Species interactions in an Andean bird-flowering plant network: phenology is more important than abundance or morphology

Oscar Gonzalez Corresp., [1, 2] , **Bette A Loiselle** [1, 3]

[1] Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, United States
[2] Grupo Aves del Peru, Lima, Peru
[3] Center for Latin American Studies, University of Florida, Gainesville, Florida, United States of America

Corresponding Author: Oscar Gonzalez
Email address: pajarologo@ufl.edu

Biological constraints and neutral processes have been proposed to explain the properties of plant-pollinator networks. Using interactions between nectarivorous birds (hummingbirds and flowerpiercers) and flowering plants in high elevation forests (i.e., “elfin” forests) of the Andes, we explore the importance of biological constraints and neutral processes (random interactions) to explain the observed species interactions and network metrics, such as connectance, specialization, nestedness and asymmetry. In cold environments of elfin forests, which are located at the top of the tropical montane forest zone, many plants are adapted for pollination by birds, making this an ideal system to study plant-pollinator networks. To build the network of interactions between birds and plants, we used direct field observations. We measured abundance of birds using mist-nets and flower abundance using transects, and phenology by scoring presence of birds and flowers over time. We compared the length of birds’ bills to flower length to identify “forbidden interactions” – those interactions that could not result in legitimate floral visits based on mis-match in morphology. *Diglossa* flowerpiercers, which are characterized as “illegitimate” flower visitors, were relatively abundant. We found that the elfin forest network was nested with phenology being the factor that best explained interaction frequencies and nestedness, providing support for biological constraints hypothesis. We did not find morphological constraints to be important in explaining observed interaction frequencies and network metrics. Other network metrics (connectance, evenness and asymmetry), however, were better predicted by abundance (neutral process) models. Flowerpiercers, which cut holes and access flowers at their base and, consequently, facilitate nectar access for other hummingbirds, explain why morphological mis-matches were relatively unimportant in this system. Future work should focus on how changes in abundance and phenology, likely results of climate change and habitat fragmentation, and

the role of nectar robbers impact ecological and evolutionary dynamics of plant-pollinator (or flower-visitor) interactions.

Species interactions in an Andean bird-flowering plant network: phenology is more important than abundance or morphology

Oscar Gonzalez[1,2] and Bette A. Loiselle[1,3]

[1] Department of Wildlife Ecology & Conservation, 110 Newins-Ziegler Hall. PO Box 110430. University of Florida. Gainesville, FL 32611-0430 USA

[2]Grupo Aves del Peru. Gomez del Carpio 135, Surquillo. Lima 34, Peru

[3]Center for Latin American Studies. 319 Grinter Hall. PO Box 115530. University of Florida. Gainesville, FL 32611-5530 USA

Corresponding author:

Oscar Gonzalez[1,2]

Email address: pajarologo@ufl.edu

Abstract

Biological constraints and neutral processes have been proposed to explain the properties of plant-pollinator networks. Using interactions between nectarivorous birds (hummingbirds and flowerpiercers) and flowering plants in high elevation forests (i.e., "elfin" forests) of the Andes, we explore the importance of biological constraints and neutral processes (random interactions) to explain the observed species interactions and network metrics, such as connectance, specialization, nestedness and asymmetry. In cold environments of elfin forests, which are located at the top of the tropical montane forest zone, many plants are adapted for pollination by birds, making this an ideal system to study plant-pollinator networks. To build the network of interactions between birds and plants, we used direct field observations. We measured abundance of birds using mist-nets and flower abundance using transects, and phenology by scoring presence of birds and flowers over time. We compared the length of birds' bills to flower length to identify "forbidden interactions" – those interactions that could not result in legitimate floral visits based on mis-match in morphology. *Diglossa* flowerpiercers, which are characterized as "illegitimate" flower visitors, were relatively abundant. We found that the elfin forest network was nested with phenology being the factor that best explained interaction frequencies and nestedness, providing support for biological constraints hypothesis. We did not find morphological constraints to be important in explaining observed interaction frequencies and network metrics. Other network metrics (connectance, evenness and asymmetry), however, were better predicted by abundance (neutral process) models. Flowerpiercers, which cut holes and access flowers at their base and, consequently, facilitate nectar access for other

hummingbirds, explain why morphological mis-matches were relatively unimportant in this system. Future work should focus on how changes in abundance and phenology, likely results of climate change and habitat fragmentation, and the role of nectar robbers impact ecological and evolutionary dynamics of plant-pollinator (or flower-visitor) interactions.

Introduction

Interactions between flowering plants and their animal visitors are frequently focused on mutualistic encounters (Bascompte & Jordano, 2014). In these mutualisms, plants provide food resources (i.e., pollen, nectar), while animals provide pollinator services. Yet, these interactions are not always mutualistic. For example, animals may visit flowers and fail to effectively transfer pollen, as in the case of “nectar-robbers”, which bypass reproductive parts of the flower via cutting a hole at the base to access nectar resources (Rojas-Nossa, 2013, Maruyama et al., 2015, Rojas-Nossa, Sanchez & Navarro, 2016). The presence of nectar-robbers in a system can change the dynamics and structure of plant-flower visitor networks. In these systems, the number and diversity of flower visitors to certain floral resources may increase as more visitors gain access to nectar, although the effectiveness of pollination may remain the same or even decline.

Plant-pollinator (or plant-flower visitor) networks have been relatively well-studied in recent years (Lewinsohn et al., 2006, Burkle & Alarcon 2011, Dalsgaard et al., 2011, Bascompte & Jordano, 2014). These networks are almost always characterized by many fewer interactions than are possible and asymmetries (e.g., Jordano, Bascompte & Olesen, 2003, Vasquez & Aizen, 2004). Mutualistic networks, such as plant-pollinator

networks and plant-frugivore networks, often tend towards a nested structure, where more specialist species interact with a subset of other species; the latter interact also with a suite of more generalist species; (Bascompte et al., 2003, Vasquez and Aizen, 2006, Bascompte, 2010, Thébault & Fontaine, 2010). Mutualistic networks also have been found to be compartmentalized or modular with groups of species well connected to each other, but less connected to others in the network, usually when they have a large number of species (e.g. Olesen et al., 2007).

Recent research suggest that how networks are structured may influence their stability and co-evolutionary dynamics (Bascompte & Jordano, 2007, Ebeling, Klein & Tscarntke, 2011, Nuismer, Jordano & Bascompte, 2013). Thus, understanding which factors explain the observed interactions and structural properties of the network are key to predicting sensitivity of networks to perturbations, such as loss of species or changes in environmental conditions. Species extinction can be preceded by the extinction of species interactions, so this study contributes to show how network theory can help to explain the web of life in an ecosystem (Bascompte & Jordano, 2014). In recent years, new analytical approaches have facilitated asking questions about the processes that drive network properties (Vasquez, Chacoff & Cagnolo, 2009, Encinas-Viso, Revilla & Etienne, 2012, Winfree et al., 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014, Olito & Fox, 2015). Two main hypotheses – neutrality and biological constraints - have emerged in these network studies. The neutrality hypothesis suggests that random interactions among species best explain network structure, such that relative species abundances predict interaction frequencies and can explain resultant structural properties (Vazquez & Aizen, 2004). In contrast, the biological

constraints hypothesis suggests that interactions are shaped by species' traits or phenological patterns (Jordano, Bascompte & Olesen, 2003, Vazquez, Chacoff & Cagnolo, 2009, Olesen et al., 2011). In the former, trait mismatches can result in "forbidden interactions" that impede or prohibit interactions among network members, such as when the length or width of the flower opening prohibits animal access to the nectar resources (Jordano, Bascompte & Olesen, 2003, Olesen et al., 2011). In the latter, phenological mismatches occur when animal presence in an area does not overlap the time when specific plants are flowering (Vazquez, Chacoff & Cagnolo, 2009).

Support for the neutral or biological constraints hypotheses have been mixed (e.g., see Olito & Fox, 2015). While information from species relative abundances (neutrality) and phenology (biological constraints) predicted components of network structure in plant-pollinator networks from Argentinean shrub land (connectance, nestedness, evenness and interaction asymmetry), neither of these hypotheses explained the observed frequencies of species interactions (Vasquez, Chacoff & Cagnolo, 2009). In contrast, in a hummingbird-flowering plant network, forbidden interactions from phenological or morphological mismatches were found to drive frequencies of observed interactions (Maglianesi et al., 2014, Maruyama et al., 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014), although they were not important predictors of network structure (e.g. nestedness, connectance, specialization, evenness and asymmetry; see Maglianesi et al., 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014). Similarly, phenological mismatches, in combination with relative abundances of network members, played a

role in explaining interaction frequencies between nectarivorous sunbirds and flowering plants (Janecek et al., 2012).

