at 65°C for 1 hour and DNA extraction was performed using a semi-automated glass fiber filtration method (Ivanova, Fazekas, & Hebert, 2008; Fazekas et al. 2012). Following established methods, we amplified a 552 bp fragment of the 5' end of the large subunit of RuBisCO (*rbc* L) and the ~350 bp second nuclear encoded internal transcribed spacer (ITS2) flanking by the partial 5.6S and 26S ribosomal genes.

Sanger sequencing was performed using a ABI 3730xl capillary sequencer (Ivanova, DeWaard, Hajibabaei, & Hebert, 2005; Ivanova & Grainger, 2006; Kuzmina & Ivanova, 2011a; Kuzmina & Ivanova, 2011b; Fazekas et al. 2012). Although plant DNA barcoding yields lower species resolution compared to fungi and animals (Hollingsworth, Graham, & Little, 2011), generally it provides robust results for identification of vascular plants at the genus level (Kress et al. 2009; Parmentier et al. 2013; Braukmann, Kuzmina, Sills, Zakharov, & Hebert, 2017). For the samples from the normal year, plant specimens collected on the sites were identified using *rbcL* and *matK* and the supplementary non-coding plastid region *trnH-psbA* (see Clare et al. 2019 for full methods).

Identification of plant DNA sequences from bat faecal samples

We initially filtered all sequences for quality and excluded low quality sequences where the PHRED score was <30 as indexed on the Barcode of Life Data Management System (BOLD) (Ratnasingham & Hebert, 2007). We compared the obtained *rbc* L and ITS2 sequences with the reference libraries of GenBank and BOLD using the BLAST algorithm with default search parameters (Altschul, Gish, Miller, Myers, & Limpman, 1990) and the combined BLAST and Hidden Markov Model methods implemented by the BOLD server (Ratnasingham & Hebert, 2007). For each reference database (BOLD, GenBank), we assigned query sequences to taxon based on highest percentage similarity, and considered a threshold of [?]97% to be a reliable assignment (Lamb, Winsley, Piper, Freidrich, & Siciliano, 2016). When there was an agreement between species-level matches for both markers (*rbc* L and ITS2) in both databases, with at least one match >97%, we assigned to the level of species. In cases where the query matched with equal similarity to multiple taxa of the same genus, we assigned the taxon to the level of the genus only, and similarly we used the same approach to assign query sequences to the level of the family. Where *rbc* L and ITS2 sequences matched different species from different genera, both at >97%, we concluded that two taxa were present in the sample and therefore assigned to both genera. Query sequences that did not show significant similarity to a reference were excluded from the analysis.

To corroborate our species assignments, for each candidate genus match, we reconstructed a gene phylogeny in which we included our query sequences together with all available reference sequences from species of the same genus present in BOLD that are also known to occur in Costa Rica. Sequences from *rbc* L and ITS2 of each plant genus were aligned with ClustalW (Larkin et al. 2007) in BioEdit v7.2.5 (Hall, 1999). For each alignment we ran a model selection test to check which would be the best method to build the phylogenetic tree based on the lowest BIC value. We ran model selection and built the phylogenetic trees using MEGA 6.06 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). These phylogenies (not shown) recovered paraphyletic groupings for some species, perhaps through a lack of reference material, and therefore such species assignments were considered unreliable. To address this issue, we took a conservative approach and reduced all data to genus-level designations and repeated our analyses to check for consistency of results (see Supplementary material).

The identification of plant DNA sequences from bat faecal samples during the normal year relied on GenBank and BOLD, with the exception of the *trn* H-*psb* A region which was not searchable within BOLD (see Clare et al. 2019 for more details) for our purposes we used the assignments as given in Clare et al. (2019).

Network matrices

We compiled the inferred interactions into interaction incidence matrices where each cell value represented the number of observed interactions between each bat-plant taxon pair. We considered one realized interaction when the DNA of a plant taxon was detected in the faeces of one individual bat. We constructed matrices for (1) each forest site in which we pooled data from both seasons during the El Nino year ('La Selva' and 'Santa Rosa'), and (2) for each forest site in which we separated the data collected for dry and wet season during the normal and El Nino ('wet' versus 'dry' for each site). Each matrix constructed for each forest site during each season and the matrices using data pooled for the whole year in each forest site were used to compare between networks and null models.

Descriptors of network structure

To determine network structure and resilience from each habitat during a whole El Nino year, and for each habitat during each season during the El Nino and normal year, we assessed network structure by measuring six key metrics. First, we quantified nestedness, which measures the extent to which the interactions of one species are a sub-set of the interactions of another species when the matrix of interaction is organized by decreasing number of links (Dormann, Frund, Bluthgen, & Gruber, 2009). We calculated nestedness using the weighted NODF approach, which is a measure of nestedness that uses overlap and decreasing fill in the weighted matrix, that has been shown to outperform other methods for estimating nestedness in binary networks (Almeida-Neto & Ulrich, 2011). Second, we quantified modularity, characterized as more interactions within a module than between modules (Dormann & Strauss, 2014), using the QuanBiMo algorithm that is based on simulated annealing and is more specifically designed for weighted bipartite networks (Dormann & Strauss, 2014). Third, we calculated weighted connectance by dividing linkage density by the number of species in the network (Tylianakis, Tscharntke, & Lewis, 2007), which reveals the number of links in the network in relation to the total number of links (Altena, Hemerik, & Ruiter, 2016). Fourth, we measured/calculated number of compartments, which are defined as isolated sub-sets of nodes interacting with each other that do not have any connections with another compartment in the network (Dormann, Frund, Bluthgen, & Gruber, 2009). Fifth, robustness was calculated as the area below the curve of secondary extinction of bats when primary extinction of plant species was simulated according to three methods: random extinction of plant species (random), extinction of most connected to least connected plant species (degree) and extinction from the least connected to most connected plant species (abundance). And finally, niche overlap among bat species was calculated using the Morisita-Horn index (Horn, 1966). Apart from robustness, all metrics chosen have little or no biases to sampling completeness and network size (Frund, McCann, & Williams, 2015). We used the function network level from the Bipartite package (Dormann, Gruber, & Frund, 2008) to determine network structure and resilience from each habitat during the whole year and for each habitat during each season and calculated the following network metrics: weighted NODF, modularity (QuanBiMo), number of compartments, niche overlap, and robustness.

Statistical analysis

To test whether in each case the network metrics deviated from the expected values and if there were differences between habitats and between seasons within each habitat, we used the swap algorithm (Dormann, Frund, Bluthgen, & Gruber, 2009). The swap algorithm initially randomizes the network matrix using the Patefield algorithm (Patefield, 1981), then swaps the interactions while constraining for connectance. Thus, it produces network matrices with the same connectance and marginal totals as the original matrix, but produces networks that are more specialized than other algorithms for randomization as some swaps are more likely than others and increases the values of high-value cells (Artzy-Randrup & Stone, 2005; Dormann, Gruber, & Frund, 2008). We followed Gotelli & Ulrich (2011) and choose swap web to randomize the network matrices because it is a more constrained null model, which are better to avoid type I error. More constrained null models are more parsimonious and conservative in testing the hypothesis when the information comes only from the occurrence matrix (Gotelli & Ulrich, 2012). In order to determine the sampling completeness of our networks and the proportion of the total arthropod species richness present in bat diets that have been sampled, we used the Chao 1 index according to the method proposed by Macgregor, Evans, & Pocock (2017) for the networks, and individual based rarefaction curves for the estimation of each bat species diet.

We generated 1,000 random matrices with the same total marginal sum and connectance as the observed networks, and we used the Monte Carlo procedure ($\alpha= 5\%$) to check if the observed network metric value was higher or lower than expected by chance. To assess whether network structure differed between between seasons within each forest, and also between forest types across the whole year, for each comparison we calculated the difference in the observed metric values, and compared this to a null distribution of 1,000 differences obtained by Monte Carlo procedure. Due to the high calculation intensity of modularity QuanBiMo, we generated only 100 random matrices using the swap algorithm to calculate its significance.