Here, we extend these studies to investigate the drivers of species' interactions and network structure in a bird-flowering plant network in "elfin" forests located within the high Andes of Peru (Brack & Mendiola, 2000). Elfin forests, like other highland sites, are characterized by flowering plants adapted largely for bird pollination, as cold temperatures and often wet conditions limit insect abundance and activity (Dalsgaard et al., 2009, Lloyd et al., 2012). In mainland Americas these forests, while dominated by hummingbirds of various sizes and bill morphologies, also are frequented by *Diglossa* flowerpiercers (Ramirez et al., 2007). Flowerpiercers feed extensively on nectar, but may offer limited pollinator services as they frequently access flowers via holes they cut at the base of flowers using their modified beaks (Rojas-Nossa, 2013). Their presence in the system may lessen the importance of morphological constraints in shaping interactions and structural properties of the network as they create opportunities for short-billed hummingbirds to also access flowers with long corollas. Thus, elfin forest networks may not fit the patterns reported earlier where interaction frequencies of networks are predicted by morphology of network members (Maruyama et al. 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014, Vizentin-Bugoni et al., 2016).

By combining information on flower visits, flower phenology, bird (hummingbirds and flowerpiercers) and plant abundance, we address the following questions: 1) How are bird-flowering plant networks of elfin forest structured?, 2) Are observed interaction frequencies and network structural properties driven by biological constraints (morphological and/or phenological mismatches) or neutral processes (i.e., species

relative abundance)?, and 3) How do visits by birds that offer little to no pollinator services affect network properties?

Methods

Study Area

Our study was conducted in the high elevation Andean forests of Peru known as “elfin forest” in Unchog, Huanuco Department, within the Carpish Mountains (9° 42' 32.33" S, 76° 9' 39.13" W; 3700 m.a.s.l.). The elfin forest of Unchog is located within the transition between cloud forest and puna grassland. The area is characterized by a dry (May-September; < 150 mm rain/month) and wet (October-March, > 200 mm rain/month) season (Supplementary material Fig. A1). The study area is known to harbor a number of endemic bird (Parker & O’Neill, 1976, Young et al., 2009) and plant species (Beltran & Salinas, 2010).

Within the Unchog area, we sampled birds and plants in three elfin forest sites that had continuous vegetative cover and were ~8 ha each - Unchog, Magma and Simeompampa; sites were from 0.6 to 1.7 km apart from each other and intervening habitat between these elfin forest patches was dominated by pasture and shrub land. To explore similarity between sites, we calculated pairwise Sorenson dissimilarity indices for plant species observed in the three sites (see Trojelsgaard et al., 2015) where values close to 0 indicate very similar community composition and values close to 1 indicate very distinct communities. For our sites, Sorenson values ranged from 0.13 to 0.25, indicating very similar plant composition. Further, the flower-visiting bird communities were also very similar. Therefore, sites were combined for network analysis given overlap in plant and bird species, increased power to characterize network with increased sample size, and the likely non-independence of the sites.

This research was conducted under permits of the Peruvian government, Resolucion 151-2014-MINAGRI-DGFFS-DGEFFS and Resolucion 182-2012-AG- DGFFS-DGEFFS and the approval of the Institutional Animal Care & Use Committee of the University of Florida; IACUC Study #201105714.

Behavioral Observations

We quantified the flowering plant-bird network with direct observations on birds and plants using transects and focal plant watches (Ortiz-Pulido et al., 2012). These observations occurred between May 2011 and August 2014. Bird-plant interactions were observed using transects to sites approximately weekly during May-July 2011, February 2012, July-November 2012, January-July 2013, September 2013, and November 2013. During these visits, one of us (OG) walked along set transects inside the forest and along forest edges observing birds and recording which plants and how many flowers they visited during visits to the sites. If the bird visited more than one flower on a given plant during a visit, this was still scored as a single visit. In January 2014 and from May-August 2014 we recorded all visits and the number of flowers visited by birds using focal plant watches during 30-minute blocks. . During these 30 minute observation periods, multiple individual plants and plant species were simultaneously observed. Focal plant observations were centered on plant species exhibiting typical floral traits found in bird pollination syndrome (Willmer, 2011), and those that were known or suspected to be visited by birds based on previous observations (e.g., see Maruyama et al., 2013). The combined observations of birds from transects and focal plants were used to build the interaction network (Walther & Brieschke, 2001).

We spent a total of 190 hours (150 h in dry and 40 h in wet season) observing interactions over 79 days; 73 h, 52 h, and 65 h in Unchog, Magma, and Simiumpampa, respectively. This effort was divided between transects (79%) and focal plant watches (21%); 50.7% and 49.3% of observed interactions were recorded by transects and focal plant watches, respectively. More time was spent during the dry season both because of increased flower abundance as well as logistics of working in the area.

Plant Phenology and Abundance

We used transects to record abundance and phenology of flowers in the three sampling sites. We set up one transect per study site; these transects were sampled once a month at times when behavioral observations occurred. The presence or absence of flowers on a monthly basis was used to characterize phenology for each plant species. We counted the numbers of flowers per individual plant, or estimated the number of flowers by counting a subsample of flowers and then extrapolated to the whole plant for plants with > 50 flowers. We converted the number of flowers to flowers per ha based on area sampled; in some transects, we corrected for effective area sampled given steep topography and inability to sample some areas at a 20 m width. We used flower density as a measure of plant relative abundance, as it has been shown to be a better estimator than the density of individual plants due to the high variability of flowers per plant (Vasquez, Chacoff & Cagnolo, 2009). For this network analysis, data were combined across sites and years due to similarities in species composition among sites and because sample sizes did not warrant more detailed examination of spatial and temporal patterns.

197 **Nectarivorous Bird Phenology and Abundance**

198 To determine the phenology of birds at sites on a monthly basis, we scored presence or
199 absence of birds based on point-counts, ad-hoc and behavioral observations, and mist-
200 netting activities. To estimate overall relative abundance of bird species, we relied on
201 mist-netting activities. We used 10-15 mist-nets (6 m or 12 m length, 36 mm mesh) by
202 sampling bout in all the sites to capture birds, collect pollen when present from bills for
203 further studies, and measure bill length and other morphological characters. Nets were
204 distributed along forest edge and within the forest interior; nets were opened on one day
205 per month overlapping periods where behavioral observations or focal plant watches
206 occurred. Over the course of the study, mist-nets were opened a total of 2399 mist-net
207 hours (one 12-m net open 1 hour = 1 mist-net hour). Vegetation height in the study area
208 is 5 m on average and, thus, most birds that use the forest are expected to be captured
209 using mist-nets. We recognize that not all birds are equally captured by mist-nets (e.g.
210 Remsen & Good, 1996), and thus estimates may be biased. Nonetheless, in montane
211 forest mist-netting is widely used as a recommended method for bird assessment (Lloyd
212 et al., 2012, Maglianesi et al., 2014). As for plants, we combined the results among sites
213 to characterize the bird community and bird-flower observations.

214 **Morphological Measurements**

215 We measured bill length and width (to nearest 0.1 mm) of birds that visited flowers
216 using individuals captured in mist nets, supplemented by measurements from museums
217 and published literature. We measured an average of 25 specimens per bird species.
218 Since hummingbirds extend their tongues to access nectar inside the flowers, we added
219 1/3rd of the total length of the bird bill following Vizentin-Bugoni, Maruyama & Sazima
220 (2014); in a later paper Vizentin-Bugoni et al. (2016) recommend using a 80% tongue

extension to correct bill measurement, although they found no difference in results when either 33% or 80% is used. We measured the length and the width (to nearest 0.1 mm) of flower corollas for plants visited by birds in the field, supplemented by measurements from herbarium specimens. The length was measured from the flower opening to the base of the nectar chamber, while the width was measured at the flower's widest aperture.