In order to better understand the effects of habitat and seasonality on the composition and interactions of the network during the ENSO event, we used the R package betalink (Poisot, Canard, Mouillot et al. 2012) and

calculated the dissimilarity of interaction matrices between habitats and between seasons within each habitat. The values for network dissimilarities were calculated based on the dissimilarity in the species composition of communities in the networks (β_S), based on the differences in the interactions observed between species common to both networks (β_{OS}), based only on differences in the interactions between both networks (β_{WN}) and based on the dissimilarity of the interaction structure that was induced by the dissimilarity in species composition (β_{ST}) (Poisot et al. 2012). In order to determine the sampling completeness of our networks and the proportion of the total plant species richness present in bat diets that have been sampled, we used the Chao 1 index according to the method proposed by Macgregor et al. (2017) for the networks, and individual based rarefaction curves for the estimation of each bat species diet. All statistical analysis and network drawings were performed using R, version 3.3.2 (R Development Core Team, 2017).

Results

In 130 sampling nights during the El Niño year, we captured 1,041 bats from 42 species, and collected guano samples from 435 frugivorous individuals of 21 species. Analyses of faecal material from these 21 bat species recovered a total of 47 plant taxa, representing a total of 374 observed interactions. Of these 47 taxa, 26 plant taxa were resolved to species, 16 to genus, five to family and one to order (though see also the supplementary material for analysis of genera only). From the normal year dataset (Clare et al. 2019), we captured a total of 801 bats from 26 species over six weeks of sampling, and collected guano samples from 112 frugivorous individuals of 12 species. Analysis of faecal material from these 12 bat species recovered a total of 20 plant taxa, representing a total of 117 observed interactions. Of these 20 taxa, 13 plant taxa were resolved to species, and seven to genus.

Network structure in dry forest and rainforest in relation to null models

Contrary to our predictions (Table 1), when data from seasons were pooled we found that El Niño was associated with similar changes to network structure in relation to the null models for both dry forest and rainforest (Figures 2-3). Compared to their respective null models, networks were more compartmentalized (Rainforest – mean= 1.38; SD= 0.59; p-value< 0.05; Dry forest – mean= 1.14; SD= 0.36; p-value< 0.01), less nested (weighted NODF) (Rainforest – mean= 20.92; SD= 0.08; p-value< 0.01; Dry forest – mean= 22.37; SD= 3.61; p-value= 0.01), less connected (weighted connectance) (Rainforest – mean= 0.12; SD= 0.01; p-value< 0.01; Dry forest – mean= 0.14; SD= 0.01; p-value= 0.01), and more modular (Rainforest – mean= 0.35; SD= 0.07; p-value= 0.01; Dry forest – mean= 0.41; SD= 0.02; p-value= 0.00) (Table 2).

Network structure in wet and dry seasons within each forest in relation to null models

For the dry forest, we found that most of the network metrics deviated from expected null distribution for the dry season, whereas there were no significant differences for the wet season during the El Niño year. However, some metrics showed deviation during the wet season of the normal year. During the dry season, the network was more compartmentalized (mean= 1.24; SD= 0.45; p-value= 0.00), less nested (weighted NODF) (mean= 15.29; SD= 2.95; p-value= 0.00), less connected (weighted connectance) (mean= 0.12; SD= 0.01; p-value= 0.05), and more modular than expected by the null models (mean= 0.50; SD= 0.03; p-value= 0.01). During the wet season of the normal year, the network was less nested (weighted NODF) (mean= 22.80; SD= 3.45; p-value= 0.01) and less connected (weighted connectance) (mean= 0.14; SD= 0.01; p-value= 0.00). Similar to the dry forest, we found that network metrics in the rainforest deviated from expected in only in the dry season. The network was less nested (weighted NODF) (mean= 12.73; SD= 3.03; p-value= 0.03) and more modular (mean= 0.37; SD= 0.04; p-value= 0.00) than expected by the null models. With regard to differences between seasons, we detected that the difference in robustness of bat species to plant extinctions was lower than expected by chance (p-value= 0.03) between seasons in the rainforest. In the dry forest, we found a higher niche overlap in the wet season of the normal year in comparison with the wet season of the El Niño year (p-value= 0.03) (Table 2).

Sampling completeness across forests and seasons

Values of sampling completeness of networks ranged from 78.85% (normal wet season) to 95.65% (Table 3).

None of the rarefaction curves built for any bat species present in our networks during each season have reached the plateau (See Supplementary Material).

Network dissimilarity across forests and seasons

All networks showed a high level of interaction dissimilarity between seasons and habitats ($\beta_{WN} > 0.800$) with only a small to intermediate portion of the dissimilarity in the structure of the interactions explained by turnover in species assemblages ($0.230 < \beta_{ST} < 0.420$). Dissimilarity in species composition between assemblages was intermediate ($0.410 < \beta_S < 0.882$). Interaction dissimilarity established between species common to both networks (β_{OS}) was also intermediate with values ranging from 0.460 to 0.590 (Table 4).

Discussion

Network structure in dry forest versus rainforest in relation to null models

Contrary to initial predictions that mutualistic networks in the rainforests would become more modular and less nested during El Niño than in a normal year, while networks in the dry forests would become less modular and more nested, we observed similar changes to network structure in response to El Niño for both forests. In both forests, aspects of the observed changes in network structure are likely to have contrasting consequences for network resilience. For example, nested mutualistic networks are thought to contribute to an increase in the maximum amount of biodiversity supported in the environment (Bastolla et al. 2009). A decrease in nestedness, as observed in both forest types, may thus be related to an increase in effective competition (Bastolla et al. 2009) driving niche separation. This is important as lower nestedness was found across most of the networks in the present study and nestedness helps to buffer against secondary extinctions and temporal fluctuations (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). Similarly, the decrease in connectance is worrying as this network metric is thought to contribute to ecosystem functional stability during fluctuating environmental conditions (Tylianakis et al. 2010).

Most observations of robustness to species extinctions also suggest a decrease in the stability of the communities and resilience of biological interactions, likely as a result of decreases in connectance and nestedness in the networks (Thébault & Faontaine, 2010). These effects are particularly important as connectance and nestedness are thought to show little temporal variation within and between years (Dupont, Padrón, Olesen, & Petanidou, 2009; Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009). In habitats such as forest and savannah, recovery to the conditions before disturbances such as floods and droughts is slow (Maron, McAlpine, Watson, Maxwell, & Barnard, 2015). Thus a significant deviation in network structure in normal years following these extreme climatic events would be expected. Overall, this effect might reduce the biodiversity supported in these ecosystems, especially when taking into consideration the expected increase in the frequency of strong El Niño events and the worldwide trend for wet areas to become wetter and dry areas to become drier (Chou et al. 2013; Cai et al. 2014).

We observed higher values of modularity than those expected under null models for both forests, also suggesting that the current interacting species are showing higher differentiation in their niche use. Modularity was not only significantly higher than expected by chance, but values for both forests were also higher than the calculated ones using a similar algorithm for previously observed mutualistic networks of phyllostomid bats in other regions of South America during normal conditions (Mello et al. 2011). Following a similar trend, the increase in compartmentalization of both habitats might reduce the number of coexisting species as fully connected networks promote a reduction in the effective interspecific competition (Bastolla et al. 2009). On the other hand, compartmentalization has been linked to greater stability, slower spread of disturbance, and smaller likelihood of trophic cascades in networks (Tylianakis et al. 2010).

It is interesting to note that the similar increases in compartmentalization and modularity alongside a decrease in nestedness might have arisen due to the same causes in each forest. Changes in rainfall have an impact in different groups of herbivorous mammal populations through alterations in the amount and quality of food resources (Mandujano, 2006; White, 2008). Severe droughts in some Pacific areas provoked by El Niño were responsible for increased production of flowers and fruit of the entire plant community (Wright &

Calderon, 2006), meanwhile in rainforests flowering was triggered by heavy rain (Wright, 1991). In Central American tropical forests, the fall of leaves after droughts that occurred during El Niño events tended to be associated with subsequent increases in seed production (Detto, Wright, Calderón, & Muller-Landau, 2018). These events, when both droughts and floods were associated with increased productivity of fruits and flowers could likely be the explanation to pattern that we have witnessed where the dry forests and rainforests showed similar changes in network structure. On the other hand, the drought that occurred in the dry forests of ACG promoted by the strong El Niño of 2015 caused a reduction in seed production that remained even after the return to normal levels of the rainfall (O'Brien et al. 2018). Thus, this effect was probably the main responsible for the changes in our observed networks for ACG, with the reduction in fruit availability leading to a higher resource specialization, which promoted an increase in modularity but a decrease in nestedness. Despite the contrasting causes, similar responses to opposite water stress in two very dissimilar species communities suggests a generalized response to stress that may become more prevalent as extreme weather cycles increase in frequency (also see Butt et al. 2015).