Network Description

Data on observed interactions at flowers were recorded as matrices with the bird flower visitors in columns, the plant species in rows and cell values representing the number of visits following Jordano, Vasquez & Bascompte (2009) and Bascompte & Jordano (2014). We examined sampling completeness of nectarivorous birds and interactions in the study area using the Chao2 estimator in EstimateS version 9.1 (Colwell, 2013) following Chacoff et al. (2012). See Supplementary material Fig. A2.

We calculated the following network metrics: connectance, nestedness, interaction evenness and interaction asymmetry (Bascompte & Jordano, 2014). We also calculated a specialization index at the network level (H2) which is resilient to sample size and network size (Blüthgen, Menzel & Blüthgen, 2006). Connectance, which varies from 0 to 1, is the realized proportion of possible links in the network (i.e., if every bird visited flowers of every plant species, then connectance would equal 1). Nestedness provides a measure of the aggregation of the distribution of interactions in the network (Nielsen & Bascompte, 2007). To calculate nestedness, we used a weighted nestedness measure (WNODF) because WNODF has been found to be more robust in quantitative networks (Almeida-Neto & Ulrich, 2011). When WNODF is close to 0 there is no evidence of aggregation in the matrix, whereas as it approaches 100, the interactions are

increasingly nested. Interaction evenness is based on Shannon's index following Tylianakis, Tscharntke & Lewis (2007) and provides a measure of the distribution of interactions in the network. High skewness in the distribution of interactions is indicative of an uneven network. Interaction asymmetry, which measures the strength and directionality of the interaction of one level to the other (birds and plants in this case), was calculated for plants and for birds separately; higher absolute values, from -1 to 1 indicate more uneven or skewed distribution of interaction frequencies. H2 measures specialization in the matrix based on the H index of Shannon-Wiener (Blüthgen, Menzel & Blüthgen, 2006). H2 describes how much the observed distribution of species interactions deviate from the frequency of the expected distribution. It ranges from 0 to 1; when H2 is closer to 1, the interactions are considered to reflect a high degree of specialization. Connectance (conn), nestedness (WNODF), evenness (interaction evenness), specialization (H2), and interaction asymmetry (intrasymm) were calculated using bipartite package version 2.05 in R (Dormann, Gruber & Fründ, 2008). See Supplementary material Table A1 for R source code.

Interaction Probability Matrices

We built interaction probability matrices using the framework proposed by Vasquez, Chacoff & Cagnolo (2009) where interaction frequencies were assumed to be determined by relative abundances, temporal (phenological) overlap, and morphological overlap. As above, these probability matrices are based on the data compiled across the three study sites. Relative abundance probability matrices will provide a test of the neutrality hypothesis, while the latter two (phenology, morphology) provide a test of the biological constraints hypothesis in explaining observed network structure and interaction frequencies.

To develop a phenological interaction probability matrix (PhenMat), we first compiled matrices of temporal overlap for plants and birds. In these matrices, plant or bird species were rows and sampling months were columns with ones and zeros for presence and absence; the total number of months with simultaneous data on both plants and birds were 15. We then used matrix multiplication to obtain temporal overlap between birds and plants. This matrix of temporal overlap was normalized such that the matrix cells added up to a total of one; individual cells with higher values indicated greater temporal overlap, or probability of interaction, of any particular bird-plant pair. An abundance interaction probability matrix (AbMat) was made in a similar way as the phenological matrix, compiling matrices of abundance for plants and for birds and overlapping them in the same months. Here the cells of the plant matrix were the number of individual flowers per ha, by species summed across the sites. The cells of the bird matrix were the number of individuals captured in mist-nets per 100 net-hours (Maglianesi et al., 2014). We multiplied the two abundance matrices and the product was normalized as explained above.

The morphology interaction probability matrix (MorMat) was generated to account for morphological mismatches in length of a bird's bill (as corrected to account for tongue, see above) and corolla length (Maruyama et al., 2014; Vizentin-Bugoni, Maruyama & Sazima, 2014). However, instead of using mean length, we used the probability of size overlap between ranges of flower length and bill length. We believe this approach is more realistic than a simple yes or no criterion because of existing intra-specific variation in morphological traits among individuals (Gonzalez-Castro et al., 2015). We first noted the range of a flower's length and the range of a bird's bill. If the lower limit of

the bill's range was longer than the lower limit of the flower's length, the interaction was scored as 100% possible with a cell value of 1. If the upper limit of the bill's range was shorter than the lower limit of the flower's length, the interaction was considered impossible and a cell value of 0 was assigned. When there was overlap of ranges between the length of a bird's bill and the length of a corolla, we calculated the proportion of overlap and assigned that value to the cell. Furthermore, we considered some exceptions when the flower's width was expansive enough for a bird's head to enter the corolla. For example, the flowers of *Puya* are longer and wider than any of the bird's bills, so we considered that all bird species could visit *Puya* and assigned a value of 1 for all possible interations with this flowering species. In cases where size overlap was zero, but the observed interaction frequency was not zero, we assigned an arbitrary value of 1×10^{-8} which is less probable than any other case in the phenology and abundance matrices (Gonzalez-Castro et al., 2015). Further, the placement of zero in the probability matrix when the observed interaction value is not zero, results in a failed calculation of the multinomial function (see next topic). As for other interaction probability matrices, we normalized this matrix so that cell values sum to 1.

We also considered the possibility that factors might act together to influence the observed bird-flower network. To do this, we used matrix multiplication to create new interaction probability matrices for all possible combinations - AbMat*PhenMat, AbMat*MorMat, PhenMat*MorMat and AbMat*PhenMat*MorMat - and then normalized these new matricies so that the cells summed to one. Following Vasquez, Chacoff & Cagnolo (2009) we also included a "Null" probability matrix where all pairwise interactions in the matrix made of observed plant and animal species had the same

probability of occurrence (i.e., all cell values in the matrix are equal to 1/IJ, where *I* and *J* are number of plant and bird species in the network).

Testing Neutrality and Biological Constraints Hypotheses

To test whether neutral processes or biological constraints best predicted observed interaction frequencies, we used a likelihood approach. Support for either of these hypotheses arises when the probability matrix can predict the observed interactions, such that higher probabilities of cells should match with higher frequencies of observed interactions (see Vasquez, Chacoff & Cagnolo, 2009, Vizentin-Bugoni, Maruyama & Sazima, 2014). Akaike information criteria (AIC) was used to compare the relative ability of these various hypothesized models to explain observed interactions. We assumed that probability of interaction between a given bird and flowering plant followed a multinomial distribution (Vasquez, Chacoff & Cagnolo, 2009). We used the number of species (44 in total), to determine the number of parameters used to weight different models' complexities when calculating AIC. So 44 was used when one factor was calculated (i.e. abundance), 88 if two factors (i.e. phenology and morphology) and 132 if three factors (i.e. phenology, morphology and abundance). As in Vizentin-Bugoni, Maruyama & Sazima (2014) we compared these results to those based on using the number of factors (abundance, phenology, morphology; either. e., 1, 2 or 3) to weight model complexity, and checked for differences. The function *dmultinomin* in the *stats* package R was used to calculate likelihood (R core team 2014).

To determine the degree to which the hypotheses predicted network metrics, such as connectance, nestedness, or asymmetry, we used a randomization algorithm *mgen* from *bipartite* package in R (Vasquez, Chacoff & Cagnolo, 2009). Using the number of

interactions actually observed, the randomization algorithm assigned interactions to each probability interaction matrix, including all combined interaction probability matrices, such that all species received at least one interaction (see Vasquez, Chacoff & Cagnolo, 2009). From these randomized matrices, we calculated network statistics (mean and 95% confidence intervals from 1000 repetitions using function *confint* in *bipartite* package in R) and compared the overlap with network statistics generated from our observed interaction matrix. If the observed metric values were found to be within the 95% confidence intervals of those generated from interaction probability matricies, we interpreted this to mean that factors (e.g., relative abundance, phenology, morphology, or their combination) could explain or were consistent with hypothesized explanations of drivers of mutualistic interactions at the community level.

Effect of Nectar-robbers on Network Properties

To examine the influence of nectar robbers on network properties, we recalculated all of the above matrices after removing interactions that likely did not result in pollination, such as visits to base of flowers through holes cut by *Diglossa* flowerpiercers or bees. This new interaction matrix is more equivalent to a pollinator-plant network than our bird-flowering plant network which included all flowering plant visits (Maruyama et al., 2015). This pollinator-plant network was then used to evaluate our third question that examined the impact of flowerpiercers on network structure and network properties as described above

Results

General Results

Bird-flower network. We observed a total of 17 bird species visiting flowers from 27 plant species in all our elfin forest sites combined.These observations included 278

362 pairwise interactions representing 74 unique interactions of bird visits to plants
363 (Supplementary Table A2). Avian flower visitors included 12 species of hummingbirds
364 (Trochilidae), 4 species of flowerpiercers (*Diglossa*: Thraupidae) and one conebill
365 (*Conirostrum*: Thraupidae). Flowering plants observed to be visited by birds included
366 plants from 24 genera, 16 families and 14 orders (Fig. 1, and Supplementary Table A3).
367 Mutualistic networks are typically characterized by many fewer observed interactions
368 than possible (e.g., Chacoff et al., 2012), and this was also true here. We detected only
369 55.2% of the estimated interactions for the whole network using Chao2 (Supplementary
370 material Fig. A2). Despite this, the observed number of unique interactions appeared to
371 be reaching an asymptote with our sampling effort.

372 **Interactions in the network.** We found that *Metallura theresiae, Pterophanes*
373 *cyanopterus* and *Diglossa mystacalis*, birds considered to be indicators of the elfin
374 forest (Parker, Stotz & Fitzpatrick, 1996), were the most important bird species in terms
375 of flowering plant interactions (Fig. 1). *Metallura* visited a total of 26 species, while *D.*
376 *mystacalis* visited 10 and *Pterophanes* visited 4 species, respectively. Among plants,
377 *Brachyotum lutescens, Tristerix longebracteatus* and *Fuchsia decussata* were the
378 species with the most interactions with visits from 8, 7, and 7 bird species, respectively
379 (Fig. 1). When compared to the “null” model, the bird-flowering plant network was found
380 to be significantly less connected and more nested (Figs. 2a, b). In addition, the network
381 was significantly less even, more specialized and exhibited greater asymmetry among
382 bird or plant species than expected (Figs. 2c-f).

383 **Plant-visitation network determinants**

384 We found that biological constraints as exemplified by phenology best explained the
385 observed interaction frequencies using the likelihood approach (Table 1). This result
386 suggests that the degree of temporal overlap among interacting players in a bird-
387 flowering plant network is an important driver of the observed interaction frequencies.
388 Results were consistent whether either the number of species or the number of matrices
389 used as parameters in likelihood analysis to compare among models (Supplementary
390 material Fig. A3).

391 Biological constraints, either through phenological constraints or phenology in
392 combination with morphology, were found to explain nestedness in the elfin forest bird-
393 plant network (Fig. 2b). Network structure also was found to be explained by neutral
394 processes, as measured by relative abundance of birds and flowering plants, in some
395 cases. For example, connectance within the network was predicted via a combination of
396 relative abundance of interacting players and biological constraints (Fig. 2a). Further,
397 relative abundance was found to explain evenness and relative abundance alone, or in
398 combination with morphology, explained asymmetry (Fig. 2e, 2f). In contrast, neither
399 biological constraints nor neutral processes were able to explain specialization (Fig. 2d).

400 **Difference in network properties with and without nectar-robbers**

401 To investigate the influence of nectar robbers in the plant-bird network, we removed all
402 interactions that involved observed ‘illegitimate” visits to flowers (i.e., birds entered
403 flower at nectar base rather than through the corolla opening). This reduced the original
404 network of 17 birds and 27 plants to 12 birds and 26 plants; all *Diglossa* species
405 dropped out of the network given that all observations were from *Diglossa* or
406 *Conirostrum* removing nectar from the base of flowers. Other interactions deleted were

Heliangelis amestyticollis - Desfontainia spinosa, Pterophanes cyanopterus - Passiflora cumbalensis, Metallura tyrianthina - Passiflora cumbalensis and *Metallura theresiae* with *Desfontainia spinosa, Fuchsia decussata* and *Passiflora cumbalensis*. Removal resulted in the loss of all interactions with *Passiflora cumbalensis*, given that all observations to this flower occurred via the floral base and were not considered "legitimate".

The exclusion of illegitimate visits by primary and secondary nectar-robber birds resulted in a decrease of connectance, nestedness and evenness, but increase in specialization when comparing metrics with the null matrix and the original matrix. Asymmetry shifted in different ways with an increase for plants and decrease for birds (compare Figs. 2 and 3). Abundance and its combination with morphology were useful to explain evenness and asymmetry for plant and birds, while phenology in combination with morphology predicted connectance. However the exclusion of the nectar-robbers in the network did not change the influence of phenology as the "best" predictor of species interactions (Table 1).

Discussion

Network Structure

We found that bird-flowering plant networks in the elfin forests studied here are characterized by fewer interactions than those possible. These results are consistent with most other pollination networks studied. For example, Chacoff et al. (2012) also observed about 55% of all possible interactions in a desert plant-pollinator network sampled over 4 years. Yet, despite their time investment, Chacoff et al. (2012) estimate that a five-fold increase in sample effort would be needed to even possibly detect 90% of the possible interactions. The sampling effort invested in our study (190 hours)

spread over multiple years matches or exceeds many other studies (e.g., Rodriguez-Flores, Stiles & Arizmendi, 2012, Ortiz-Pulido et al., 2012, Maruyama et al., 2014), but is considerably less than studies that use video-cameras to record interactions (Maglianesi et al., 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014, Vinzentin-Bugoni et al., 2016). The use of remote technology in flowering plant observational studies hold much promise, but are nonetheless, difficult or expensive to use in sites where flowering plant diversity is high.

Like several mutualistic networks, the elfin forest network was also found to be nested (Fig.3b; see also Rodriguez-Flores, Stiles & Arizmendi, 2012, Bascompte et al., 2003). Our results, however, contrast with some studies in tropical dry forests (Arizmendi & Ornelas, 1990) and Atlantic forests (Vizentin-Bugoni, Maruyama & Sazima, 2014) where the plant-bird network was not nested using the same qualitative metric (WNODF). However in a more recent analysis an updated version of this Atlantic forest network was nested using a binary measure (Vinzentin-Bugoni et al., 2016). Bascompte et al. (2003) suggest that increases in the number of species in networks might result in greater nestedness. Indeed, when we reduced the network to only include species and observations that resulted in “legitimate” flower visits, we found nestedness values were lower although the network was still more nested than expected. In the elfin forest the abundance of the flowerpiercers facilitating access to hummingbirds would take out several “forbidden links” as limitations, diminishing nestedness. Sampling effort did not likely bias our estimate of nestedness given that WNODF is known to be a robust estimator for nestedness (Vizentin-Bugoni et al., 2016).

453 The important species in networks, based on their abundance and frequency of
454 interactions, often provide insights about the ecological or evolutionary implications of
455 the network (Bascompte & Jordano, 2007). In this system the most abundant flower
456 visitor in elfin forests (*Metallura theresiae*) also had the greatest number of connections
457 and interacted with the most flowering plant species (Fig. 1). *Metallura theresiae* is quite
458 aggressive and its behavior may interfere with other flower visitors, and thus, may affect
459 visitation rates (Justino, Maruyama & Oliveira, 2012). In contrast, the plant which had
460 the greatest number of flowers in this system, *Brachyotum lutescens*, did not have the
461 greatest number of flower visits nor the greatest number of visiting species. Similar
462 results were reported by Rodriguez-Flores, Stiles & Arizmendi (2012) in a plant-
463 hummingbird network in Colombia, where hermit hummingbirds were the most
464 abundant birds, visiting the greatest number of plant species in the lowland Amazon.
465 In the elfin forest system we found that abundance models combined with phenology or
466 morphology can explain network connectance, as well as evenness and asymmetry for
467 both plants and birds. Nestedness was predicted by phenology and phenology with
468 morphology, matching results from an insect-plant network in a subalpine community
469 (Olito & Fox, 2015). In contrast, in plant-hummingbird networks in the Brazilian Atlantic
470 forest (Vizentin-Bugoni, Maruyama & Sazima, 2014) neither abundance, morphology
471 nor phenology were associated with network metrics, except the mixed model of
472 phenology, morphology and abundance for the asymmetry of the birds in the network.