One of the limitations of our comparisons is that we do not have data collected for a normal year during both seasons from any of the forest types. Thus, it is hard to fully understand how our results are limited to the data and null models that we have used for the comparisons, or if they also reflect a real comparison with values gathered from a normal year for both forests. Another limitation is that for all almost all networks, except for two, we have lower values of sampling completeness than the rule of thumb proposed by Macgregor et al. (2017) (90%), though not by much. In addition, most of the rarefaction curves built to estimate the number plant species present in the diet of each bat species did not reach an asymptote. However, we focused our study mostly on network metrics that do not show a strong bias by network size which should minimize the impact of these issues. Finally, it is hard to assess the influence of markers choice that we used for plant identification on the values of network metrics. Multiple genetic markers have been proposed in various combinations to identify different plant species ($matK$, $trnH$-$psbA$, $rbcL$, ITS2), but still not sufficient to discriminate closely related species in some taxonomic groups, especially those with recent and intense species radiation (Hollingsworth et al. 2011). For example, the fig tree ($Ficus$), one of the common genera consumed by bats, is extremly specious and demonstrated poor resolution on species level using $rbcL$ and ITS (Ronsted, Weiblen, Clement, Zerega, & Savolainen, 2008). As such, some of our identificaitons should be treated provisionally. However, our analysis of data limited only to genera (see supplement) suggests our observations are robust to these effects. One major benefit of our molecular approach is the inclusion of plant species which might otherwise be missed when their seeds are not consumed. Our ability to identify plants from consumed pollen or fruit pulp provides a more complete perspective than many previous analytical approaches.

Network structure in wet versus dry seasons within each forest in relation to null models

We predicted that increased seasonality in the rainforest and decreased seasonality in the dry forest, would lead to different impacts on the structure of mutualistic networks. In the dry forest, we found that while the wet season during the El Niño year showed no changes in network structure in relation to the null models, the network in the dry season showed several metrics that deviated from expectations, and that these occurred in different directions. On the other hand, two network metrics during the wet season of the normal year (weighted NODF and weighted connectance) showed similar trends to the dry season and were lower than expected by chance. Explanations for these observations are likely to reflect changes in fruit availability. Notably, in the dry forest, most of the consumption of fleshy fruits occurs at the beginning of the wet season (Vieira & Aldicir, 2006). Although there was a big decrease in the rainfall in the wet season during this study, the second month of the wet season (June) had rainfall within the historical standard deviation that may have restored some of the normal conditions of the forest in terms of fruit availability. This may explain why nestedness (weighted NODF) was low during the dry season and why the network did not show any significant deviation in structure in the wet season. Another possibility is that the drought could have also led to an increase in fruit availability during the beginning of the wet season, which usually happens after a period of drought and leaf fall (Detto, Wright, Calderón, & Muller-Landau, 2018).

During the normal year, the low values of nestedness and connectance are likely explained by the low niche overlap between bat species during this season. The low niche overlap is likely linked with the low number of plant species in the diet of each bat species that was showed by the low value of weighted connectance in relation with the null model. The low niche overlap can promote a decrease in nestedness due to a low overlap in the diet of generalists and specialists. Even though the values of niche overlap were lower than expected by chance during the wet seaon of the normal year, it was higher than the values of the wet season of the El Niño year according to our null model comparison. This suggests that even though our null models did not detect a significant difference during one season only, there was a decrease in relation to what would be expected during a normal year.

In the rainforest, the changes across the seasons were also not consistent, which might also reflect changes in food availability across the year. The lower nestedness and higher modularity of the network during the dry season might be reflecting the bat niche specialization during this season due to a reduction in food availability. On the other hand, the absence of any significance difference in relation to the null models during the wet season might be happening due to an increase in fruit production where bats are exploiting more common resources.

Network dissimilarity across forests and seasons

We observed high interaction dissimilarity between seasons in both forests. Similar observations have been made for other mutualistic networks over time (years) where the percentage of retained interactions was similarly low, ranging from 5% to 31% (Petanidou et al. 2008; Alarcón, Waser, & Ollerton, 2008; Vázquez et al. 2009). It's likely that most variation in interactions between seasons in the dry forest in our study can be explained by differences in fruit availability, which tends to show temporal variation (Kushwaha, Tripathi, Tripathi, & Singh, 2011). The dissimilarity in species composition between the rainforest and dry forest of our observed networks is in accordance with what has been observed for the species turnover between lowland dry forests and rainforests in Costa Rica, where 50%-100% of the flora and fauna were common to both forests (Janzen, 1986). Mello (2009) suggested that patterns of temporal species turnover in phyllostomid bats are related to the abundance of preferred food items with the abundance of understory and canopy frugivores positively correlated with the rainfall in the Atlantic rainforest. Therefore, the impact of El Niño is unlikely to be equally distributed across all bat species. While species that forage in the canopy tend to be more specialized on tree species that produce big numbers of fruits for short periods of time, understory bats feed mainly on plants that produce few fruits over many months of the year (Mello, 2009).

Although El Niño causes floods in some regions of the world, the overall trend is to promote droughts in tropical rainforests (Holmgren et al. 2001) with occurrences of high annual rainfall and low seasonality considered unlikely (Borchert, 1998). This trend is usually reversed during the year after El Niño due to La Niña (Holmgren et al. 2001). However, most studies evaluate the effects of droughts, but not floods, in rainforests (Wright et al. 1999; Harrison, 2000). Dunham, Erhart, & Wright (2011) worked in Madagascar, and reported one of the few studies that examined the impact of heavy rains caused by an ENSO event on a rainforest, where he observed a disruption in the cycle of the primary fruit food sources, with a consequent increase in infant mortality in lemurs. Working in semi-deciduous forest in Panama during the strong ENSO event of 1982-1983, Leigh, Windsor, Rand, & Foster (1990) reported a drought that led to tree mortality that was 5 times higher than usual, yet resulted in no clear serious negative consequences for animal populations. They suggested that the forest might have adapted to surviving droughts provoked by ENSO events without too much damage.

El Niño seems to be impacting network structure in contradictory ways, which might promote biodiversity on one hand through increasing compartmentalization, but might deplete it on the other by increasing competition and decreasing stability via lower nestedness and connectance. It is especially interesting that different phenomena related to El Niño (floods and droughts) induced similar effects in the structure of mutualistic seed dispersal networks. This has broad consequences as increasingly strong El Niño events are expected to impact large portions of Latin America, where phyllostomid bats are distributed. More studies are required to see if there are similar responses in mutualistic networks to different stressors such as habitat

fragmentation or other scenarios that potentially boost the effects of extreme climatic events (Butt et al. 2015).

Acknowledgements

Oliveira H. F. M., Rodríguez-Herrera B., Kuzmina M., Rossiter S. J., & Clare E. L.; 2020; Seed dispersal by bats; Bold Systems; Version 4.

References

Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a

plant–pollinator interaction network. *Oikos, 117*, 1796-1807. doi: 10.1111/j.0030-1299.2008.16987.x

Almeida-Neto, M., & Ulrich, W. (2011). A straightforward computational approach for

measuring nestedness using quantitative matrices. *Environmental Modelling and Software, 26*, 173-178. doi: 10.1016/j.envsoft.2010.08.003

Altena, C., Hemerik, L., & Ruiter, P. C. (2016). Food web stability and weighted

connectance: the complexity-stability debate revisited.*Theoretical Ecology, 9*, 49-58. doi: 10.1007/s12080-105-0291-7

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Limpman, D. J. (1990). Basic local

alignment search tool. *Journal of Molecular Biology, 215*, 403-410. doi: 10.1016/S0022-2836(05)80360-2

Artzy-Randrup, Y., & Stone, L. (2005). Generating uniformly distributed random

networks. *Physical Review E , 72* , 056708. doi: 10.1103/PhysRevE.72056708

Asensio, N., Schaffner, C. M., & Aureli, F. (2015). Quality and overlap of individual core

areas are related to group tenure in female spider monkeys. *American Journal of Primatology, 77*, 777-785. doi: 10.1002/ajp.22400

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of

plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences, 100*, 9383-9387. doi: 10.1073/pnas.1633576100

Bastolla, U., Fortuna, M. A., Pascual-Garcia, A., Ferrera, A., Luque, B., & Bascompte, J.

(2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature, 458*, 1018-1021. doi: 10.1038/nature07950

Borchert, R. (1998). Responses of tropical trees to rainfall seasonality and its long-term

changes. *Climatic Change, 39* , 381-393. doi: 10.1007/978-94-017-27330-3_10

Bradley, B. J., Stiller, M., Doran-Sheehy, D. M., Harris, T., Chapman, C. A., Vigilant, L., &

Poinar, H. (2007). Plant DNA sequences from feces: potential means for assessing diets of wild primates. *American Journal of Primatology, 69*, 699-705. doi: 10.1002/ajp20384

Braukmann, T. W. A., Kuzmina, M. L., Sills, J., Zakharov, E. V., & Hebert, P. D. N. (2017).

Testing the efficacy of DNA barcodes for identifying the vascular plants of Canada. *PLoS one, 12*, e0169515. doi: 10.1371/journal.pone.0169515

Brown, D. S., Burger, R., Cole, N., Vencatasamy, D., Clare, E. L., Montazam, A., &

Symondson, W. O. C. (2014). Dietary competition between the alien Asia Musk Shrew (*Suncus murinus*) and a re-introduced population of Telfair's Skink (*Leiolopisma telfairii*). *Molecular Ecology, 23*, 3695-3705. doi: 10.111/mec.12445

Burgess, K. S., Fazekas, A. J., Kesanakurti, P. R., Graham, S. W., Husband, B. C.,

Newmaster, S. G., ... & Barrett, S. C. H. (2011). Discriminating plant species in a local temperate flora using the rbcL+matK DNA barcode. *Methods in Ecology and Evolution, 2*, 333–340. doi: 10.1111/j.2041-210X.2011.00092.x

Butt, N., Seabrook, L., Maron, M., Law, B. S., Dawson, T. P., Syktus, J., & McAlpine, C.A.

(2015). Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. *Global Change Biology, 21*, 3267-3277. doi: 10.1111/gcb.12869

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., ... & Jin, F.

(2014). Increasing frequency of extreme El Nino events due to greenhouse warming. *Nature Climate Change, 4*, 111-116. doi: 10.1038/nclimate2100

CBOL Plant Working Group (2009). A DNA barcode for land plants.

Proceedings of the

National Academy of Sciences , 106 , 12794–12797. doi: 10.1073/pnas.0905845106

Chanin, P., O'Reilley, C., Turner, P., Kerslake, L., Birks, J., & Woods, M. (2015). Insects in

the diet of the hazel dormouse (*Muscardinus avellanarius*): a pilot study using DNA barcoding. *Mammalian Communications,1*, 1-7.

Chou, C., Chiang, J. C., Lan, C. W., Chung, C. H., Liao, Y. C., & Lee C. J. (2013). Increase

in the range between wet and dry season precipitation. *Nature Geoscience, 6 ,* 263-267. doi: 10.1038/ngeo1744

Clare, E. L. (2014). Molecular detection of trophic interactions: emerging trends, distinct

advantages, significant considerations and conservation applications.

Evolutionary

Applications, 7 , 1144-1157. doi: 10.1111/eva.12225

Clare, E. L., Symondson, W. O. C., Broders, H., Fabianek, F., Fraser, E. E., MacKenzie, A.,

... & Reimer, J. P. (2014). The diet of *Myotis lucifugus* across Canada: assessing foragin quality and diet variability. *Molecular Ecology, 23*, 3618-3632. doi: 10.1111/mec.12542

Clare, E. L., Fazekas, A. J., Ivanova, N. V., Floyd, R. M., Hebert, P. D., Adams A. M., ... &

Fenton M. B. (2019). Approaches to integrating genetic data into ecological networks. *Molecular Ecology, 28*, 503-519. doi: 10.1111/mec.14941

Dalsgaard, B., Trojelsgaard, K., Gonzalez, A. M., Bigues-Bravo, D., Ollerton, J., Petanidou,

T., . . . & Olesen, J. M. (2013). Historical climate-change influences modularity and nestedness of pollination networks.*Ecography, 36*, 1331-1340. doi: 10.1111/j.1600-0587.2013.00201.x

Delmas, E., Besson, M., Brice, M. H., Burkle, L. A., Dalla, R. G. V., Fortin, M. J., . . . &

Poisot, T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, *94*, 16-36. doi: 10.1111/brv.12433

Detto, M., Wright, S. J., Calderon, O., & Muller-Landau, H. C. (2018). Resource acquisition

and reproductive strategies of tropical forest in response to the El Nino–Southern Oscillation. *Nature Communications* , *9* , 1-8. doi: 10.1038/s41467-018-03306-9

Donatti, C. I., Guimaraes, P. R., Galetti, M., Pizo, M. A., Marquitti F., & Dirzo, R. (2011).

Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters, 14*, 773-781. doi: 10.1111/j,1461-0248.2011.01638.x

Dormann, C. F., Gruber, B., & Frund, J. (2008). Introducing the bipartite package: analysing

ecological networks. *Interaction, 1* , 8-11.

Dormann, C. F., Frund, J., Bluthgen, N., & Gruber, B. (2009). Indices, graphs and null

models: analyzing bipartite ecological networks. *The Open Ecology Journal, 2*, 7–24. doi: 10.2174/187421300090210007

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative

bipartite networks. *Methods in Ecology and Evolution, 5*, 90-98. doi: 10.1111/2041-210X.12139

Dunham, A. E., Erhart, E. M., & Wright, P. C. (2011). Global climate cycles and cyclones:

consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, *17*, 219-227. doi: 10.1111/j.1365-2486.2010.02205.x

Dupont, Y. L., Padron, B., Olesen, J. M., & Petanidou, T. (2009). Spatio-temporal variation

in the structure of pollination networks. *Oikos, 118*, 1261-1269. doi: 10.1111/j.1600-0706.2009.17594.x

Evans, D. M., Kitson, J. J., Lunt, D. H., Straw, N. A., & Pocock, M. J. (2016). Merging DNA

metabarcoding and ecological network analysis to understand and build resilient terrestrial ecosystems. *Functional Ecology, 30*, 1904-1916. doi: 10.1111/1365-2435.12659

Fazekas, A. J., Burgess, K. S., Kesanakurti, P. R., Graham, S. W., Newmaster, S. G.,

Husband, B. C., . . . & Barrett, S. C. (2008). Multiple multilocus DNA barcodes from the plastid genome discriminate plant species equally well. *PloS one*, *3*, e2802. doi: 10.1371/journal.pone.0002802

Fazekas, A. J., Kuzmina, M. L., Newmaster, S. G., & Hollingsworth, P. M. (2012). DNA

barcoding methods for land plants. In W. J. Kress & D. L. Erickson (Eds.), *DNA barcodes: methods and protocols* (pp. 223-252). Totowa: Humana Press.

Fenton, M. B., & Simmons, N. (2015). Bats: a world of science and mystery. USA:

University of Chicago Press.

Ford, C. S., Ayres, K. L., Toomey, N., Haider, N., van-Alpen-Stahl, J., Kelly, L. J., . . . &

Wilkinson, M. J. (2009). Selection of candidate DNA barcoding regions for use on land plants. *Botanical Journal of the Linnean Society,159*, 1–11. doi: 10.1111/j.1095-8339.2008.00938.x

Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., &

Bascompte, J. (2010). Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology,79*, 811-817. doi: 10.1111/j.1365-2656.2010.01688.x

Fredriksson, G. M., & Wich, S. A. (2006). Frugivory in sun bears (Helarctos malayanus) is

linked to El Nino-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society, 89*, 489-508. doi: 10.1111/j.1095-8312.2006.00688.x

Frund, J., McCann, K. S., & Williams, N. M. (2015). Sampling bias is a challenge for

quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos, 125*, 502-513. doi: 10.1111/oik.02256

Galimberti, A., Spinelli, S., Bruno, A., Mezzasalma, V., Mattia, F., Cortis, P., & Labra, M.