473 **Observed interaction frequencies**

474 In this study, the observed interactions, either with the full suite of avian flower visitors
475 or the reduced set of “legitimate” visitors, were best explained by phenology. Greater
476 phenological overlap in birds and plants led to greater number of interactions between

pairs of species. The importance of phenology in explaining pairwise interactions has also been found in other studies, but was still found to be a poor predictor of observed interactions in some cases (Encinas-Viso, Revilla & Etienne, 2012, Olito & Fox, 2015). In contrast, morphology alone, or morphology interacting with phenology, have been found to explain observed pairwise interactions in some hummingbird-plant networks (Maglianesi et al., 2014, Maruyama et al., 2014, Vizentin-Bugoni, Maruyama & Sazima, 2014). The importance of phenology in driving interactions highlight the potential vulnerabilities of these mutualism networks to climate change, which can alter phenological patterns (Dalsgaard et al, 2011, Rafferty, CaraDonna & Bronstein, 2015). Elfin forests which are located at the top of tropical mountains are likely to be particularly impacted by climate change and, thus, as phenological patterns change, nectarivorous birds, a number of which are endemic, may face lowered availability of resources and potential invasion of competitors (Sekercioglu, Primack & Wormworth, 2012).

The nectar robber effect in the network

Morphological constraints were not an important driver in our system, or only were important when combined with abundance or phenology for some network metrics. This result is likely due to the presence of *Diglossa* flowerpiercers. The opportunities for morphological constraints to operate in this system are many as several flowering plant species have corollas that exceed the length of a number of flower visitors. Yet, the forbidden interactions in this network, which hypothetically should restrict access to nectar for small-billed birds for a number of flowering species, were allowed. *Diglossa*, which cut holes in base of flowers to gain access to nectar, act as facilitators for other species (hummingbirds with small bills) that would not be able to access to long-corolla

flowers (Bruno, Stachowicz & Bertness, 2003); large bees are also known to cut holes at base of flowers in this system and may also serve as “facilitators”. Consequently, connectance in the network increases with flowerpiercers in the system (Fig. 2a with Fig. 3a). In contrast, we found that network specialization increased markedly when nectar-robbers were removed from the network (Fig. 2d with Fig. 3d).

In this study several factors might influence our results. First, we observed only about 55% of all possible pairwise interactions. If our system were undersampled, including potentially “missing” interactions due to not capturing flowering events because of limited sampling, we might have been less likely to see biologically constrained interactions, and thus, may have overestimated their effect. However, we did find that the number of observed pairwise interactions appeared to be reaching an asymptote, suggesting we had sufficiently characterized the network. Second, as most observations were based on transects, we might expect that abundance may emerge as a driver of network interactions and properties as abundant species may be sampled more often in flocal plant watches. Nevertheless, the amount of interactions detected by transects was almost the same as the interactions detected by focal watch. The importance of relative abundance as a driver, however, did not play a large role in explaining observed interactions when compared to other factors. Third, we also did not examine the importance of body size of birds and nectar production in explaining network structure. Nectar production can be highly variable both within and among plants and is difficult to adequately measure when dealing with many plant species. Large-bodied birds, in particular, might focus more on plant species that produce more nectar. These factors might be especially important in explaining network properties

such as specialization. Further studies would benefit from including additional predictors of networks.

In summary, in elfin forests biological processes were important in predicting observed interactions between flowering plants and birds, while neutral and biological processes interacted to explain network components. In particular, the importance of neutral processes (i.e., abundance) was the single best predictor for four of six network metrics in networks with and without illegitimate interactions. However, the importance of phenology for both species interactions and network structure suggests that the ecological and evolutionary dynamics of networks are likely to be altered with climate change. As such, future studies should focus on how phenological changes, as well as changes in abundance impact network dynamics.

Acknowledgements

We thank Camilo Diaz, Bernie Britto and Juan Diego Shoobridge for plant identification. OG thanks Jessica Burnett and J. Vizentin-Bugoni for their help in R codes.

References

Almeida-Neto M, Ulrich W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software 26:173-178. DOI:10.1016/j.envsoft.2010.08.003

Arizmendi MD, Ornelas JF. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. Biotropica 22:172-180. DOI: 10.2307/2388410

Bascompte J. 2010. Structure and Dynamics of Ecological Networks. Science 329:765-766. DOI: 10.1126/science.1194255

547 Bascompte J, Jordano P. 2007. Plant-animal mutualistic networks: The architecture of
548 biodiversity. Annual Review of Ecology and Systematics 38:567-593. DOI:
549 10.1146/annurev.ecolsys.38.091206.095818

550 Bascompte J., Jordano P. 2014. Mutualistic networks. Monographs in Population
551 Biology Series, no. 53. Princeton University Press.

552 Bascompte J, Jordano P, Melian C, Olesen JM. 2003. The nested assembly of plant-
553 animal mutualistic networks. Proceedings of the National Academy of Sciences of the
554 United States of America 100:9383-9387. DOI: 10.1073/pnas.1633576100

555 Beltran H, Salinas I. 2010. The vascular flora and vegetation of the Carpish Humid
556 Montane Forests (Huanuco - Peru). Arnaldoa 17(1): 107 - 130

557 Blüthgen N, Menzel F, Blüthgen N. 2006. Measuring specialization in species
558 interaction networks. BMC Ecology 6:9. DOI: 10.1186/1472-6785-6-9

559 Brack A, Mendiola C. 2000. Ecologia del Peru. Lima: Bruño.

560 Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological
561 theory. Trends in Ecology and Evolution 18:119-125. DOI: 10.1016/S0169-
562 5347(02)00045-9

563 Burkle LA, Alarcon R. 2011. The future of plant-pollinator diversity: understanding
564 interaction networks across time, space, and global change. American Journal of
565 Botany 98:528-538. DOI: 10.3732/ajb.1000391

566 Chacoff NP, Vazquez DP, Lomascolo SB, Stevani EL, Dorado J, Padron B. 2012.
567 Evaluating sampling completeness in a desert plant-pollinator network. Journal of
568 Animal Ecology 81:190-200. DOI: 10.1111/j.1365-2656.2011.01883.x

569 Colwell RK. 2013. EstimateS: Statistical estimation of species richness and shared
570 species from samples. Version 9. Persistent URL <purl.oclc.org.estimates>

571 Dalsgaard, B., Magård E., Fjeldså J., Martín González A.M., Rahbek C., Olesen J.M.,
572 Ollerton J., Alarcón R, Cardoso Araujo A, Cotton PA, Lara C, Machado CG, Sazima I,
573 Sazima M, Timmermann A, Watts S, Sandel B, Sutherland WJ, Svenning JC. 2011.
574 Specialization in plant-hummingbird networks is associated with species richness,
575 contemporary precipitation and quaternary climate-change velocity. PLoS ONE 6,
576 e25891. DOI: http://dx.doi.org/10.1371/journal.pone.0025891

577 Dormann CF, Gruber B, Fründ J. 2008. Introducing the bipartite package: Analysing
578 Ecological Networks. R News 8(2):8-11.

579 Ebeling A, Klein A-M, Tscharntke T. 2011. Plant-flower visitor interaction webs:
580 Temporal stability and pollinator specialization increases along an experimental plant
581 diversity gradient. Basic and Applied Ecology 12:300-309. DOI:
582 10.1016/j.baae.2011.04.005

583 Encinas-Viso T, Revilla A, Etienne R. 2012. Phenology drives mutualistic network
584 structure and diversity. Ecology Letters 15:198-208. DOI: 10.1111/j.1461-
585 0248.2011.01726.x

586 Gonzalez-Castro A, Yang S, Nogales M, Carlo TA. 2015. Relative importance of
587 phenotypic trait matching and species' abundances in determining plant-avian seed
588 dispersal interactions in a small insular community. - AoB PLANTS 7.
589 DOI: 10.1093/aobpla/plv017.

590 Janecek S, Riegert J, Sedlacek O, Bartos M, Horak D, Reif J, Padysakova E, Fainova
591 D, Antczak M, Pesata M, Mikes V, Patacova E, Altman J. 2012. Food selection by avian
592 floral visitors: an important aspect of plant-flower visitor interactions in West Africa.
593 Biological Journal of the Linnean Society 107:355-367. DOI: 10.1111/j.1095-
594 8312.2012.01943.x

595 Jordano P, Bascompte J, Olesen JM. 2003. Invariant properties in coevolutionary
596 networks of plant-animal interactions. Ecology Letters 6:69-81. DOI: 10.1046/j.1461-
597 0248.2003.00403.x

598 Jordano P, Vázquez D, Bascompte J. 2009. Redes complejas de interacciones
599 mutualistas planta-animal. *in* Medel, R, Aizen M & Zamora R, editors. Ecología y
600 evolución de las interacciones planta-animal: conceptos y aplicaciones. Santiago de
601 Chile: Editorial Universitaria, 17-41.