(2016). Evaluating the efficacy of restoration plantings through DNA barcoding of frugivorous bird diets. *Conservation Biology,30*, 763-773. doi: 10.1111/cobi.12687

Galindo-Gonzalez, J., Guevara, S., & Sosa, V. J. (2000). Bat and bird-generated seed rains at

isolated trees in pastures in a tropical rainforest. *Conservation Biology, 14*, 1693–1703. doi: 10.1111/j.1523-1739.2000.99072.x

Gillespie, T. W., Grijalva, A., & Farris, C. N. (2000). Diversity, composition, and structure of

tropical dry forests in Central America. *Plant Ecology,147*, 37-47. doi: 10.1023/A:1009848525399

Gotelli, N. J., & Ulrich, W. (2011). Over-reporting bias in null model analysis: a response to

Fayle and Manica (2010). *Ecological Modelling, 222*, 1337-1339. doi: 10.1016/j.ecolmodel.2010.11.2008

Gotelli, N. J., & Ulrich, W. (2012). Statistical challenges in null model analysis. *Oikos, 121* ,

171-180. doi: 10.1111/j.1600-0706.2011.20301.x

Gunarathne, R. M. U. K., & Perera, G. A. D. (2014). Climatic factors responsible for

triggering phenological events in *Manilkara hexandra* (Roxb.) Dubard., a canopy tree in tropical semi-deciduous forest of Sri Lanka.*Tropical Ecology, 55*, 63-73.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis

program for windows 95/98/NT. *Nucleic Acids Symposium Series,41*, 95–98. doi: 10.14601/Phytopathol_-Mediterr-14998u1.29

Harrison, R. D. (2000). Repercussions of El Nino: drought causes extinction and the

breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London B: Biological Sciences, 267*, 911-915. doi: 10.1098/rspb.2000.1089

Hollingsworth, P. M., Graham, S. W., & Little, D. P. (2011). Choosing and using a plant

DNA barcode. *PloS one, 6* , e19254. doi: 10.1371/journal.pone.0019254

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J. R., & Mohren, G. M. (2001). El Nino

effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution, 16*, 89-94. doi: 10.1016/S0169-5347(00)02052-8

Horn, H. (1966). Measurement of "Overlap" in comparative ecological studies. *American*

Naturalist, 100 , 419-424. doi: 10.1086/282436

Ings, T. C., Montoya, J. M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C. F., . . . &

Woodward, G. (2009). Review: ecological networks –beyond food webs.*Journal of Animal Ecology, 78*, 253-269. doi: 10.1111/j.1365-2656.2008.01460.x

Ivanova, N. V., DeWaard, J. R., Hajibabaei, M., & Hebert, P. D. N. (2005). Protocols for

high volume DNA barcoding. http://www.dnabarcoding.ca/.

Ivanova, N. V., & Grainger, C. (2006). Pre-made frozen PCR and sequencing plates.

http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_Sequencing.pdf.

Ivanova, N. V., Fazekas, A. J., & Hebert, P. D. N. (2008). Semi-automated, membrane-based

protocol for DNA isolation from plants. *Plant Molecular Biology Reporter, 26*, 186–198. doi: 10.1007/s11105-008-0029-4

Ivanova, N., Kuzmina, M., & Fazekas, A. (2011). CCDB Protocols. Manual

protocolemploying centrifugation: glass fiber plate DNA extraction protocol for plants, fungi, echinoderms and mollusks; http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_DNA_Extraction-Plants.pdf.

Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., &

Bograd, S. J. (2016). Impacts of the 2015–2016 El Nino on the California current system: early assessment and comparison to past events. *Geophysical Research Letters, 43*, 7072-7080. doi: 10.1002/2016GL069716

Janzen, D. H. (1986). Guanacaste National Park: tropical ecological and cultural restoration.

Costa Rica: Editorial Universidad Estatal a Distancia.

Jedlicka, J. A., Sharma, A. M., & Almeida, R. P. P. (2013). Molecular tools reveal diets of

insectivorous birds from predator fecal matter. *Conservation Genetic Resources, 5*, 879-885. doi: 10.1007/s12686-013-9900-1

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M.

L., . . . & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores.*Proceedings of the National Academy of Sciences, 112*, 8019-8024. doi: 10.1073/pnas.1503283112

Krasnov, B. R., Fortuna, M. A., Mouillot, D., Khokhlova, I. S., Shenbrot, G. I., & Poulin, R.

(2012). Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *The American Naturalist, 179*, 501-511. doi: 10.1086/664612

Kress, W. J., Wurdack, K. J., Zimmer, E. A., Weigt, L. A., & Janzen, D. H. (2005). Use of

DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences, 102*, 8369-8374. doi: 10.1073/pnas.0503123102

Kress, W. J., Erickson, D. L., Jones, F. A., Swenson, N. G., Perez, R., Sanjur, O., &

Bermingham, E. (2009). Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proceedings of the National Academy of Sciences USA, 106*, 18621–18626. doi: 10.1073/pnas.0909820106

Kruger, F., Clare, E. L., Symondson, W. O. C., Keiss, O., & Petersons, G. (2014). Diet of the

insectivorous bat *Pipistrellus nathusii* during autumn migration.*Molecular Ecology, 23*, 3672-3632. doi: 10.1111/mec.12547

Kunz, T. H., Braun, de Torrez, E., Bauer, D., Lobova, T., & Fleming, T. H. (2011).

Ecosystem services provided by bats. *Annals of the New York Academy of Sciences, 1223*, 1-38. doi: 10.1111/j.1749-6632.2011.06004.x

Kushwaha, C. P., Tripathi, S. K., Tripathi, B. D., & Singh, K. P. (2011). Patterns of tree phenological diversity in dry tropics. *Acta Ecologica Sinica,31*, 179-185. doi: 10.1016/j.chnaes.2011.04.003

Kuzmina, M., & Ivanova, N. (2011a). PCR amplification for plants and fungi. http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_Amplification-Plants.pdf.

Kuzmina, M., & Ivanova, N. (2011b). Primer sets for plants and fungi. http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_PrimerSets-Plants.pdf

Lamb, E. G., Winsley, T., Piper, C. L., Freidrich, S. A., & Siciliano, S. D. (2016). A high-throughput belowground plant diversity assay using next-generation sequencing of the *trn*L intron. *Plant and Soil, 404*, 361-372. doi: 10.1007/s11104-016-2852-y

Larkin, M. A., Blackshields, G., Brown, N. P., Chenna, R., McGettigan, P. A., McWilliam, H., . . . & Higgins, D. G. (2007). Clustal W and Clustal X version 2.0. *Bioinformatics, 23*, 2947–2948. doi: 10.1093/bioinformatics/btm404

LaVal, R. K., & Rodriguez-Herrera, B. (2002). Murcielagos de Costa Rica. Costa Rica : Instituto Nacional de Biodiversidad (InBio).

Lahaye, R., van der Bank, M., Bogarin, D., Warner, J., Pupulin, F., Gigot, G., . . . & Savolainen, V. (2008). DNA barcoding the floras of biodiversity hotspots. *Proceedings of the National Academy of Sciences of the USA*, *105*, 2923–2928. doi: 10.1073/pnas.0709936105

Leigh, E. G., Windsor, D. M., Rand, A. S., & Foster, R. B. (1990). The impact of the "El Nino" drought of 1982-83 on a Panamanian semieciduous forest.*Elsevier Oceanography Series, 52*, 473-486. doi: 10.1016/S0422-9894(08)70046-1

Macgregor, C. J., Evans, D. M., & Pocock, M. J. (2017). Estimating sampling completeness of interactions in quantitative bipartite ecological networks: incorporating variation in species specialization.*bioRxiv*, 1-32. doi: 10.1101/195917

Malhi, Y., & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical rainforests regions. *Philosophical Transactions of the Royal Society B, 359*, 311-329. doi: 10.1098/rstb.2003.1433

Mandujano, S. (2006). Preliminary evidence of the importance of ENSO in modifying food availability for white-tailed deer in a Mexican tropical dry forest.*Biotropica, 38*, 695-699. doi: 10.1111/j.1744-7429.2006.00184.x

Maron, M., McAlpine, C. A., Watson, J. E., Maxwell, S., & Barnard, P. (2015). Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions, 21*, 731-743. doi: 10.1111/ddi.12339

Mello, M. A. R. (2009). Temporal variation in the organization of a Netropical assemblage of leaf-nosed bats (Chiroptera: Phyllostomidae). *Acta Oecologica,35*, 280-286. doi: 10.1016/j.actao.2008.11.008

Mello, M. A. R., Marquitti, F. M. D., Guimaraes, P. R., Kalko, E. K. V., Jordano, P., &

Aguiar, M. A. M. (2011). The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS one, 6,* e17395. doi: 10.1371/journal.pone.0017395

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination neworks to

species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences, 271*, 2605-2611. doi: 10.1098/rspb.2004.2909

O'brien, M. J., Perez-Aviles, D., & Powers, J. S. (2018). Resilience of seed production to a

severe El Nino-induced drought across functional groups and dispersal types. *Global Change Biology, 24*, 5270-5280. doi: 10.1111/gcb.14416

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of

pollination networks. *Proceedings of the National Academy of Sciences, 104*, 19891-19896. doi: 10.1073/pnas.0706375104

Parmentier, I., Duminil, J., Kuzmina, M., Philippe, M., Thomas, D. W., Kenfack, D., . . . &

Hardy, O. J. (2013). How effective are DNA barcodes in the identification of African rainforest trees?. *PLoS one, 8*, e54921. doi: 10.1371/journal.pone.0054921

Patefield, W. (1981). An efficient method of generating random R x C tables with given row

and column totals. *Applied Statistics, 30,* 91–97. doi: 10.2307/2346669

Petanidou, T., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P., & Pantis, J. D. (2008).

Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters, 11*, 564-575. doi: 10.1111/j.1451-0248.2008.01170.x

Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of

species interaction networks. *Ecology Letters, 15* , 1353-1361. doi: 10.1111/ele.12002

Quemere, E., Hibert, F., Miquel, C., Lhuillier, E., Rasolondraibe, E., Champeau, J., . . . &

Chikhi, L. (2013). A DNA metabarcoding study of a primate dietary diversity and plasticity across its entire fragmented range. *PLoS one, 8*, e58971. doi: 10.1371/journal.pone.0058971

R Core Team (2017). R: A language and environment for statistical omputing. R Foundation

for Statistical Computing, Vienna, Austria. URL: htp://www.R-project.org/.

Ratnasingham, S., & Hebert, P.D.N. (2007). BOLD: The Barcode of Life Data System.

Molecular Ecology Resources, 7 , 355-364. doi: 10.1111/j.1471-8286.2007.01678.x

Reid, F. (1997). A field guide to the mammals of Central America and Southeast Mexico.

United Kingdom: Oxford University Press.

Rico-Gray, V., Diaz-Castelazo, C., Ramirez-Hernandez, A., Guimaraes, Jr P.R., & Holland,

J.N. (2012). Abiotic factors shape temporal variation in the structure of an ant–plant network. *Arthropod-Plant Interactions, 6*, 289-295. doi: 10.1007/s11829-011-9170-3

Rojas, D., Vale, A., Ferrero, V., & Navarro, L. (2012). The role of frugivory in the

diversification of bats in the Neotropics. *Journal of Biogeography, 39*, 1948-1960. doi: 10.1111/j.1365-2699.2012.02709.x

Ronsted, N., Weiblen, G. D., Clement, W. L., Zerega, N. J., & Savolainen, V. (2008).

Reconstructing the phylogeny of figs (Ficus, Moraceae) to reveal the history of the fig pollination mutualism. *Symbiosis (Rehovot)*, *45*, 45-55.

Roslin, T., & Majaneva, S. (2016). The use of DNA barcodes in food web construction-

terrestrial and aquatic ecologists unite!. *Genome, 59*, 603-628. doi: 10.1139/gen-2015-0229

Schleuning, M., Ingmann, L., Strauss, R., Fritz, S. A., Dalsgaard, B., Dehling, M., Plein, M.,

Saavedra, F., Sandel, B., Svenning, J., & Bohning-Gaese, K. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters, 17*, 454-463. doi: 10.1111/ele.12245

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., ... &

Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In C. B. Field, V. Barros, T. F. Stocker & Q. Dahe (Eds.), *Managing the risks of extreme events and disasters to advance climate change adaptation* (pp. 109-230). Cambridge, UK: Cambridge University Press.

Sigel, B. J., Sherry, T. W., & Young, B. E. (2006). Avian community response to lowland

tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conservation Biology, 20*, 111-121. doi: 10.1111/j.1523-1739.2005.00293.x

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: molecular

evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution, 30*, 2725-2729. doi: 10.1093/molbev/mst197

Thebault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture

of mutualistic and trophic networks. *Science, 329*, 853-856. doi: 10.1126/science.1188321

Timm, R. M., & LaVal, R. K. (1998). A field key to the bats of Costa Rica. *Occasional*

Publication , *22* , 1-30. doi: 10.1093/jmammal/gyz150

Trojelsgaard, K., & Olesen, J. M. (2013). Macroecology of pollination networks. *Global*

Ecology and Biogeography, 22 , 149-162. doi: 10.1111/j.1466-8238.2012.00777.x

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the

structure of tropical host-parasitoid food webs. *Nature, 445*, 202-205. doi: 10.1038/nature05429

Tylianakis, J. M., Laliberte, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species

interaction networks. *Biological Conservation, 143*, 2270-2279. doi: 10.1016/j.biocon.2009.12.004

Vazquez, D. P., Bluthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and

process in plant–animal mutualistic networks: a review. *Annals of Botany, 103*, 1445-1457. doi: 10.1093/aob/mcp057

Vieira, D. L., & Scariot, A. (2006). Principles of natural regeneration of tropical dry forests

for restoration. *Restoration Ecology, 14*, 11-20. doi: 10.1111/j.1526-100X.2006.00100.x

Waylen, P., Caviedes, C., Poveda, G., Mesa, O., & Quesada, M. (1998). Rainfall distribution

and regime in Costa Rica and its response to the El Nino -Southern Oscillation. *Conference of Latin Americanist Geographers*,*24*, 75-84.

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of

animals. *Biological Reviews, 83* , 227-248. doi: 10.1111/j.1460-185X.2008.00041.x

Wirta, H. K., Hebert, P. D., Kaartinen, R., Prosser, S. W., Varkonyi, G., & Roslin, T. (2014).

Complementary molecular information changes our perception of food web structure. *Proceedings of the National Academy of Sciences,111*, 1885-1890. doi: 10.1073/pnas.1316990111

Wolfe, J. D., Ralph, C. J., & Elizondo, P. (2015). Changes in the apparent survival of a

tropical bird in response to the El Nino Southern Oscillation in mature and young forest in Costa Rica. *Oecologia, 178*, 715-721. doi: 10.1007/s00442-015-3256-z

Wright, S. J. (1991). Seasonal drought and the phenology of understory shrubs in a tropical

moist forest. *Ecology, 72* , 1643–1657. doi: 10.2307/1940964

Wright, S. J., Carrasco, C., Calderon, O., & Paton, S. (1999). The El Nino Southern

Oscillation, variable fruit production, and famine in a tropical forest.*Ecology, 80*, 1632-1647. doi: 10.1890/0012-9658(1999)080[1632:TENOSO]2.0.CO;2

Wright, S. J., & Calderon, O. (2006). Seasonal, El Nino and longer term changes in flower

and seed production in a moist tropical forest. *Ecology Letters,9*, 35-44. doi: 10.1111/j.1461-0248.2005.00851.x

Data accessibility

Raw data associated with this paper are available form the BOLD website in the project "Seed dispersal by bats" and will be made publicly accessible on acceptance