602 Justino DG, Maruyama PK, Oliveira PE. 2012. Floral resource availability and
603 hummingbird territorial behaviour on a Neotropical savanna shrub. Journal of
604 Ornithology 153:189-197. DOI: 10.1007/s10336-011-0726-x

605 Lewinsohn T, Prado P, Jordano P, Bascompte J, Olesen JM. 2006. Structure in plant-
606 animal interaction assemblages. Oikos 113:174-184. DOI: 10.1111/j.0030-
607 1299.2006.14583.x

608 Lloyd H, Sevillano Rios S, Marsden SJ, Valdes-Velasquez A. 2012. Bird community
609 composition across an Andean tree-line ecotone. Austral Ecology 37(4):470-478. DOI:
610 10.1111/j.1442-9993.2011.02308.x

611 Maglianesi MA, Blüthgen N, Boehning-Gaese K, Schleuning M. 2014. Morphological
612 traits determine specialization and resource use in plant-hummingbird networks in the
613 neotropics. Ecology 95:3325-3334. DOI: 10.1890/13-2261.1

614 Maruyama PK. Oliveira GM, Ferreira C, Dalsgaard B, Oliveira PE. 2013. Pollination
615 syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna
616 hummingbirds. Naturwissenschaften 100:1061-1068. DOI: 10.1007/s00114-013-1111-9

617 Maruyama PK, Vizentin-Bugoni J, Oliveira GM, Oliveira PE, Dalsgaard B. 2014.
618 Morphological and Spatio-Temporal Mismatches Shape a Neotropical Savanna Plant-
619 Hummingbird Network. Biotropica 46:740-747. DOI: 10.1111/btp.12170

620 Maruyama PK., Vizentin-Bugoni J, Dalsgaard B, Sazima I, Sazima M. 2015. Nectar
621 robbery by a hermit hummingbird: Association to floral phenotype and its influence on
622 flowers and network structure. Oecologia 178: 783793.

623 Nielsen A, Bascompte J. 2007. Ecological networks, nestedness and sampling effort.
624 Journal of Ecology 95:1134-1141. DOI: 10.1111/j.1365-2745.2007.01271.x

Nuismer SL, Jordano P, Bascompte J. 2013. Coevolution and the architecture of mutualistic networks. Evolution 67:338-354. DOI: 10.1111/j.1558-5646.2012.01801.x

Olesen JM, Bascompte J, Dupont Y, Jordano P. 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences of the United States of America 104:19891-19896. DOI:10.1073/pnas.0706375104

Olesen JM, Bascompte J, Dupont Y, Elberling H, Rasmussen C, Jordano P. 2011. Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B-Biological Sciences 278:725-732. DOI: 10.1098/rspb.2010.1371

Olito C, Fox JW. 2015. Species traits and abundances predict metrics of plant-pollinator network structure, but not pairwise interactions. Oikos 124:428-436. DOI: 10.1111/oik.01439

Ortiz-Pulido R, Diaz SA, Valle-Diaz OI, Fisher A. 2012. Hummingbirds and the plants they visit in Tehuacan-Cuicatlan Biosphere Reserve, Mexico. Revista Mexicana de Biodiversidad 83:152-163.

Parker III TA, O'Neill JP. 1976. Introduction to bird-finding in Peru: Part II. The Carpish Pass region of the eastern Andes along the Central Highway. Birding 8: 205-216.

Parker III TA, Stotz DF, Fitzpatrick JW. 1996. Ecological and distributional databases. Pages 113-436 *in* Stotz DF, Fitzpatrick JW, Parker III TA, Moskovits DK, editors. Neotropical birds: ecology and conservation. Chicago: University of Chicago Press.

644 R Core Team 2014. R: A language and environment for statistical computing. - R
645 Foundation for Statistical Computing. http://www.R-project.org/.

646 Rafferty NE, CaraDonna PJ, Bronstein JL. 2015. Phenological shifts and the fate of
647 mutualisms. Oikos 124:14-21. DOI: 10.1111/oik.01523

648 Ramirez O, Arana M, Bazan E, Ramirez A, Cano A. 2007. Assamblages of two mammal
649 and bird communities in two major ecological units in the high Andean plateau of
650 southern Peru. Ecologia Aplicada 6(1-2):1-15.

651 Remsen JV, Good DA. 1996. Misuse of data from mist-net captures to assess relative
652 abundance in bird populations. Auk 113:381-398.

653 Rodriguez-Flores CI, Stiles FG, Arizmendi MC. 2012. Pollination network of a hermit
654 hummingbird community (Thochilidae, Phaetornitidae) and their nectar resources in the
655 Colombian Amazon. Ornitologia Neotropical 23:85-100.

656 Rojas-Nossa SV. 2013. Asociación entre el robo de néctar y las características florales
657 en una comunidad montana de los Andes colombianos. Revista Ecosistemas
658 22(2):107-112. DOI: 10.7818/ECOS.2013.22-2.16

659 Rojas-Nossa SV, Sánchez, JM, Navarro L. 2016, Nectar robbing: a common
660 phenomenon mainly determined by accessibility constraints, nectar volume and density
661 of energy rewards. Oikos. DOI: 10.1111/oik.02685

662 Sekercioglu CH, Primack RB, Wormworth J. 2012. The effects of climate change on
663 tropical birds. Biological Conservation 148:1-18. DOI:10.1016/j.biocon.2011.10.019

664 Thébault E, Fontaine C. 2010. Stability of Ecological Communities and the Architecture
665 of Mutualistic and Trophic Networks. Science 329: 853-856. DOI:
666 10.1126/science.1188321

667 Trojelsgaard K, Jordano P, Carstensen DW, Olesen JM. 2015. Geographical variation in
668 mutualistic networks: similarity, turnover and partner fidelity. Proceedings. Biological
669 sciences / The Royal Society 282.

670 Tylianakis JM, Tscharntke T, Lewis OT. 2007. Habitat modification alters the structure
671 of tropical host-parasitoid food webs. Nature 445:202-205. DOI: 10.1038/nature05429

672 Vazquez DP, Aizen MA. 2004. Asymmetric specialization: A pervasive feature of plant-
673 pollinator interactions. Ecology 85:1251-1257. DOI: 10.1890/03-3112

674 Vasquez DP, Aizen MA. 2006. Community-wide pattern of specialization in Plant-
675 Pollinator interactions revealed by null models. *In*: Waser NM, Ollerton J, editors. Plant-
676 Pollinator Interactions: From specialization to generalization. Chicago: University of
677 Chicago Press, 200-219.

678 Vazquez DP, Chacoff NP, Cagnolo L. 2009. Evaluating multiple determinants of the
679 structure of plant-animal mutualistic networks. Ecology 90:2039-2046. DOI:10.1890/08-
680 1837.1

681 Vizentin-Bugoni J, Maruyama PK, Sazima M. 2014. Processes entangling interactions
682 in communities: forbidden links are more important than abundance in a hummingbird-
683 plant network. Proceedings of the Royal Society B-Biological Sciences 281:20132397
684 DOI: 10.1098/rspb.2013.2397

685 Vizentin-Bugoni J, Maruyama PK, Debastiani VJ, Duarte LD, Dalsgaard B, Sazima M.
686 2016. Influences of sampling effort on detected patterns and structuring processes of a
687 Neotropical plant-hummingbird network. Journal of Animal Ecology 85:262-272.
688 DOI: 10.1111/1365-2656.12459

689 Walther BA, Brieschke H. 2001. Hummingbird-flower relationships in a mid-elevation
690 rainforest near Mindo, Northwestern Ecuador. International Journal of Ornithology
691 4:115-135.