Author's contribution

HFMO, SJR, and ELC designed the project; HFMO, SJR, ELC, and MK identified plant DNA sequences; HFMO conducted fieldwork and performed statistical analysis; HFMO, BHR, MK, SJR, and ELC wrote the manuscript.
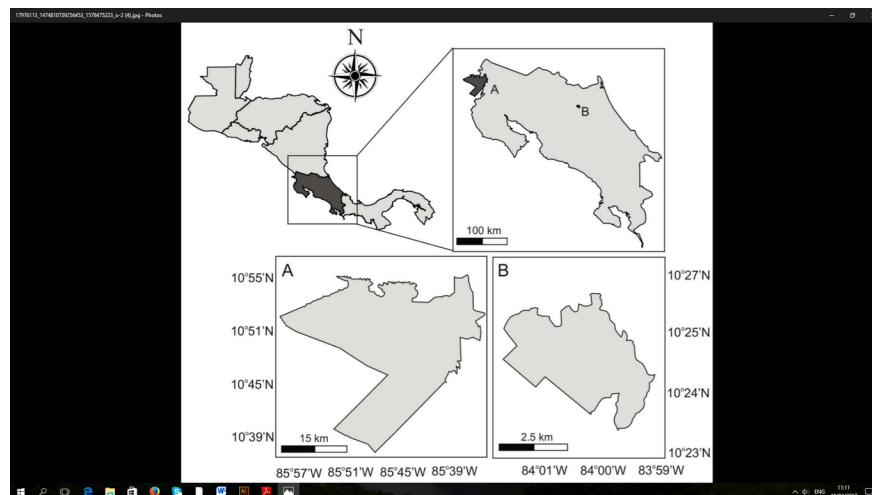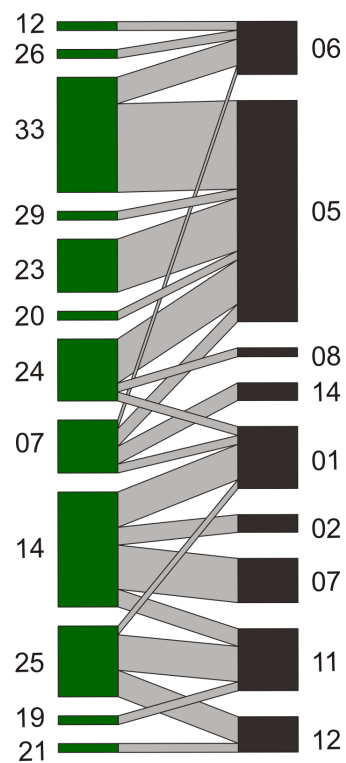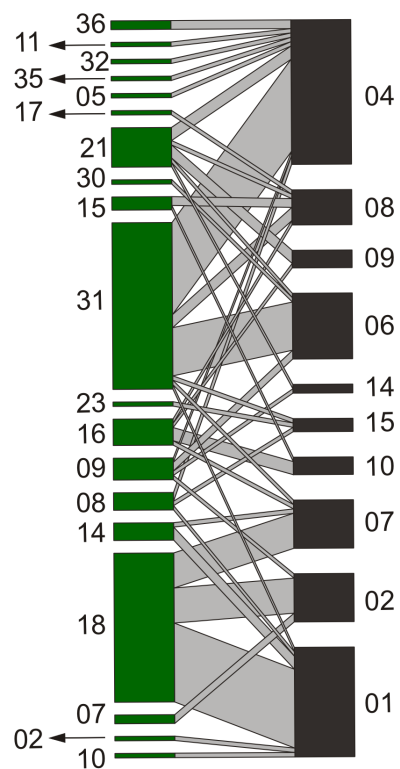

Figure 1. Map of Central America with Costa Rica and the field sites of the present study highlighted. A= Sector Santa Rosa (of Área de Conservación Guanacaste); B= La Selva Biological Station.
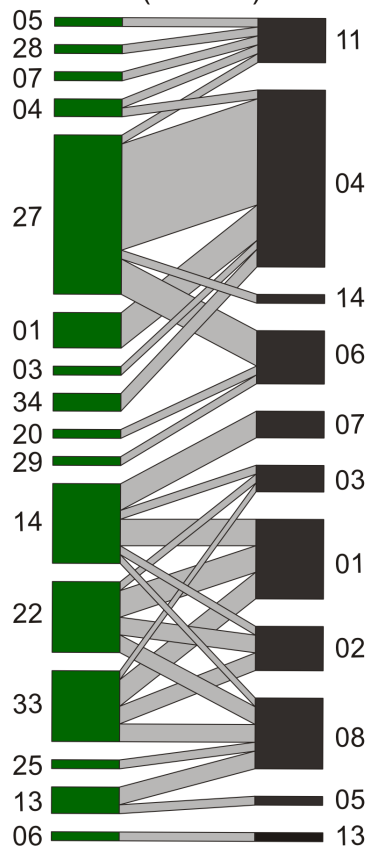
Wet season
(El Niño)

Wet season
(normal year)
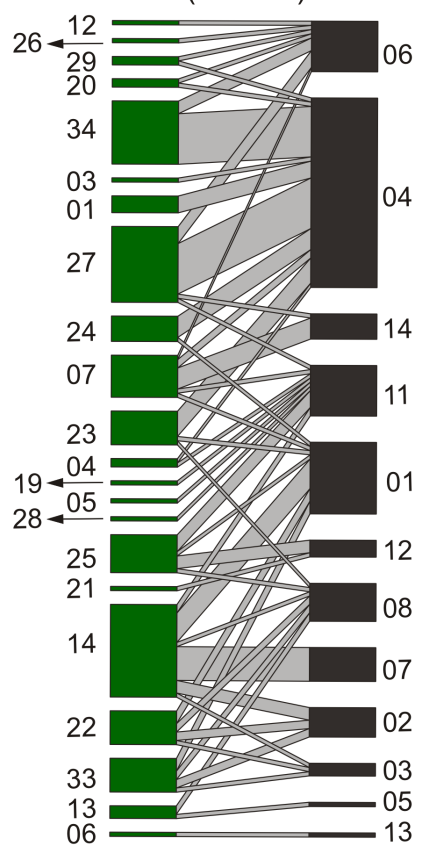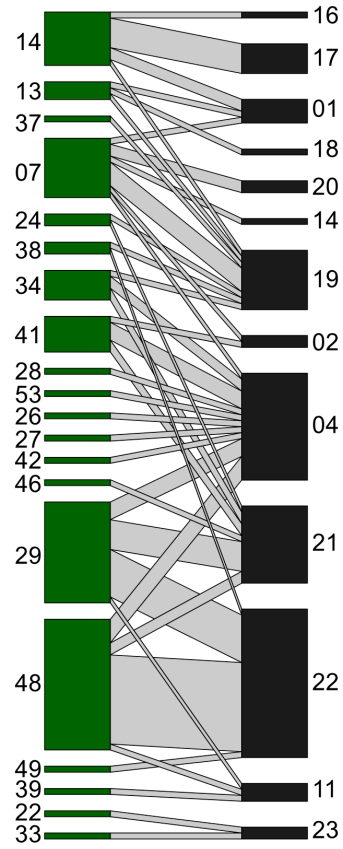
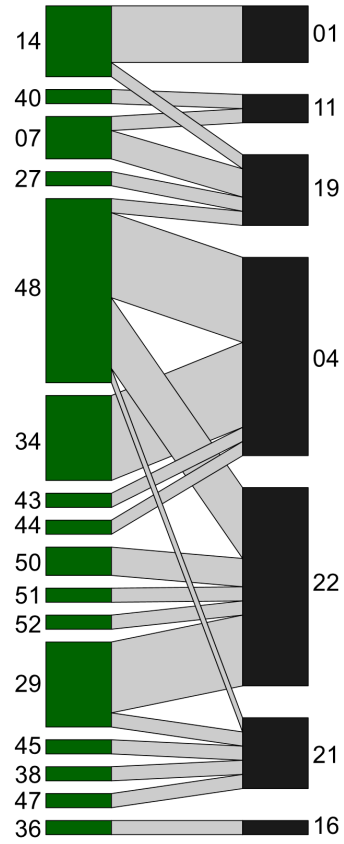Dry season
(El Niño)

Both seasons
(El Niño)

Figure 2. Mutualistic networks of interactions between frugivorous bats (upper boxes) and the plant species (bottom boxes) present in their diet in the wet and dry season within the dry forest of Área de Conservación Guanacaste (Costa Rica) during a normal (2009) and an extreme El Niño year (2015).

Bats: 01 – *Artibeus jamaicensis* ; 02 – *Artibeus lituratus* ; 03 – *Dermanura tolteca* ; 4 – *Carollia perspicillata* ; 05 – *Centurio senex* ; 06 – *Carollia subrufa* ; 07 – *Chiroderma villosum* ; 08 – *Dermanura phaeotis* ; 09 – *Glossohaga leachii* ; 10 – *Glossophaga soricina* ; 11 – *Glossophaga* sp.; 12 – *Lonchophylla concava* ; 13 - *Micronycteris microtis* ; 14 – *Platyrrhinus helleri* ; 15 – *Sturnira parvidens* . **Plants:** 01 –*Annona reticulata;* 02 – *Apocynum* ; 03 – *Bernardia nicaraguensis* ; 04 – *Bauhinia ungulata* ; 05 – *Bauhinia* ; 06 – *Casearia* ; 07 – *Cecropia* ; 09 - *Cecropia* sp. 1; 10 – *Cecropia* sp. 3; 11 – *Enterolobium* ; 12 –*Erythroxylum* ; 13 – *Ficus citrifolia* ; 14 – *Ficus* ; 15 – *Ficus* sp. 1; 16 – *Ficus* sp. 2; 17 – *Ficus*sp. 3; 18 – *Ficus* sp. 4; 19 – *Helicteres* ; 20 –*Karwinskia* ; 21 – *Muntingia calabura* ; 22 – Manilkara chicle; 23 – *Maclura tinctoria* ; 24 – Moraceae; 25 –*Piper amalago* ; 26 – *Piper auritum* ; 27 – *Piper marginatum* ; 28 – *Pinus* ; 29 – *Piper* ; 30 – *Solanum erianthum* ; 31 – *Solanum hazenii* ; 32 – *Solanum schlechtendalianu* ; 33 – Sapotaceae; 34 – Solanum; 35 – *Vismia collinsi* ; 36 – *Vismia* .

Wet season
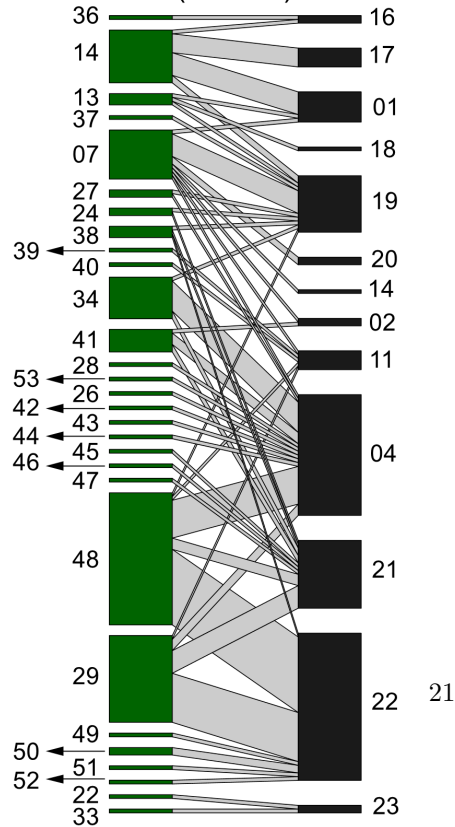(El Niño)

Dry season
(El Niño)

Both seasons
(El Niño)

Figure 3. Mutualistic networks of interactions between frugivorous bats (top boxes) and the plant species (bottom boxes) present in their diet in the wet and dry season within the rainforest of La Selva Biological Station (Costa Rica) during an extreme El Niño year (2015).

Bats: 01 – *Artibeus jamaicensis* ; 02 – *Artibeus lituratus* ; 04 – *Carollia perspicillata* ; 11 –*Glossophaga* sp.; 14 – *Platyrrhinus helleri* ; 16 –*Uroderma convexum* ; 17 – *Ectophylla alba* ; 18 –*Vampyerssa thyone* ; 19 – *Dermanura watsoni* ; 20 –*Vampyriscus nymphaea* ; 21 – *Carollia sowelli* ; 22 –*Carollia castanea* ; 23 – *Phyllostomus discolor* .**Plants:** 07 – *Cecropia* ; 13 – *Ficus citrifolia* ; 14 – *Ficus* ; 24 – Moraceae; 26 – *Piper auritum* ; 27 –*Piper marginatus* ; 28 – *Pinus* ; 29 – *Piper* ; 32 –*Solanum schlechtendalianum* ; 33 – Sapotaceae; 34 –*Solanum* ; 36 – *Vismia* ; 37 – *Ficus dewolfii;* 38 – Zingiberales; 39 – Bromeliaceae; 40 – *Ochroma pyramidale* ; 41 –*Vismia macrophylla* ; 42 – *Senna papillosa* ; 43 – Saxifragaceae; 44 – *Philodendron* ; 45 – *Pourouma* ; 46 –*Epippremum* ; 47 – *Piper glabrescens* ; 48 – *Piper multiplinervium* ; 49 – *Columnea purpurata* ; 50 – *Piper sanctifelicis* ; 51 – *Piper reticulatum* ; 52 – *Piper peltatum* ; 53 - Juglandiaceae.

Tables

Table 1. Expected changes of food resources and different metrics of mutualistic networks of frugivorous bats and the plants they eat in the dry forest of Sector Santa Rosa (of Área de Conservación Guanacaste) and rainforest of La Selva Biological Station in Costa Rica during an extreme El Niño event (2015) in relation to null models (network metrics) and historical patterns (food resources).

Habitat	Season	Network metrics	Rainfall (obs.)	Food resources
Dry forest	Dry	Low modularity High nestedness and other metrics	Normal	Low availability
Dry forest	Wet	Lower modularity Higher nestedness and other metrics	Decreased (drought)	Lower fruit availability than normal
Rainforest	Dry	High modularity Low nestedness and other metrics	Normal	High fruit availability
Rainforest	Wet	Higher modularity Lower nestedness and other metrics	Increased (flood)	Higher fruit availability than normal

Table 2. Network metrics of frugivorous bat mutualistic networks in the wet and dry season of the dry forest of Sector Santa Rosa (of Área de Conservación Guanacaste) and rainforest of La Selva Biological Station in Costa Rica during a normal year and extreme an El Niño year (2015). Significance tested in relation to 1,000 random generated networks for each season according to the swap algorithm using the Monte Carlo procedure.

Network metric	Dry forest	Dry forest	Dry forest	Dry forest	Dry forest	Rainforest	Rainforest	Rainforest	Rainforest
	Whole year Dry Wet normal	*Dry Wet normal*	*Whole year Dry Wet normal*	*Whole year Dry Wet normal*	*Whole year Dry Wet*	*Whole year Dry Wet*	*Whole year Dry Wet*	*Whole year Dry Wet*	*Whole year Dry Wet*
Number of compartments	— 2.00**	— 3.00**	1.00	1.00	1.00	— 2.00*	2.00	2.00	2.00
Weighted NODF	— 13.94*	— 6.57**	18.23	— 15.37*	— 15.37*	— 13.72**	— 6.92*	18.24	18.24
Weighted connectance	— 0.12*	— 0.11*	0.14	— 0.10**	— 0.10**	— 0.09**	0.11	0.14	0.14
Modularity (QuanBiMo)	— 0.53**	— 0.57*	0.50	0.52	0.52	— 0.46*	— 0.55**	0.48	0.48
Niche overlap (bats)	0.18	0.18	0.20	— 0.22**	— 0.22**	0.18	0.14	0.20	0.20
Robustness (bats)									
Random	0.66	0.61	0.63	0.61	0.61	0.61	0.56	0.65	0.65
Degree	0.43	0.43	0.38	0.42	0.42	0.30	0.39	0.38	0.38
Abundance	0.82	0.80	0.82	0.78	0.78	0.80	0.68	0.82	0.82

* Indicates a p-value < 0.05; ****** Indicates a p-value < 0.01

Table 3. Sampling completeness of mutualistic networks of frugivorous bats in the dry forest of Sector Santa Rosa (of Área de Conservación Guanacaste) (wet and dry season) and rainforest of La Selva Biological Station (wet and dry season) of Costa Rica during a normal year (2009) and an extreme El Niño event (2015).

Type of forest (year – season)	Sampling completeness (%)
Dry forest (El Niño – whole year)	86.44
Dry forest (Normal year – wet season)	78.85
Dry forest (El Niño – dry season)	86.49
Dry forest (El Niño – wet season)	94.74
Rainforest (El Niño – whole year)	79.71
Rainforest (El Niño – dry season)	95.65
Rainforest (El Niño – wet season)	83.17

Table 4. Values of β dissimilarities between mutualistic networks of frugivorous bats in the dry forest of Sector Santa Rosa (of Área de Conservación Guanacaste) (wet and dry season) and rainforest of La Selva Biological Station (wet and dry season) of Costa Rica during a normal year (2009) and an extreme El Niño event (2015).

Differences	Dry forest – Rainforest	Dry forest Wet – Dry	Dry forest El Niño wet season – normal wet season	Rainforest Wet – Dry
Dissimilarity in the species composition of the communities in the networks (β_S)	0.632	0.417	0.882	0.536
Dissimilarity of interaction established between species common to both networks (β_{OS})	0.462	0.583	-	0.520
Dissimilarity of interactions (β_{WN})	0.868	0.821	1.000	0.812
Dissimilarity of interactions based due to species turnover between both networks (β_{ST})	0.406	0.238	-	0.292