692 Willmer P. 2011. Pollination and Floral Ecology. Princeton: Princeton University Press.

693 Winfree R, Williams NM, Dushoff J, Kremen C. 2014. Species abundance, not diet
694 breadth, drives the persistence of the most linked pollinators as plant-pollinator
695 networks disassemble. American Naturalist 183:600-611. DOI: 10.1086/675716

696 Young BE, Franke I, Hernandez PA, Herzog SK, Paniagua L, Tovar C, Valqui T. 2009.
697 Using spatial models to predict areas of endemism and gaps in the protection of
698 Andean slope birds. Auk 126(3):554-565.
699 DOI: http://dx.doi.org/10.1525/auk.2009.08155

Figure 1(on next page)

Pairwise interactions in the bird-flowering plant visitation network in the elfin forest of Unchog (Peruvian Andes). Each green box represents a plant species; blue boxes are hummingbirds, orange are flowerpiercers. The lines represent the interactions an

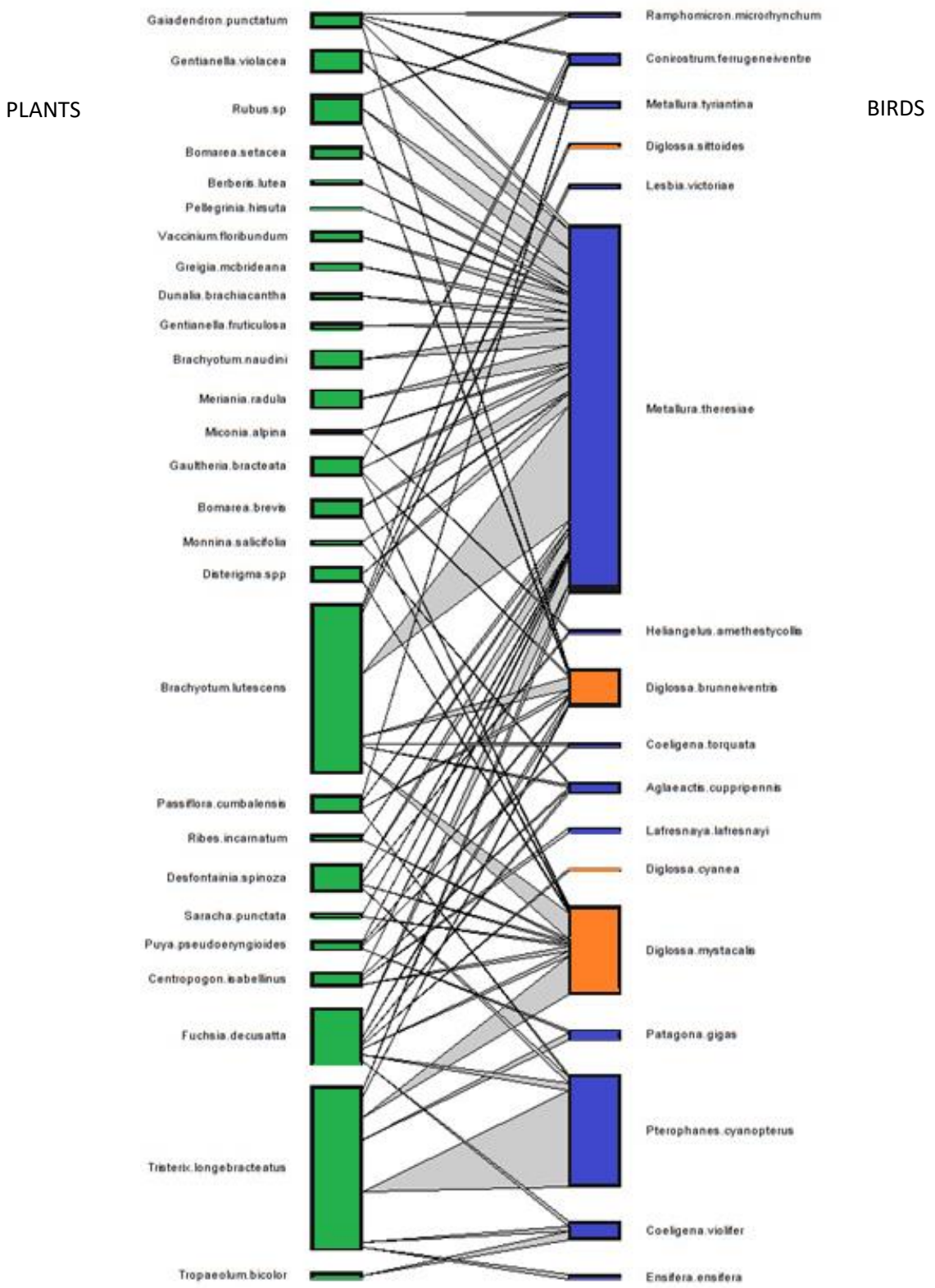

PLANTS
BIRDS
Gaiadendron.punctatum
Gentianella.violacea
Rubus.sp
Bomarea.setacea
Berberis.lutea
Pellegrinia.hirsuta
Vaccinium.floribundum
Greigia.mcbrideana
Dunalia.brachiacantha
Gentianella.fruticulosa
Brachyotum.naudinii
Meriania.radula
Miconia.alpina
Gaultheria.bracteata
Bomarea.brevis
Monnina.salicifolia
Disterigma.spp
Brachyotum.lutescens
Passiflora.cumbalensis
Ribes.incarnatum
Desfontainia.spinosa
Saracha.punctata
Puya.pseudoeryngioides
Centropogon.isabellinus
Fuchsia.decussata
Tristerix.longebracteatus
Tropaeolum.bicolor
Ramphomicron.microrhynchum
Conirostrum.ferrugineiventre
Metallura.tyriantina
Diglossa.sittoides
Lesbia.victoriae
Metallura.theresiae
Heliangelus.amethestycolis
Diglossa.brunneiventris
Coeligena.torquata
Aglaeactis.cupripennis
Lafresnaya.lafresnayi
Diglossa.cyanea
Diglossa.mystacalis
Patagona.gigas
Pterophanes.cyanopterus
Coeligena.violifer
Ensifera.ensifera

Table 1(on next page)

Difference of the AIC values between various models predicting observed interaction frequencies and the model with lowest AIC value.

Ab= Abundance, Phen= Phenology, Mor= Morphology, Null= Null matrix. The visitation network includes all bird species and the pollination network excludes interactions where birds did not visit flowers legitimately. In both matrices, phenology was the best predictor of interaction frequencies.

Table 1. Difference of the AIC values between various models predicting observed interaction frequencies and the model with lowest AIC value. Ab= Abundance, Phen= Phenology, Mor= Morphology, Null= Null matrix. The visitation network includes all bird species and the pollination network excludes interactions where birds did not visit flowers legitimately. In both matrices, phenology was the best predictor of interaction frequencies.

Matrix	Δ AIC visitation network	Δ AIC pollination network
Phen	0	0
Ab	428.2	180.3
Null	588.6	433.4
Ab*Phen	660.1	387.0
Phen*Mor	1262.9	122.9
Ab*Mor	1846.8	365.0
Mor	1912.1	575.9
Ab*Phen*Mor	2067.4	563.7

Figure 2(on next page)

Comparison of the network metrics produced by probability matrices (mean and 95% confidence intervals) and the observed network values for the bird-flowering plant network of the elfin forest.

Network metrics are: (a) connectance, (b) weighted nestedness (WNODF), (c) evenness, (d) specialization, (e) asymmetry of plants (f) asymmetry of birds. The dashed vertical lines in each graph represents the value for the observed matrix. Matrix codes: Ab= Abundance, Phen=Phenology, Mor=Morphology, Null= Null matrix.

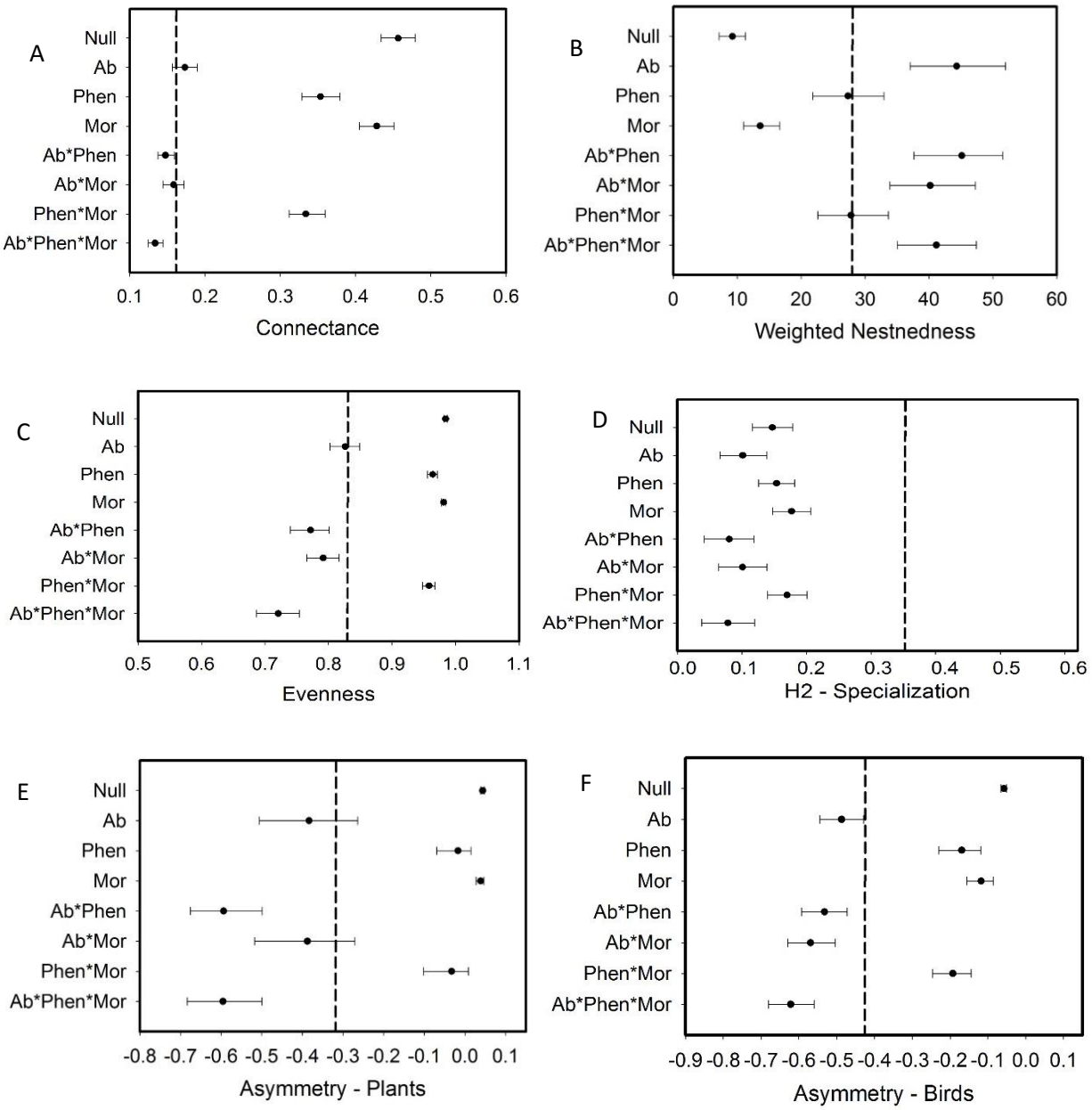
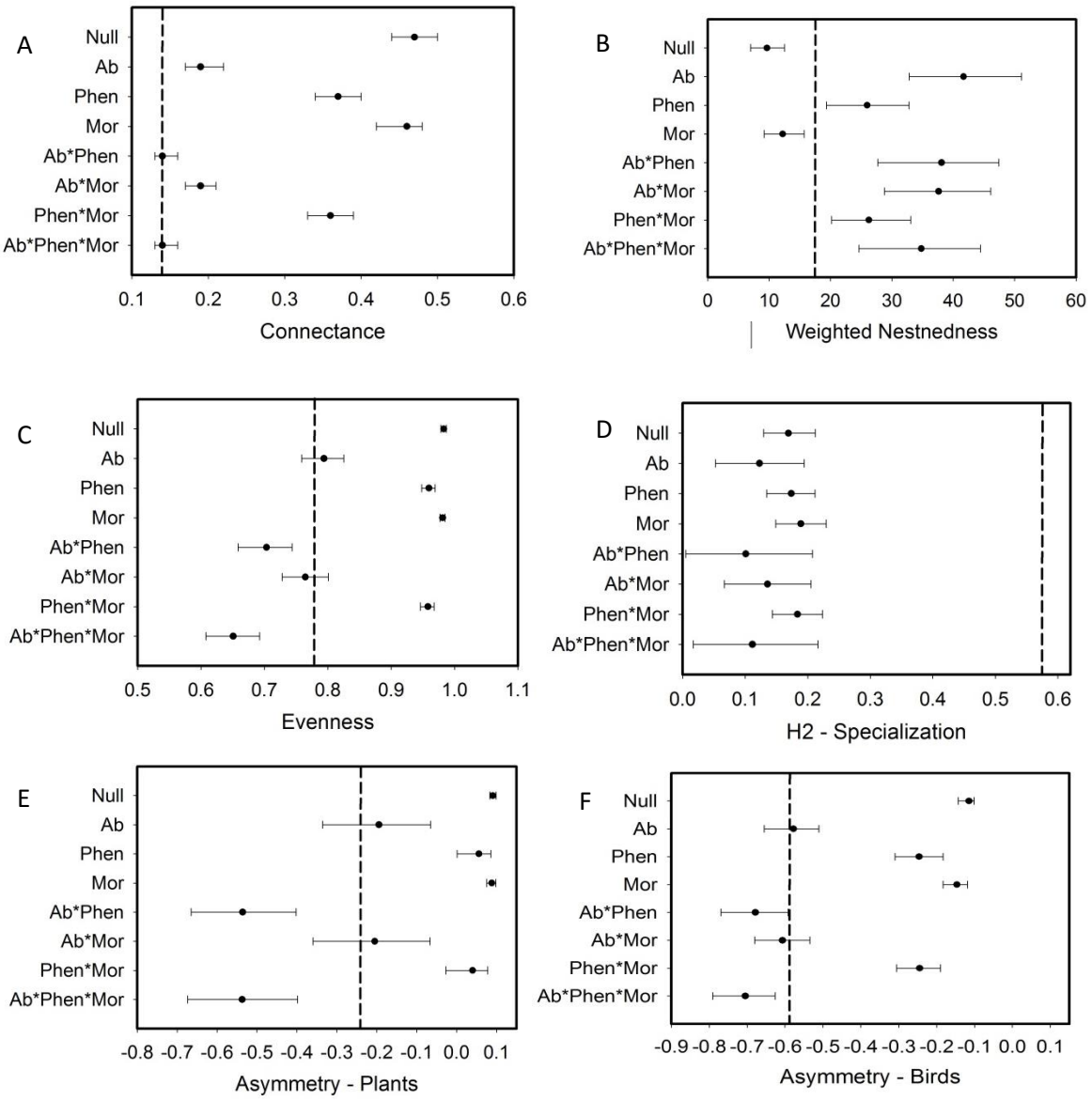

A
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.1 0.2 0.3 0.4 0.5 0.6
Connectance
B
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0 10 20 30 40 50 60
Weighted Nestedness
C
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.5 0.6 0.7 0.8 0.9 1.0 1.1
Evenness
D
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.0 0.1 0.2 0.3 0.4 0.5 0.6
H2 - Specialization
E
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
-0.8 -0.7 -0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1
Asymmetry - Plants
F
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
-0.9 -0.8 -0.7 -0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1
Asymmetry - Birds

Figure 3(on next page)

Comparison of the network metrics produced by probability matrices after removal of interactions involving nectar-robbers

Network metrics are: (a) connectance, (b) weighted nestedness (WNODF), (c) evenness, (d) specialization, (e) asymmetry of plants, (F) asymmetry of birds. The dashed vertical lines in each graph represents the value for the observed matrix. Matrix codes: Ab= Abundance, Phen=Phenology, Mor=Morphology, Null= Null matrix.


A
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.1 0.2 0.3 0.4 0.5 0.6
Connectance
B
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0 10 20 30 40 50 60
Weighted Nestedness
C
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.5 0.6 0.7 0.8 0.9 1.0 1.1
Evenness
D
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
0.0 0.1 0.2 0.3 0.4 0.5 0.6
H2 - Specialization
E
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
-0.8 -0.7 -0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1
Asymmetry - Plants
F
Null
Ab
Phen
Mor
Ab*Phen
Ab*Mor
Phen*Mor
Ab*Phen*Mor
-0.9 -0.8 -0.7 -0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1
Asymmetry - Birds